Institut für Erd- und Umweltwissenschaften
Arbeitsgruppe Environmental Modelling

Integrating dynamic and statistical modelling approaches in order to improve predictions for scenarios of environmental change

Kumulative Dissertation
zur Erlangung des akademischen Grades
"doctor rerum naturalium"
(Dr. rer. nat.)
in der Wissenschaftsdisziplin "Geoökologie"

eingereicht an der
Mathematisch-Naturwissenschaftlichen Fakultät
der Universität Potsdam

von
Damaris Zurell
aus Templin

Potsdam, den 05.05.2011

if tha eva does owt for nowt do it for thi sen

Yorkshire saying

Contents

Summary

Species respond to environmental change by dynamically adjusting their geographical ranges. Robust predictions of these changes are prerequisites to inform dynamic and sustainable conservation strategies. Correlative species distribution models (SDMs) relate species' occurrence records to prevailing environmental factors to describe the environmental niche. They have been widely applied in global change context as they have comparably low data requirements and allow for rapid assessments of potential future species' distributions. However, due to their static nature, transient responses to environmental change are essentially ignored in SDMs. Furthermore, neither dispersal nor demographic processes and biotic interactions are explicitly incorporated. Therefore, it has often been suggested to link statistical and mechanistic modelling approaches in order to make more realistic predictions of species' distributions for scenarios of environmental change.

In this thesis, I present two different ways of such linkage. (i) Mechanistic modelling can act as virtual playground for testing statistical models and allows extensive exploration of specific questions. I promote this 'virtual ecologist' approach as a powerful evaluation framework for testing sampling protocols, analyses and modelling tools. Also, I employ such an approach to systematically assess the effects of transient dynamics and ecological properties and processes on the prediction accuracy of SDMs for climate change projections. That way, relevant mechanisms are identified that shape the species' response to altered environmental conditions and which should hence be considered when trying to project species' distribution through time. (ii) I supplement SDM projections of potential future habitat for black grouse in Switzerland with an individual-based population model. By explicitly considering complex interactions between habitat availability and demographic processes, this allows for a more direct assessment of expected population response to environmental change and associated extinction risks. However, predictions were highly variable across simulations emphasising the need for principal evaluation tools like sensitivity analysis to assess uncertainty and robustness in dynamic range predictions. Furthermore, I identify data coverage of the environmental niche as a likely cause for contrasted range predictions between SDM algorithms. SDMs may fail to make reliable predictions for truncated and edge niches, meaning that portions of the niche are not represented in the data or niche edges coincide with data limits.

Overall, my thesis contributes to an improved understanding of uncertainty factors in predictions of range dynamics and presents ways how to deal with these. Finally I provide preliminary guidelines for predictive modelling of dynamic species' response to environmental change, identify key challenges for future research and discuss emerging developments.

Zusammenfassung

Das Vorkommen von Arten wird zunehmend bedroht durch Klima- und Landnutzungswandel. Robuste Vorhersagen der damit verbundenen Arealveränderungen sind ausschlaggebend für die Erarbeitung dynamischer und nachhaltiger Naturschutzstrategien. Habitateignungsmodelle erstellen statistische Zusammenhänge zwischen dem Vorkommen einer Art und relevanten Umweltvariablen und erlauben zügige Einschätzungen potentieller Arealveränderungen. Dabei werden jedoch transiente Dynamiken weitgehend ignoriert sowie demographische Prozesse und biotische Interaktionen. Daher wurden Vorschläge laut, diese statistischen Modelle mit mechanistischeren Ansätzen zu koppeln. In der vorliegenden Arbeit zeige ich zwei verschiedene Möglichkeiten solcher Kopplung auf. (i) Ich beschreibe den sogenannten ‚Virtuellen Ökologen'-Ansatz als mächtiges Validierungswerkzeug, in dem mechanistische Modelle virtuelle Testflächen bieten zur Erforschung verschiedener Probenahmedesigns oder statistischer Methoden sowie spezifischer Fragestellungen. Auch verwende ich diesen Ansatz, um systematisch zu untersuchen wie sich transiente Dynamiken sowie Arteigenschaften und ökologische Prozesse auf die Vorhersagegüte von Habitateignungsmodellen auswirken. So kann ich entscheidende Prozesse identifizieren welche in zukünftigen Modellen Berücksichtigung finden sollten. (ii) Darauf aufbauend koppele ich Vorhersagen von Habitateignungsmodellen mit einem individuen-basierten Populationsmodell, um die Entwicklung des Schweizer Birkhuhnbestandes unter Klimawandel vorherzusagen. Durch die explizite Berücksichtigung der Wechselwirkungen zwischen Habitat und demographischer Prozesse lassen sich direktere Aussagen über Populationsentwicklung und damit verbundener Extinktionsrisiken treffen. Allerdings führen verschiedene Simulationen auch zu hoher Variabilität zwischen Vorhersagen, was die Bedeutung von Sensitivitätsanalysen unterstreicht, um Unsicherheiten und Robustheit von Vorhersagen einzuschätzen. Außerdem identifiziere ich Restriktionen in der Datenabdeckung des Umweltraumes als möglichen Grund für kontrastierende Vorhersagen verschiedener Habitateignungsmodelle. Wenn die Nische einer Art nicht vollständig durch Daten beschrieben ist, kann dies zu unrealistischen Vorhersagen der Art-Habitat-Beziehung führen. Insgesamt trägt meine Arbeit erheblich bei zu einem besseren Verständnis der Auswirkung verschiedenster Unsicherheitsfaktoren auf Vorhersagen von Arealveränderungen und zeigt Wege auf, mit diesen umzugehen. Abschließend erstelle ich einen vorläufigen Leitfaden für Vorhersagemodelle und identifiziere Kernpunkte für weitere Forschung auf diesem Gebiet.

1 General Introduction

1.1 Motivation and objectives

Why does a species occur in a particular place on Earth or why does it not occur? This fascinating question central to the discipline of biogeography has a long-standing history and inspired many important naturalists, such as Alexander von Humboldt and Charles R. Darwin, to seek explanations or even develop more general theories of the diversity of life. Biodiversity is not evenly distributed across our planet but species' distributions are fundamentally constrained by physiological tolerances to environmental conditions. If environmental conditions change beyond the species' tolerances, then species may respond by range shifts, phenology shifts, (genetic and/or behavioural) adaptation or (local) extinction (Parry et al. 2007). Community-level changes are likely to follow these species-level changes and may include changing biotic interactions and changing species compositions. Already at the end of the 19th century, famous biogeographer Alfred R. Wallace warned about the impacts human activities such as deforestation can have on ecosystems and, through complex interactions, also on the climate system (Wallace 1878). Over the last centuries, virtually all of Earth's ecosystems have experienced significant transformations caused by human actions (MEA 2005). Today, the most critical direct drivers causing ecosystem changes are habitat change, climate change, invasive species, overexploitation, and pollution (Sala et al. 2000). While land use change and pollution are currently the most important drivers of biodiversity change in terrestrial ecosystems, the impact of climate change is expected to rapidly increase during the 21st century (Pereira et al. 2010). This is alarming because climate change is probably the most pervasive threat to Earth's biodiversity as it has the potential to influence all ecosystems, including those that are far from human populations and development and are still classified as wilderness (MEA 2005). Evidence is accumulating that recent anthropogenic change in climate, especially warmer regional temperatures, have already affected biodiversity in many parts of the world. Species' responses included changes in geographic distributions, population sizes and community structures (Thomas et al. 2001, Walther et al. 2002, Parmesan and Yohe 2003), timing of reproduction and migration (Menzel and Fabian 1999, Visser and Both 2005, Both et al. 2009) as well as an increase in the frequency of epidemic diseases (Harvell et al. 2002, Pounds et al. 2006, Bosch et al. 2007). With growing concern about irrevocable species loss, predictive modelling of species' distributions has become an increasingly important tool in climate change research and conservation biogeography. Projections facilitate better understanding of possible environmental change impacts which, in turn, is essential for management actions and policy aimed at mitigating negative impacts. Therefore, a growing number of modelling studies has attempted to project

21st century species extinctions for scenarios of environmental change (e.g. Thomas et al. 2004, Malcolm et al. 2006, van Vuuren et al. 2006, Jetz et al. 2007) and more studies are constantly appearing.

Generally, projections of future species' distributions can build on models ranging from purely statistical models to complex mechanistic models. These two types of models can be thought of as alternative ends on a trade-off gradient between precision and generality (Levins 1966, Sharpe 1990), or between specificity and transferability, although, in practice, many models exist with components of both types. Mechanistic models are powerful in modelling spatiotemporal population responses to environmental change as, by definition, they are grounded in mechanistic understanding of underlying processes. However, they are highly data demanding, usually involve more complex model structures and, thus, rely on extensive knowledge on species' biology and population processes. This information is not readily available for the majority of species, thus limiting the general use of mechanistic models in conservation biogeography and biodiversity assessment. Statistical species distribution models (SDMs) are an alternative approach that fit the environmental niche of a species by relating species' occurrence records to environmental characteristics (Guisan and Zimmermann 2000, Guisan and Thuiller 2005). Here, future projections of species' distributions do not depend on profound prior knowledge on the species (although, in my perception, the fitted relationships should be consistent with fundamental theory). SDMs are less complex and less 'data hungry', and currently remain one of few practical approaches for assessing the impact of projected climate change on a wide range of species (Huntley et al. 2004, Guisan and Thuiller 2005, Elith and Leathwick 2009). Nevertheless, it has to be acknowledged that SDMs are not designed for extrapolation under climate change because this widely stresses key assumptions of SDMs: that species are at equilibrium with their environment (ignoring transient dynamics, dispersal capacity and pathways, persistence); that all environmental factors limiting species' distribution are included in the model and that these environmental gradients have been adequately sampled; that biotic interactions will be the same under extrapolated conditions; that genetic variability, phenotypic plasticity and adaptive mechanisms are negligible (Austin 2002, Dormann 2007, Elith and Leathwick 2009). Further, different algorithms, each with their own specific assumptions, have partially led to controversial projections (Thuiller 2004, Pearson et al. 2006, Buisson et al. 2010), and validation of model predictions under climate change is challenging and rarely done (Araújo et al. 2005, Franklin 2010). As future is unknown, ecological models are often validated with data gathered in present conditions (e.g. validation with 'space for time' substitutes). But this way, we implicitly assume that prediction accuracy in the case of present climate guarantees realism of the model and thus prediction accuracy in the case of changing climatic conditions as well which may not necessarily be the case (Hänninen 1995, Hampe 2004, Elith et al. 2010).

Several authors have proposed to link or supplement the statistical modelling approaches by more mechanistic models in order to improve the realism of key assumptions presumably leading to more robust model projections (Guisan and Thuiller 2005, Araújo and Guisan 2006, Thuiller et al. 2008). In this context, with mechanistic models researchers mostly mean process-oriented, dynamic population models that simulate demographic processes and are able to describe non-equilibrium dynamics explicitly by incorporating modifying mechanisms such as migration limitations, source-sink dynamics, evolutionary changes, or species interactions. Guisan and Thuiller (2005) identified two major avenues for linking SDMs and dynamic population models that may lead to improved biodiversity forecasts: (1) SDMs may be improved by incorporating theoretical information from population dynamics. For instance, knowledge about inherent stochasticity in a system exhibiting source-sink dynamics may help to determine the maximum amount of deviance that can possibly be explained by SDMs. (2) SDMs can lend support to population studies. For example, in spatially explicit metapopulation models SDMs may aid the definition of patches by providing maps of habitat suitability for given environmental conditions. In fact, the latter approach has repeatedly been employed by researchers over the last two decades, and more recently, has also been utilised in climate change research (for an overview see Franklin 2010). Here, SDMs are used to project habitat suitability for scenarios of climate change. Then, time series of habitat suitability maps are fed into spatially explicit stochastic population models. Recent applications of this approach promised better understanding of species' vulnerability and of non-linear responses to environmental change, and insights of how these responses may be mediated by interactions with other processes such as disturbance regimes (Keith et al. 2008, Anderson et al. 2009, Brook et al. 2009, Cheung et al. 2009).

With this thesis, I want to add some more aspects to this discussion. First of all, I want to add a third point to the above list how SDMs and more mechanistic, dynamic modelling components may be linked to improve forecasts: Mechanistic models may serve as virtual playground for thoroughly validating statistical methods in a 'virtual ecologist' approach. Here, we essentially imitate the entire process of ecological analysis and modelling by simulating ecosystems and species therein as well as observer behaviour and subsequent data processing. As we have full control over this 'virtual world' and full access to all information created therein, in contrast to reality, we are able to draw strong conclusions about sampling methods and about (statistical) modelling methods used for interpretation and prediction. In SDM context, this allows rigorous evaluation of all steps in the model building strategy such as the choice of appropriate sampling designs or model algorithms for a given purpose. But what is much more appealing and particularly relevant to climate change research, such a virtual ecologist approach allows direct evaluation of SDM predictions under transient dynamics and other complicating ecological processes. Part of this thesis is aimed at promoting this virtual ecologist approach and its manifold applications (chapter 2). Thereby, I do not only critically discuss its capabilities and relevance for various ecological disciplines but I also demonstrate how it may foster the integration of theoretical and empirical work, and outline possible future applications that I find especially promising. This review is complimented by a case study in which I utilise such a virtual ecologist approach to explore the applicability of SDMs for making predictions under changing climatic conditions (chapter 3). To this end, I present a spatially explicit, multi-species dynamic population model incorporating species-specific and interspecific ecological processes, environmental stochasticity, and climate change. The effects of transient dynamics and ecological properties and processes as well as the effect of different algorithms on SDM prediction accuracy are explicitly investigated in a full factorial design. That way, relevant mechanisms are identified that shape the species' response to altered environmental conditions and which should hence be considered when trying to project potential species' distribution through time. In subsequent chapter 4, I am asking whether incorporating these processes into our models will really render predictions more robust or whether consideration of these processes may not, at the same time, introduce immense additional uncertainty. I explore this question in a case study for black grouse (*Tetrao tetrix*) in Switzerland. Predictions of climate-induced range dynamics are made by linking models of habitat suitability and spatially explicit population dynamics similar to the approaches described above (Keith et al. 2008, Anderson et al. 2009). Then, in an extensive sensitivity analysis, I apportion variation in key model outputs (population size, probability of extinction, elevational range, and mean population centre) to different sources of uncertainty: statistical methods (SDM algorithms), dynamic population model parameters, regional circulation models and emission scenarios. Thereby, I demonstrate both the merits but also the weaknesses of such an integrated approach. On the one hand, it allows for a more direct assessment of expected population response to environmental change and associated extinction risks as we can study the complex interplay between habitat availability and demographic processes explicitly. On the other hand, both quantitative and qualitative predictions of range and population dynamics may be highly variable. This underscores the necessity of sensitivity analysis in dynamic range predictions because robustness can never be a model property *per se* but needs to be assessed contingent on explicit simulation runs. Additionally, I outline important challenges that remain with this type of species vulnerability assessment. For example, one recurrent issue here is why predictions made by different SDM algorithms differ. In chapter 5 of this thesis, I again employ simulated data to explore this question and identify data coverage of the species environmental niche to be a crucial factor. Different SDM algorithms may in fact perform and predict equally well if the entire niche is encompassed by data. However, SDM algorithms may fail to make reliable predictions if the niche is truncated, meaning that portions of the niche are not represented in the data, or if the niche edge coincides with data limit. Thus, SDMs will need to extrapolate the full shape of the environmental niche and different algorithms will assume different shapes. This will pose a problem to subsequent predictions, if these unobserved portions of the niche get unclosed following environmental change. In my concluding chapter (chapter 6), I summarise the key results of this thesis and put these into broader context. I provide general conclusions regarding range predictions and coupled model systems; identify other complicating factors in climate change research and conservation biogeography, and outline emerging developments and future directions. But first of all, in the remaining part of this chapter, I spend a few more words to introduce the reader to the concepts of statistical and mechanistic models of species distributions and the hybrids between them.

1.2 State of the art

This thesis covers a broad range of ecological model types. Because I suspect many readers to have expertise knowledge in one particular field rather than in all model types, I will shortly summarise important properties of the different modelling philosophies. Thereby, I will indicate where these model types appear in subsequent chapters. Note, that this is not a comprehensive review of available biodiversity models (Pereira et al. 2010), but rather I want to provide a short overview of available models to make spatial predictions of environmental change response at the species level for large scales.

1.2.1 Correlative species distribution models

As the main focus of this thesis is on correlative species distribution models (SDMs) they have earned especial attention here. Thereby, I define species distribution models (SDMs) as phenomenological (statistical, correlative) models that relate species location data (presences, presence/absences or abundances) to environmental variables to describe the environmental conditions within which a species occurs. These models are aimed at understanding and explaining the species-environment relationship and/or aimed at predicting the potential distribution. Rather than reiterating what is already said about species distribution models in general, I want to refer the reader to some comprehensive reviews about SDMs in the literature, for example Guisan and Zimmermann (2000), Guisan and Thuiller (2005), Schröder (2008a) as well as Elith and Leathwick (2009). Here, I will confine myself to summarising theoretical underpinnings that I find central to understanding SDMs and possible problems and limitations in global change context. Note that the following overview does not present a critical discussion but is simply a summary of current practice and believes. Thus when stating that things should be done in specific ways this merely means that this is currently regarded as good scientific practice. I will supply more critical views and add my own voice to this subject in subsequent chapters, and I will provide a critical synopsis in chapter 6.

1.2.1.1 Theoretical framework

Numerous synonyms for the term species distribution model exist including ecological niche model, habitat suitability model, resource selection function, or environmental envelope model among others (Elith and Leathwick 2009). Despite smaller differences in emphasis and meaning, all these models have similar theoretical concepts and essentially follow the same basic modelling process. Although the term species distribution modelling is now (maybe the most) widespread, and I will use it throughout this thesis, SDMs do not actually model the species' distribution *per se* as the name might imply but rather the distribution of suitable habitat (Pearson 2007). The outputs of SDMs are habitat suitability maps.

SDMs aim at describing the species' range limits in geographic space by identifying the environmental space that is physiologically suitable for the species, the environmental niche (Hutchinson 1957). Predictions of potential distributions are made by projecting the environmental niche back onto geographic space, either to current environmental conditions or to selected scenarios of environmental change (Fig. 1.1). We can envision environmental space as an n-dimensional conceptual space that is defined by the environmental factors to which the species responds. Thereby, we need to appreciate that environmental variables included in SDMs are likely to represent only a subset of all possible dimensions of the environmental niche. Moreover, different dimensions may be important at different spatial scales, often resulting in a hierarchical structure (Mackey and Lindenmayer 2001, Guisan and Thuiller 2005). Generally, it is desirable to include only causal, functionally relevant environmental variables that exert direct effects on species and that constitute limiting factors or resources to the species or describe disturbances (Austin 2002). Only models that are consistent with fundamental theory are likely to be robust and facilitate understanding of underlying processes.

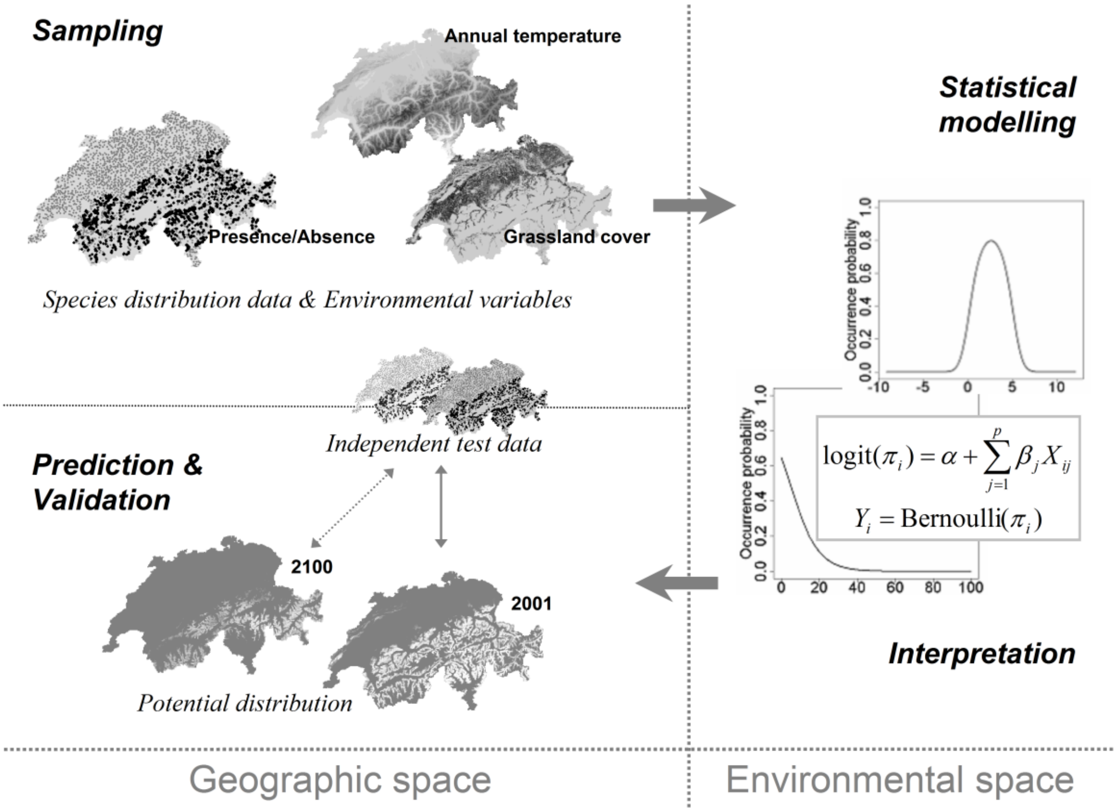


Figure 1.1. Schema of predictive species distribution modelling. Species' distributional data (e.g. presence-absence data of black grouse in Switzerland) and a suite of environmental variables (e.g. climatic such as annual temperature [°C] or land use such as grassland cover [%]) are sampled in geographic space according to underlying hypotheses regarding species' ecology. Statistical models (e.g. generalised linear model) are used to characterise the environmental space within which the species occurs. Current and future potential distribution are modelled by projecting the environmental niche back onto geographic space, either to current environmental conditions or to selected environmental change scenarios. The predictive power of the species distribution model should ideally be evaluated against independent test data.

Guisan and Thuiller (2005) identify six important steps in the model-building procedure: conceptualisation, data preparation, model fitting, model evaluation, spatial predictions, and assessment of model applicability. Although, or maybe because, recent years have seen an upsurge of available methods and rapid improvements of existing ones, both assisted by the spread of easy computation, integration with ecological theory often remains insufficient (Austin 2002, Huston 2002, Guisan and Thuiller 2005). That means that we generally like to regard descriptive, empirical models as black boxes that take any input and produce some system output (in our case potential distribution of habitat) without explicitly considering the driving processes. Easy to use software packages of recent years may well have fuelled this way of thinking as they allow automated modelling of multiple species simultaneously including automatic selection of predictors out of hundreds of possible input variables ('data mining'), automatic decisions about the species' response shape to those predictors etc. In contrast 'out in the fields', I dare say, an ecologist will never regard species' behaviour and distribution as black box response but will formulate hypotheses about the species under study and build a conceptual model in his mind which can and should be compared to computational outputs. Such systematic consideration of ecological theory at each model-building step will greatly improve our models' realism. For example, this may involve the selection of most causal environmental predictors, the choice of ecologically realistic response curves for each predictor, determination of restricted set of competing models in multi-model inference or in ensemble framework, discussion of likely causes and cost of prediction errors as well as validity assessment of underlying model assumptions when projecting into the future (for more examples see Table 2 in Guisan and Thuiller 2005).

1.2.1.2 Extrapolation and robustness

While in their beginnings, SDMs were primarily used as explanatory models, nowadays, they are increasingly used for making predictions to new times and places (Mac Nally 2000, Elith and Leathwick 2009). Generally, when transferring a model in time and space, the model needs to extrapolate beyond environmental conditions it was calibrated on. The crux is that SDMs are not intended for extrapolation, especially not for extrapolation under environmental change. Foremost, SDMs assume that species are in pseudo-equilibrium with their environment (Guisan and Theurillat 2000) which brings out two problems for extrapolation. On the one hand, species may not be in equilibrium with environment (Leathwick 1998). For example, Svenning and Skov (2004) measured low range filling for many European tree species suggesting that many present-day species' ranges may still be controlled by post-glacial dispersal limitations. On the other hand, when extrapolating, we implicitly assume an instantaneous realisation of a new equilibrium situation essentially ignoring transient dynamics. But of course, if suitable habitat is predicted to shift for about 100 km, then the species will first have to migrate into the newly available habitat and then will have to establish a viable population there (Thuiller and Münkemüller 2010). In most projections, species' migration abilities are inappropriately taken into consideration corresponding to two extreme assumptions, namely 'null' (zero) or 'full' (unlimited and instantaneous) migration (e.g. Thomas et al. 2004, Thuiller 2004). Furthermore, the limiting environmental factors may differ throughout a species' geographic range and trends may not be valid beyond the calibrated environmental range (Dormann 2007). Also, limiting factors may change substantially in environmental change context as do biotic interactions because of different migration rates, different food resources, and different competitors among others (Davis et a. 1998). And most probably, species' long-term response will be influenced by genetic variability, phenotypic plasticity and evolutionary changes (Elith and Leathwick 2009). Summarising, we need to be aware that we make numerous assumptions on the way when extrapolating and we should, thus, be careful not to put faith in our projections too lightheartedly (Dormann 2007). In contrast, we should constantly scrutinise not only our model-building steps as explained above but also our predictions in order to reduce or expose errors (Elith and Leathwick 2009). This may involve quantifying differences between sampled environmental space and prediction space (Elith et al. 2010; also see chapter 5), employing multiple models and reducing error by consensus (e.g. in ensemble framework, Araújo and New 2007; for application see chapter 4) or discovering why predictions differ (Elith and Graham 2009; also see chapter 5).

In order to assess the robustness and reliability of predictions we need to evaluate predictive ability of our models (cf. Fig. 1.1). This is a non-trivial task as predictions generally concern events that have not yet occurred (Heikkinen et al. 2006). Often, data resampling methods are utilised to test predictive performance because independent data are often unavailable. This may involve split samples, cross-validation or bootstrapping (Araújo et al. 2005, Elith and Leathwick 2009). Independent testing could be achieved by using retrospective data (Hill et al. 1999, Araújo et al. 2005, Pearman et al. 2008a). Availability of such is rare, however, and thus perfect validation may not be conceptually possible for every species and study (Araújo et al. 2005). Another possible route is to use virtual data generated by mechanistic models as I will show in subsequent chapters (Zurell et al. 2009, 2010; chapters 2 and 3). This allows explicit investigation of the effects of transient dynamics and confounding ecological properties and processes on SDM prediction accuracies. Overall, the usefulness of models and their predictions is contingent on both underlying questions and on the methods used (Araújo et al. 2005). Multiple assessments based on several accuracy measures should be preferred over using a single measure (Fielding 2002, Zurell et al. 2009, chapter 3). Also, accuracy measures should be closely linked to the intended use of the model and the species' biology. For example, higher commission errors (false presences) may be expected for species experiencing range expansions because not all suitable locations may have been colonised yet while we may expect higher omission errors (false absences) at places that are characterised by source-sink dynamics (Thuiller and Münkemüller 2010).

1.2.2 Mechanistic models of species distributions

Mechanistic or process-based models aim at providing a more general image of real world processes by reproducing the assumed internal structure of the studied systems. Predictions are grounded in real cause and effect links between different system components. Thereby, setting up a mechanistic model that is a faithful, one-to-one reflection of real world's complexity would be the most naïve approach (Levins 1966). Such a one-to-one reflection is not possible, however, and, more importantly, not desirable because it would most probably hamper rather than facilitate understanding (Wissel 1992). Models need to make artificial assumptions, simplifications and idealisations in order to gain insights into selected attributes of the studied system. Therefore, we will only ever consider specific processes in any one model depending on the purpose of the model, on the temporal and spatial scales involved, on available information and data among others.

When speaking of mechanistic or process-based modelling of species distributions, we need to be aware that there are sometimes misunderstandings about what mechanistic or process-based means in ecological modelling context. In its classical meaning, mechanistic or process-based models are *ab initio*, based on first principles. These models start directly at the level of established laws of nature (physics). However, many natural systems are (computationally) irreducible systems and have so many interacting elements that it is not possible to reduce the system's behaviour and evolution to a law in nature (Wolfram 1984 a,b). For example, the exact form of a post-glacial species' range depends not only on species' physiological traits but also on behaviour as well as site history and other confounding factors and may be determined only by following each step in the colonisation history of the species. Thus, in an ecological model that is based on 'first principles' the system's behaviour and development emerges from modelling its physiological as well as behaviourally relevant dynamic processes and their interactions with the physical environment (Bossel 1992, Grimm and Railsback 2005, Grimm et al. 2007). These models do not make assumptions such as fitting parameters but only include real process parameters that are empirically measurable (Bossel 1992). In practice however, the term process-based often is attributed also to models that do not strictly follow these principles. Rather, such models incorporate key dynamic processes of an ecosystem in an aggregate form which requires model fitting (calibration) because these 'process' parameters are not empirically measurable (Bossel 1992) but imposed (Grimm and Railsback 2005). In the following, I briefly introduce process-based models relevant to modelling species distributions in space and time. Thereby, I want to draw a distinction between models that primarily focus on representing key demographic processes and models that are based on first principles, i.e. models that incorporate ecophysiological and/or behavioural mechanisms and are, thus, process-based in the narrower sense.

1.2.2.1 Modelling demographic processes

Population dynamics, the distribution and abundance of species through time, are determined by the demographic processes of birth, death and migration which are, in turn, influenced by environmental factors. The fundamental demographic processes can be described by the simple single-population equation $N_{t+1} = N_t + B - D + I - E$, where N is population size at time t, B is the number of births, D is the number of deaths, I is the number of immigrants to and E the number of emigrants from the site (Begon et al. 2006). We can link these demographic processes and the dynamic patterns we observe in nature by means of mathematical modelling. Model systems describing population dynamics may differ in how they approach space and time, which ecological level they focus on (individual, population, species etc.), what life cycle details are included, the number of state variables they require, whether stochasticity is considered, whether parameters need to be fitted or are empirically derived etc. Thereby, classical (analytical) models from theoretical ecology such as the Lotka-Volterra equations and their variants or the logistic growth model that use population size as a state variable are considered most general. The more detail such as age, space or habitat we include in our models the less general and the more specific to e.g. particular populations they become (Grimm and Railsback 2005).

In the context of range dynamics, as we are interested in the spatial distribution of populations or species, models, self-evidently, need to be spatially explicit. This leads us to so-called spatially explicit population models (SEPMs; Dunning et al. 1995) that are mostly bottom-up which means that smaller system components are modelled in detail and system dynamics emerge from the interactions between these components (Grimm and Railsback 2005). Lattice models are examples of models whose components can be characterised by or as spatial units. Thereby, a regular (usually square) lattice or grid is composed of cells with properties such as amount of suitable area, number of individuals or species. Cellular automata are stochastic, discrete-time lattice models in which the value of each site is determined by the values of its neighbours from the previous time step. Coupled-map lattices (CML) model local population (within-patch) dynamics and extend these in space by linking local populations by dispersal whereby local population dynamics are often described by analytical models (Hassel et al. 1991, Comins et al. 1992, for application see Zurell et al. 2009, chapter 3). Similar to CMLs, many spatially explicit metapopulation models link local and regional population dynamics with the main difference that space is not divided into regular grid cells but into suitable habitat patches of varying sizes (Hanski and Thomas 1994, Hanski 1999, Hanski and Gaggiotti 2004). Here, more sophisticated approaches are taken to describe local population dynamics, for example stage-structured matrix models (Beissinger and Westphal 1998, Akçakaya 2000, Söndgerath and Schröder 2002). In individual-based models (IBMs), we follow, by definition, the state of all individual organisms within an ecological community through an entire simulation (Grimm 1999, for application see Zurell et al. 2011, chapter 4). IBMs can incorporate a wide range of individual behaviour and landscape structures, and direct links between these, for example through resource depletion (DeAngelis and Mooij 2005, Grimm and Railsback 2005).

In the context of modelling species distributions, SEPMs allow us to study effects of large-scale patterns and processes on population dynamics and, thus, provide better mechanistic understanding of how populations react to and are influenced by the environmental conditions and landscape context. Relative importance of different processes in shaping population response can be assessed. In contrast to phenomenological models, understanding is facilitated by more interpretable parameters as they relate to specific traits of organisms. Even aggregate parameters can tell us a lot about the species, for example mortality rates can inform us about species' persistence ability (Cabral 2009). Likewise, the degree of environmental stochasticity can indicate important processes acting at smaller spatial or temporal scales that have not yet been considered. However, as mentioned above, the more detail the models include the more specific they become to the organism, to the landscape or study area, to initial conditions etc. Also, demographic parameters are generally derived from field observations or fitted to observations within a statistical framework. That way, these parameters are only valid for the environmental conditions under which the model was designed, a fact that we have already learned about correlative SDMs. Thus, similar to correlative models, dynamic population models are not intended for extrapolation to novel environments unless they build on first principles as I will explain in the next paragraph.

1.2.2.2 Modelling ecophysiological and behavioural processes

This thesis does not actually include any models of this type. Nevertheless, as 'first principles' are mentioned at different places throughout the thesis, I feel that some introductory words are appropriate here. As an organism's fitness is driven by interactions between environmental factors and an organism's physiological and behavioural traits, it seems only natural to also allow model organisms to respond to their direct environment in their best physiological and behavioural capability (Grimm and Railsback 2005, Grimm et al. 2007, Kearney et al. 2010). For this, we need to base our models on first principles.

For example, mechanistic niche models are physiological models that describe the potential niche of a species based on functional traits of organisms (Kearney and Porter 2009). These models follow the concepts of biophysical ecology. They adhere to the conservation laws of thermodynamics (energy and mass balance) and are, thus, primarily concerned with transport phenomena (Gates 2003). For example, heat is transferred through the skin of ectotherms if they bask in the sun or mass is transferred through the gut when drinking or eating (Kearney and Porter 2009). In contrast to correlative species distribution models which merely yield indices of habitat suitability, the output of mechanistic niche models relates to key fitness components such as survival and reproduction. Validation of mechanistic niche models is (potentially) more straight-forward than that of correlative models because observed distribution data, for example, are not needed for model calibration and, hence, provide truly independent test data (Morin and Thuiller 2009). As mechanistic niche models are grounded in sound physics they are highly general and transferable, and, thus, allow predictions to novel climates and in non-equilibrium situations. However, it is useful to note that precision of the predictions may be low (Kearney and Porter 2009). Because mechanistic niche models merely map the fundamental niche of the species they are subject to the same basic caveat as correlative species distribution models are. They aim to identify areas with suitable environmental conditions that can potentially support a viable population, but they do not inform us which areas are actually occupied (Pearson 2007).

What we often like to ignore is that organisms actively respond to their environment and are able to adapt their behaviour (Grimm et al. 2007). From a natural selection perspective, fitness maximising behaviours are favoured (Salant et al. 1995). Thereby, an organism will assume the optimal behavioural strategy with the best trade-off between optimal feeding location, locomotion costs, reproduction effort, competition, predation risk among others. For example, the ectotherm needs to bask in the sun to heat up body temperature but through extensive basking it will lose time for foraging and also extensive basking will make it more detectable for predators. Thus, the ectotherm will only spend so much time with basking as it needs for acquiring optimal body temperature for subsequent activities (Kearney et al. 2010).

As mentioned in the previous paragraph, individual-based models (IBMs) are well suited to study behaviour and performance of individuals and explore emergent properties at the population, community or species level (Grimm and Railsback 2005). Here, we need to distinguish between IBMs that are demography-based and rely on empirically derived demographic parameters as described above, and behaviour-based IBMs (Grimm and Railsback 2005, Goss-Custard et al. 2006, Grimm et al. 2007). The latter represent the physiology and behavioural decision making of individuals explicitly. Demographic functions emerge from the behavioural decisions of individuals instead of being imposed properties of the model. Behaviour-based IBMs base on the assumption that even if these behavioural decisions of individuals change with altered environmental conditions, the fitness-maximising strategy the individuals base their decisions on will not change and will hold even for non-analogue environments (for an independent test see Goss-Custard et al. 2006). However, behaviour-based models are highly data-demanding, they may take a long time to develop and require fundamental knowledge on behaviour and bioenergetics which probably will not be available for many species thus constraining their overall practicality.

1.2.3 ‘Hybrid’ models of species distributions

In recent years, it has often been suggested to supplement correlative SDMs with more mechanistic approaches that are able to describe non-equilibrium dynamics by explicitly simulating dispersal and migration, landscape dynamics and demographic processes (Guisan and Thuiller 2005, Thuiller et al. 2008). The rationale is to keep the practicality of correlative SDMs for rapid impact assessments over a wide range of species as well as their predictive accuracy at large spatial scales while overcoming some principal limitations associated with their static nature by taking into account modifying demographic mechanisms such as dispersal or local extinctions among others (Brook et al. 2009, Franklin 2010, Gallien et al. 2010). One way to achieve this is to use SDMs to predict maps of habitat suitability which are then fed into spatially explicit population models to constrain the population models' demographic parameters (Akçakaya 2000; for applications under climate change see Keith et al. 2008, Anderson et al. 2009, Zurell et al. 2011, chapter 4 of this thesis, Fig. 1.2). Sometimes, this kind of models are referred to as ‘hybrid’ models (Thuiller et al. 2008, Gallien et al. 2010, Thuiller and Münkemüller 2010), probably to underscore that these models are meant to ‘capitalize on the strength and advantage of both approaches and concepts to make more reliable and useful predictions’ (Gallien et al. 2010). For better recognition, I also used this term in this section's title. Nevertheless, I find the name a little misleading and rather imprecise because from the onset one cannot know what kinds of models are ‘hybridised’, to which purpose and, moreover, within which scientific discipline this is done. In fact, these models belong to the category (demography-based) spatially explicit population models with the specific feature that the spatial structure of the population is determined by a habitat suitability map which can be derived by SDMs. Akçakaya (2000) coined the term habitat-based SEPMs for this kind of models. Thereby, demographic parameters such as carrying capacity (Keith et al. 2008, Anderson et al. 2009, Cheung et al. 2009) and intrinsic growth rate (Pagel and Schurr 2011) are constrained by local habitat suitability. Hence, habitat suitability acts as surrogate for the species' habitat requirements and may represent factors such as suitable climate space, resources and shelter.

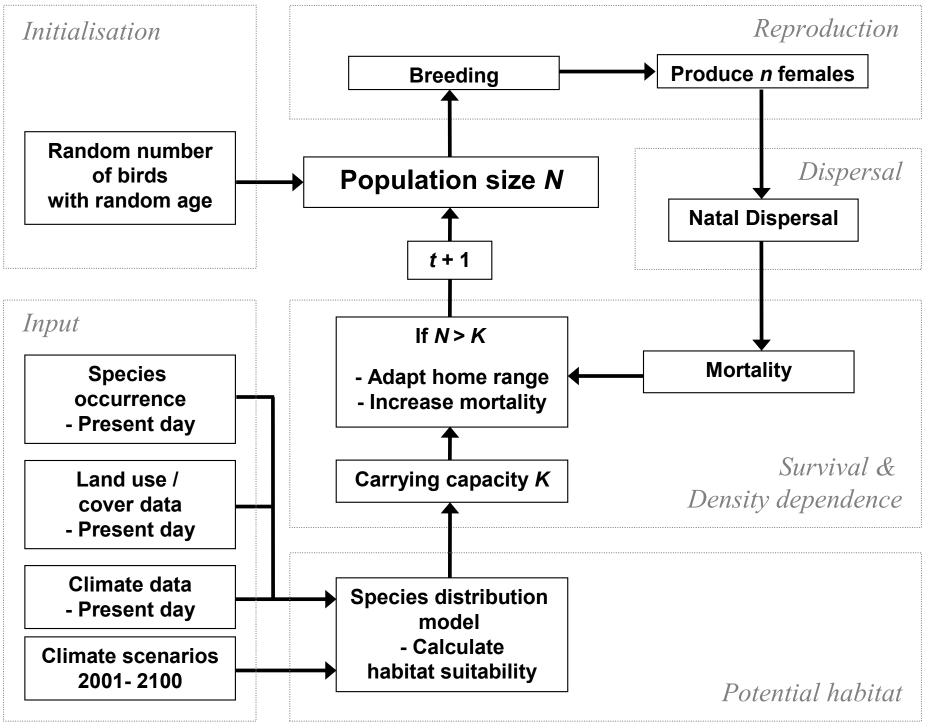


Figure 1.2. Simplified flow chart of habitat-based, spatially explicit individual-based model for Swiss black grouse population (cf. chapter 4). The correlative species distribution model is external to the individual-based model and provides a habitat suitability map for each time step given the environmental conditions. Habitat suitability is related to carrying capacity which regulates density. Each time step starts in spring and includes the processes reproduction, dispersal and death.

Only few attempts have been made yet to apply this approach in environmental change context (Keith et al. 2008, Anderson et al. 2009, Cheung et al. 2009; for review on other applications see Franklin 2010). Therefore, many questions remain regarding their practical use and general guidelines some of which are dealt with in chapter 4. I will provide further considerations in chapter 6.

1.3 Thesis structure

Given the cumulative character of this thesis, the core part of the present work (chapters 2-5) consists of four thematically related yet stand-alone articles that are published in or are in review for international peer-reviewed, ISI-listed scientific journals (for full references, see front pages of the respective chapters). These chapters can be read independently as they focus on specific aims and, thus, constitute autonomous contributions to scientific literature. Some information contained in the articles may be overlapping though, especially regarding introductions. In contrast to the general introduction (chapter 1) and the synthesis (chapter 6), the articles presented in the core chapters 2-5 are written in first-person plural because they are co-authored. However, as the lead author of all articles I have performed the main work described in these chapters, and the views expressed throughout the entire thesis are mine. Nevertheless, I want to acknowledge support by the co-authors in terms of data collection and provision, fruitful and invaluable discussions as well as proof-reading.

Further, I want to acknowledge that the idea for this thesis was born during my diploma thesis (Zurell 2007) and that fundamental experimental design concepts were recycled for parts of this PhD thesis (the virtual ecologist approach, chapter 3). Nonetheless, all findings presented here are original and result from work that I have done independently during the course of this thesis.

2 The virtual ecologist approach: simulating data and observers[1]

---

[1] An article with equivalent content has been published as:

Zurell, D., Berger, U., S. Cabral, J., Jeltsch, F., Meynard, C.N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B. and Grimm, V. 2010: The virtual ecologist approach: simulating data and observers. Oikos 119: 622-635.

2.1 Abstract

Ecologists carry a well-stocked toolbox with a great variety of sampling methods, statistical analyses and modelling tools, and new methods are constantly appearing. Evaluation and optimisation of these methods is crucial to guide methodological choices. Simulating error-free data or taking high-quality data to qualify methods is common practice. Here, we emphasise the methodology of the “virtual ecologist” (VE) approach where simulated data and observer models are used to mimic real species and how they are ‘virtually’ observed. This virtual data are then subjected to statistical analyses and modelling, and the results are evaluated against the ‘true’ simulated data. The VE approach is an intuitive and powerful evaluation framework that allows a quality assessment of sampling protocols, analyses and modelling tools. It works under controlled conditions as well as under consideration of confounding factors such as animal movement and biased observer behaviour. In this review, we promote the approach as a rigorous research tool, and demonstrate its capabilities and practical relevance. We explore past uses of VE in different ecological research fields, where it mainly has been used to test and improve sampling regimes as well as for testing and comparing models, for example species distribution models. We discuss its benefits as well as potential limitations, and provide some practical considerations for designing VE studies. Finally, research fields are identified for which the approach could be useful in the future. We conclude that VE could foster the integration of theoretical and empirical work and stimulate work that goes far beyond sampling methods, leading to new questions, theories, and better mechanistic understanding of ecological systems.

2.2 Introduction

Models permeate every field in ecology. They have become an indispensable tool for a wide range of tasks, including the understanding of mechanisms, capturing the processes behind the emergence of ecological phenomena, quantifying relationships between species presence or abundance and environmental conditions, and forecasting effects of changing environments on broad spatial and temporal scales (DeAngelis and Mooij 2005, Araújo and Rahbek 2006, Thuiller et al. 2008).

There is, however, a further important field of application of ecological models that so far has not been thoroughly acknowledged in ecological research: evaluating methods for data sampling, analysis and modelling methods by means of virtual data. Here, the idea is to generate virtual data by simulating not only ecological processes, but also the sampling processes that are used to collect these data in reality and the methodological tools used to analyse them. We propose to call this the "virtual ecologist" (VE) approach (see Box 2.1). The virtue of this approach is its ability to rigorously test method performance against a known truth. The VE approach is concerned with practical questions regarding ecological methods: Is a method able to identify patterns that we know exist (Grimm et al. 1999)? Can we infer the mechanisms underlying these patterns given a certain set of data (Tyre et al. 2001)? Can we correctly and reliably predict future events (Zurell et al. 2009, chapter 3)?

Descriptive model: a model that describes system behaviour quantitatively without explaining any underlying mechanisms. The system is regarded as a black box and is described by input-output analysis or by statistical means, e.g. regression analysis.

Species distribution model: a descriptive model that relates species occurrence to environmental (biotic and abiotic) factors to describe environmental conditions within which a species occurs. (Synonyms: habitat model, habitat-suitability model, environmental niche model)

Mechanistic model: a model that simulates the processes under study by reproducing the assumed internal structure, i.e. the cause and effect links between components of the studied system. Depending on spatial and temporal scale, only specific processes are considered in any mechanistic model.

Virtual Ecologist approach: a framework for evaluating sampling schemes and methods, (statistical) analysis tools, model approaches and structures. Virtual data is generated by simulating (a) a virtual ecological model which includes key processes of the ecological system, (b) a virtual sampling model mimicking the observation procedure, and (c) the methodological tools used to analyse the 'virtually' observed data. Results are evaluated against 'true' simulated data.

Box 2.1. Glossary.

To evaluate methods of data collection, statistical analysis, and modelling we would ideally compare their outcome to reality. This would allow us to assess whether existing patterns were detected correctly, whether correct estimates of process rates were obtained, or whether the distribution of a species was predicted correctly. However, we have no privileged access to reality independent of and beyond field observations and analytical methods. The ability of field data to represent reality depends not only on the time interval and the spatial extent of observation but also on the disturbances the observation procedure might induce. We can never know the complete "truth" because any knowledge about the real world is based on (limited) data, because the methods to derive and analyse real world data sets are subject to constraints and biases (Austin et al. 2006, Grimm et al. 1999, Halle and Halle 1999, Hirzel et al. 2001), and because amount of data is limited by time and costs. Many factors cannot be controlled: underlying environmental factors; historical factors such as disturbances, catastrophes, past land uses; and ecological processes such as competition, dispersal, and diseases.

With the VE approach all relevant information can be obtained at all times in the virtual world which is taken as a surrogate of reality. We know, for example, the full movement path of model animals, or the exact location of all individuals or subpopulations at a given time. In the virtual reality, we can generate certain patterns *a priori* as well as biases introduced by the (virtual) observer.

The idea of generating virtual data to evaluate different methods is quite natural and not new. An early example for evaluating sampling methods is given by Stickel (1954). Stickel analysed the quality of mark-recapture data describing the dispersal of small mammals. For this, the author used as a virtual habitat a sheet of paper divided into grid cells. Some of the grid cells marked traps. Animal movement was simulated by random movements of a pencil. Based on the virtual capture data, movement indices were calculated and compared to those derived from the full trajectories of the pencil. By this the accuracy of different observational algorithms was evaluated.

In statistics it is quite common praxis to use high-quality data or artificially created, error-free data to qualify different sampling or modelling methods (cf. Hirzel et al. 2001). For example, Fortin et al. (1989) subsampled a large, real vegetation data set of sugar-maple (*Acer saccharum* L.) in southwestern Québec, simulating three different types of sampling designs (random, systematic and systematic-cluster). This allowed them to evaluate the effects of these sampling designs and of different sampling efforts on the estimation of spatial structures as well as the sensitivity of different spatial analysis methods. Statistical ecologists also build replicate or simulated data sets with known properties to demonstrate the unbiasedness of new modelling methods they have developed or to show their superior efficiency in comparison to previous methods (Bolker 2008). Many introductory textbooks on statistics deal with such topics. Bolker (2008) recommends using simulated data as a "best-case scenario" to test whether correct estimates of the parameters of an ecological system can be inferred from the data before proceeding to real data.

In this review, we identify two main fields of application for VE: (i) Testing and improving sampling schemes and methods; (ii) Testing and comparing models. The first includes the evaluation of spatial and temporal sampling designs, and the assessment of sampling bias as well as the sensitivity of sampling methods to extrinsic conditions, trappability or observability (Halle and Halle 1999). For the latter, VE may help to assess whether a particular model fitted to the virtual data is principally capable of describing and predicting underlying patterns and processes. Also, contests can be arranged between competing models (Hanski 1999), and their application domain can be circumscribed theoretically (Hirzel et al. 2001). In this way, VE helps to select the most appropriate model for a given situation.

The primary aim of this review is to give the VE approach, which emerged and keeps emerging independently under different names in the literature, a common name and summarise its potential and current limitations. We want to introduce VE as a generic, rigorous and unifying approach that can be used as a common basis for testing methods of data collection and for testing modelling methods. First we will characterise the virtual ecologist approach and its elements in more detail. Secondly, we will review past uses of VE and list specific examples within the two above-mentioned main fields of application. We will thereby show that VE can be applied in a broad and diverse range of problems in ecology. Then we will discuss potential uses for empirical ecologists and ecological modellers, and give some practical guidelines which might help to design VE studies for given purposes. Finally, we will outline future directions and list specific research fields that we feel would benefit from VE.

2.3 The virtual ecologist approach

The virtual ecologist approach requires four elements (Fig. 2.1): (a) the virtual ecological model, (b) the virtual sampling model, (c) (statistical) modelling and (d) evaluation. The virtual ecological model (a) represents the virtual species and/or ecosystem, and includes key processes of the ecological system relevant to the question under study. Thus, the virtual ecological model may comprise a single or multiple species, single individuals or entire populations; it may be temporally and spatially implicit or explicit, fine-scaled or coarse-scaled; it may be governed by abiotic factors etc. The virtual sampling model (b) simulates the observation process. Data are collected from the virtual ecosystem (by a "virtual ecologist") according to a sampling scheme mimicking the way the data would be collected by real ecologists in real ecosystems. (Statistical) Modelling (c) is used to draw inferences from the collected data. Examples include estimation of population size, identification of factors influencing species distribution or abundance, and estimation of process parameters. (Statistical) Modelling can also be used to predict the effects of ecological processes. Finally, the results are evaluated against 'true' simulated data (d). Essentially, the "virtual ecologist" operates in the same way as an empirical ecologist (Fig. 2.1). However, in a VE study we have full access to all information created by the virtual ecological model which allows us to draw strong conclusions about our sampling and (statistical) modelling methods.

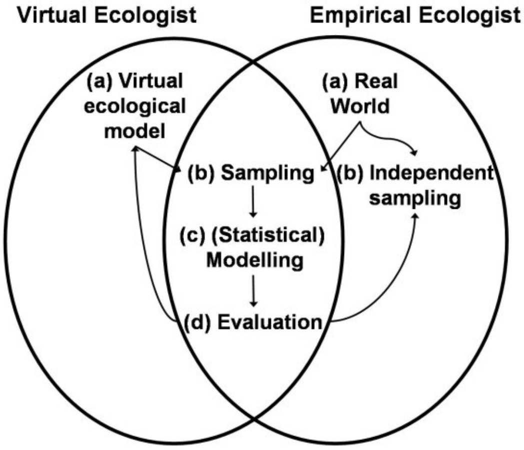


Figure 2.1. The elements of the virtual ecologist approach.

Different names have emerged throughout the literature for the very same approach: "artificial data" or "artificial species" (Austin et al. 2006, Meynard and Quinn 2007, Cabral and Schurr 2010), "virtual species" (Hirzel et al. 2001), "virtual ecologist" (Grimm et al. 1999, Tyre et al. 2001, Zurell et al. 2009, chapter 3), "simulated data" (Hanski 1999, Dormann et al. 2007), "virtual ecology" (Grimm et al. 1999, Nehrbass et al. 2006), to name but a few. Of these, virtual ecologist approach seems to best capture the central idea that not only a virtual reality is created but that the sampling itself or the observer's behaviour is also being simulated in a second model in a hierarchical way. The term virtual ecologist is thus not ambiguous in contrast to terms such as "virtual experiment" or "virtual ecology" which are also used for studies simply employing conceptual models for hypothesis testing where the effect of different scenarios on some system response is explored (Parysow and Gertner 1997, 1999). The current inconsistent terminology emphasises the importance to give the approach a common name which, we believe, will make it more visible and coherent.

In addition to various studies that we simply knew from regular scanning of the ecological literature, our overview of applications of the virtual ecologist approach is based on extensive literature searches carried out between autumn 2008 and spring 2009 using both the search engines http://www.scirus.com and http://www.sciencedirect.com. We used multiple keywords such as "virtual ecologist", "virtual biologist", "virtual experiment", "virtual species", "artificial species", "artificial data" and "simulated data". Due to the lack of a general terminology, it is possible that we have not detected all studies that would have been relevant to our review of the VE approach. However, we are confident that we included a representative set of worked examples and of ecological research fields.

Both the virtual ecological model and the virtual sampling model can be of different complexities. Depending on how much process detail is put into these models the VE approach covers quite a broad range of scientific questions and applications. Generally, we can distinguish descriptive and mechanistic models representing the virtual species/ecosystem (see Box 2.1). In the same way, the virtual sampling model, i.e. the virtual ecologist, may be descriptive or mechanistic.

Throughout our literature survey, we found an approximately equal ratio between descriptive and mechanistic representations of the virtual ecological model (Appendix A Table A.1; 21 descriptive models vs. 25 mechanistic models). In most studies that aimed at testing and improving sampling regimes (n=14) the virtual ecosystem was simulated by means of mechanistic modelling (12). Within the second field of application, testing and comparing models, 19 out of 32 reviewed studies used descriptive models of the virtual ecosystem. The field of mechanistic modelling is vast and, thus, mechanistic modelling types employed in VE studies are manifold (Appendix A Table A.1). They range from grid-based models and patch network models (cf. Hanski 1998) to individual-based models (cf. Grimm 1999, Grimm and Railsback 2005).

Likewise, the virtual sampling model (Fig. 2.1, b) covers a wide range of complexities and model types. In most studies we reviewed within the two main fields of application, virtual sampling was modelled as simple subsampling from the full simulated data, and in rare cases virtual sampling was modelled probabilistically (Appendix A Table A.1; 37 out of 46 VE studies employed subsampling, eight of which carried out a full census; seven VE studies employed probabilistic sampling). Simple subsampling means that the virtual ecologist acts flawlessly according to a certain sampling design, makes no observational or measurement errors and does not interact with the virtual species in any way (Tyre et al. 2001). Probabilistic sampling includes e.g. probability of detection and regards observation as a stochastic process (Reese et al. 2005). For instance, even if the species is present, it may not be detected. Still the virtual sampling includes no interaction between virtual species and virtual ecologist. If the virtual ecosystem is based on a mechanistic model, direct feedbacks may be included between the models of virtual species and virtual sampling, such as observer induced individual escapes (Berger et al. 1999, Nott 1998).

2.4 Past use of VE

2.4.1 Testing and improving sampling schemes and methods

In many field studies, ecologists obtain data that are known to be biased. Nevertheless, such data may provide valuable information particularly in cases where the ratio of measured variables between ecological systems is of interest. Knowledge about the error range of each variable is essential, as it might differ depending on the particular observation scenario. An increasing number of studies already optimise the error ranges of their chosen observation scenario by a virtual or theoretical comparison of optional scenarios beforehand (Appendix A Table A.1). In the following we chose three of these studies to illustrate the range of potential fields of application.

Entomologists frequently use mark-recapture methods to monitor the position of grasshoppers or ground beetles in order to understand their behaviour and mobility depending on habitat quality, intra-daily variable climatic conditions, or interactions with con-specific and other animals. Based on the resulting data on positions at different times, various mobility variables are calculated, for example the mean daily movement, maximal distance between two locations an individual was captured, or mean activity radius. These indices may be biased and their quality may differ depending on the particular observation scheme, sample size, edge effects, and spatial discretisation among others (Berger et al. 1999).

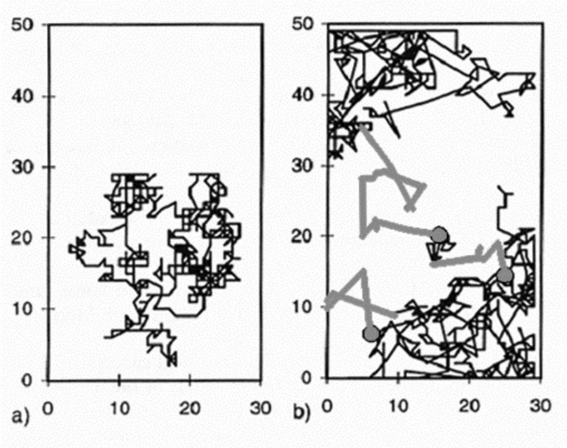


Figure 2.2. Movement of one exemplary individual over a 100 day period; (a) undisturbed and (b) influenced by an observer's motion during daily surveys (after Berger et al. 1999).

It seems reasonable to assume that the quality of mobility variables increases with the frequency of observations. However, too frequent or dense observations will disturb the individuals and might artificially increase their activity (Fig. 2.2). It is thus necessary to optimise the observation scenario related to the minimisation of the observation error and, simultaneously, to minimise the disturbance effect by the observer. The VE approach was used for this optimisation (Berger et al. 1999). The "virtual ecologist" samples the data according to the observation schemes applied in the field and disturbance effects on grasshopper are included in the model. The comparison of the "real" mobility variables (obtained in the virtual world) with the sampled variables provides a quality assessment of the various variables depending on the particular survey method and allows to rank their suitability.

The VE approach can also be used for assessing the compatibility of different sampling methods across spatial scales (Mac Nally 2001). Mac Nally asks whether comparing experimental units of different size may cause scaling artefacts. He tests the ability of the two most common methods to estimate the strength of interaction between competing species, enclosures and quadrate- or transect-based techniques, and whether information from the two sources can be mixed, which often is done for parameterising so-called community matrix models (e.g. Wootton 1995). In his simulation model, Wootton (1995) describes three types of foragers (mimicking micro-algal grazers on rocky shores) which are distinguished by their foraging strategy ("random walkers", "homing", "searcher"). Mac Nally (2001) found that for foragers that apply a more "intelligent" foraging strategy, including dynamic decision-making capabilities, the mixing of data from field-enclosure experiments and quadrate-based methods is ill-advised because the error of these two methods scales differently with the size of the sampling plot.

A third example is related to tree-mortality relationships. Tree mortality is a key process in forest dynamics. In many cases, tree death is preceded by periods of slow growth, and many forest succession models incorporate growth-mortality relationships. Few studies, however, quantify the growth-mortality relationship from empirical data. One question concerns the accuracy of growth-mortality models that are based on tree-ring data, forest inventory data or a combination of both. Wunder et al. (2008) address this question with a VE approach. An individual-based virtual forest model included growth, mortality, snag standing time and regeneration of trees. The forest was subjected to alternative sampling regimes (tree-coring, forest inventories). Growth-mortality relationships were estimated with statistical models of varying flexibility, and were compared to the *a priori* specified relationships. Highest accuracies were found for tree-ring based models, which require only a small sample size (60 dead trees). High model accuracies were also found for forest inventory-based models, starting at sample sizes of 500 trees. Overall, the study provided guidelines for efficient sampling schemes in real forests.

2.4.2 Testing and comparing models

Within this field of application we can compare the efficiency of different modelling approaches including algorithmic choices, or the effects of different model structures and complexities. We distinguish different classes of problems that can be unified conceptually or technically: first, we list examples of VE studies testing and comparing species distribution models (see Box 2.1), followed by studies that tested descriptive models in the context of community assembly theory. Finally, we present studies that used VE to test statistical modelling frameworks to parameterise dynamic population models of differing complexity.

2.4.2.1 Species distribution models

Species distribution models are commonly used to characterise suitable environmental conditions for a species by relating incidence data to environmental variables (Guisan and Zimmermann 2000). The resulting species-habitat relationship can be extrapolated in space and time to identify the spatial distribution of potentially suitable habitats. Steps in species distribution modelling involve data acquisition, selection of modelling algorithm, model calibration including selection of important predictor variables and parameters, creation of habitat suitability maps, and model evaluation. VE studies usually focussed on specific steps of this model building procedure.

Several VE studies tested and compared the performance of alternative modelling algorithms (Austin et al. 2006, Dormann et al. 2007, Hirzel et al. 2001, Legendre et al. 2002, Meynard and Quinn 2007, Moisen and Frescino 2002, Reese et al. 2005, Tyre et al. 2003) conditional on e.g. response shapes, direct and indirect predictor variables, prevalence, sample size, spatial autocorrelation, or colonisation history. Reineking and Schröder (2006) compared regularisation and variable selection methods for model calibration. Other studies tested different threshold criteria (Jiménez-Valverde and Lobo 2007) or the use of favourability functions (Albert and Thuiller 2008, Real et al. 2006) to convert the species distribution model output to maps of presence or absence.

All these studies focussed on the methods' ability to correctly reproduce the current distribution pattern of the virtual species. Simple descriptive models were used to create these patterns. Only few studies were concerned with the processes behind those distribution patterns, and simulated the virtual ecosystem and driving processes by means of mechanistic modelling (Tyre et al. 2001, Railsback et al. 2003, de Marco et al. 2008, Zurell et al. 2009, chapter 3).

Tyre et al. (2001) examined whether species distribution models are capable of identifying source habitats with high birth rates and low death rates and, thus, whether demographic processes can be inferred from simple distribution patterns. De Marco et al. (2008) evaluated the performance of SDMs coupled with Spatial Eigenvector Mapping under range expansion. Railsback et al. (2003) and Zurell et al. (2009, chapter 3) assessed whether species distribution models are able to project species distribution into the future when species undergo transient dynamics due to environmental change. Species distribution models are increasingly used to project shifts in species distributions for different scenarios of climate change (Thomas et al. 2004, Thuiller 2004) and land use change (Pompe et al. 2008). Since the future is unknown, these expected distributional changes are difficult to evaluate, and the use of species distribution models for global change projections remains hotly debated (Dormann 2007).

Zurell et al. (2009, chapter 3) utilised VE to explore the performance of species distribution models under climate change scenarios, and tested the effects of transient dynamics and ecological processes on projection accuracies. To accomplish this, they created a virtual ecosystem by means of mechanistic modelling that included three species, a butterfly, a host plant and a predator, and incorporated species-specific properties and processes such as ecological niche width, dispersal and reproduction, interspecific ecological processes such as competition and predation, environmental stochasticity, and climate change. Virtually sampled data were used to calibrate species distribution models; then, future potential species distribution was projected and evaluated against the simulated "true" distribution of the virtual species. With the VE approach, Zurell et al. (2009, chapter 3) were able to show that the performance of species distribution models for climate change projections strongly depends on the dispersal ability of the species and the extinction rate at the trailing edge of range shifts. Furthermore, their results indicated that species distribution models were useful tools in most of their tested situations. Zurell et al. (2009, chapter 3) were the first to rigorously assess the potential impacts of such factors like dispersal, demographic processes and biotic interactions on global change projections. Nevertheless, they also point out, that their study only scratched the surface of what could be done by using VE with mechanistic models of the virtual ecosystems to test species distribution models. In the future, the complicating effects of several other factors could be explored with this approach such as changing biotic interactions under environmental change, the effects of changing disturbance regimes, local ecological adaptation or the evolution of species niches.

2.4.2.2 Descriptive community assembly models

Several studies on community structure and assembly rules utilised the virtual ecologist approach. Local communities can be considered as a subset of the larger regional pool of potential community members. Numerous processes (including niche differentiation, environmental filtering, limited dispersal, niche conservatism and convergence) contribute to the formation of the local community from the regional species pool by fostering some species and excluding others. From certain patterns in distributional data, underlying community processes can be inferred by employing different metrics that characterise the community structure and by testing these for significant deviations from the null hypothesis (e.g. the community is locally neutral). Therefore, the question is twofold. First, do different processes result in different patterns of phenotypic, genotypic and trait diversity? Second, do the metrics and null models successfully distinguish between different patterns? The VE approach has been mainly used to address the second question, i.e. to test the performance of different metrics and null models in identifying non-random patterns in biodiversity distribution data.

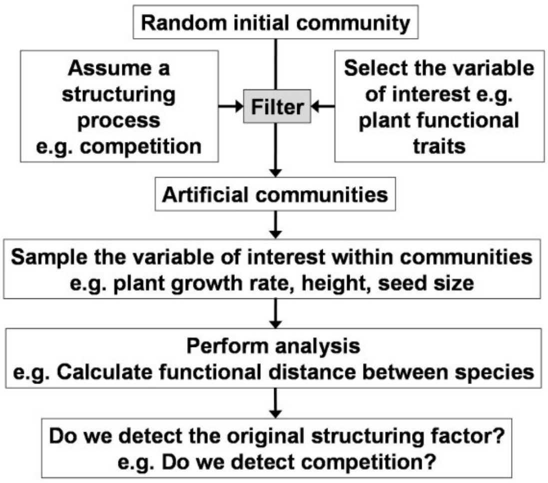


Figure 2.3. Example of a typical VE approach within community ecology.

Here, artificial communities that result from any of the proposed processes are created, for example by using simple filtering algorithms (Fig. 2.3). For instance, limiting similarity has been modeled by the stepwise exclusion of species with the lowest trait based Euclidean distances to other species while neutrality was modelled by random exclusion (Kraft et al. 2007). Then different metrics and null models are applied and their performance at distinguishing patterns created by different community processes is assessed. Patterns tested have considered nestedness (Fischer and Lindenmayer 2002, Greve and Chown 2006, Higgins et al. 2006, Ulrich and Gotelli 2007a, 2007b) and trait, phylogenetic and species diversity (Kraft et al. 2007).

Hardy (2008) studied how phylogenetic community metrics and null models perform in identifying neutral processes by using an individual-based model to represent the virtual ecosystem. In contrast to Kraft et al. (2007), he found inflated type I error rates for some null model tests. Hardy argues that the difference in results are due to differences in the structure of the virtual ecological model, Kraft et al.’s (2007) model being much simpler (based on simple algorithms and neglecting individual differences, abundances, the influence of dispersal limitation, and the influence of community size variation). However, Hardy only simulated a neutral community. It would be interesting to see, what happens to the performance of the different indices and null models when applied to a range of distributional patterns generated not by simple filtering algorithms but by mechanistic models.

2.4.2.3 Dynamic (meta-)population models

The VE approach has also achieved prominence for models of population dynamics, whenever these are parameterised from data. A class of models which has been extensively explored with VE are metapopulation models or stochastic patch occupancy models (SPOMs, Hanski 1999, Hanski et al. 2000). SPOMs describe metapopulation dynamics in a patch network by rates of local extinction and colonisation and are parameterised either from recorded turnover events or spatial data on patch occupancy. For the latter, Moilanen (1999) presents an improved technique for parameter estimation based on maximising the likelihood of observed transitions in patch occupancy. By evaluating the new method with a VE approach, Moilanen (1999) demonstrates that parameter estimates were generally more accurate than those produced by the original method. In a similar study, the new method showed to be less susceptible to the prediction of spurious trend in metapopulation size than other methods (e.g. logistic regression of turnover rates), especially when only snapshot data from two years is used (Moilanen 2000). While both these studies used exact data, Moilanen (2002) imposed error on the virtual measurements of both patch area and patch occupancy and simulated oversight of patches during survey in order to study the effect of different error types on parameter estimation and predictions and, thus, to guide survey efforts accordingly. Extending the VE approach further by using an IBM for the ecological simulation enabled Hilker et al. (2006) to compare the performance and data needs of a patch-based SPOM against a grid-based analogue.

Another field of population modelling studied by VE experiments is population viability analysis (PVA). For example, McCarthy et al. (2003) assessed absolute and relative predictions of extinction risks for a total of 160 parameter scenarios using the stochastic Ricker model. To scrutinise common assumptions of single-species PVA, Sabo and Gerber

(2007) simulated time series of population abundance with a stochastic stage-based predator-prey model. Both demographic PVA models and time-series PVA methods were tested for the effect of neglected species interactions on predictions of quasi-extinction risk for the prey.

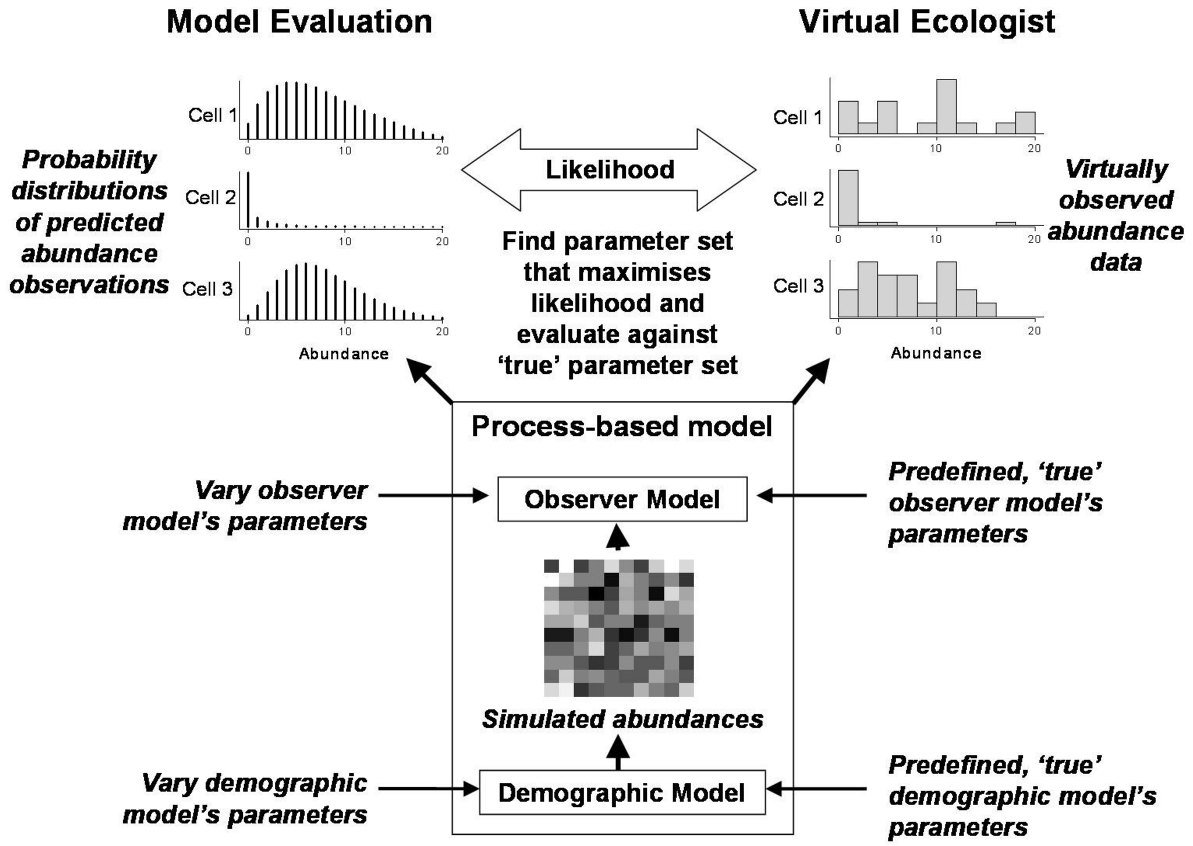


Figure 2.4. Schematic representation of the likelihood framework introduced by Cabral and Schurr (2010). The process-based model of range dynamics consists of a demographic and an observation component and is fitted to spatial abundance data. Virtual data are simulated by running the process-based model with predefined, 'true' parameter values against which the estimated parameters are evaluated.

A more challenging task is the parameterisation of spatially explicit demographic models from species' count data. For the development and verification of parameterisation techniques the VE approach can be an (in-)valuable tool. An example was performed by Cabral and Schurr (2010) using hybrid models of species distribution (Fig. 2.4). The authors aimed to parameterise both the mechanistic demographic model, which simulated the range dynamics of a species within its suitable habitat, and the observation model, which incorporated sampling error of the survey data set used for parameterisation. With a selected combination of demographic and observation parameter values, they simulated virtual data in five different fractal landscapes. Using these virtual survey data, they assessed whether the applied parameterisation framework was able to recover the underlying parameters. Although the fitted parameter values could vary around the correct values, the median values over the five different landscapes were strikingly close to the correct values, confirming the suitability of the parameterisation technique.

2.5 Discussion

The VE approach provides an important, unifying framework to test sampling methods as well as statistical analysis and modelling methods (Hilker et al. 2006). More and new methods are constantly appearing in ecology, especially as more computer power becomes available. These methods need to be tested rigorously and continuously before applying them to real data. VE is an intuitive and powerful method to do so. It has been used in ecology for a long time without being properly recognised or acknowledged. We think that VE deserves a more prominent place in the ecological toolbox.

VE is particularly suitable for synthesising our mechanistic understanding of factors influencing our study results: system-immanent properties and processes such as animal movement, methodological aspects such as observer behaviour and analysis tools as well as interactions of both. The VE models can incorporate an increasing level of complexity that allows the separation of different factors, and it can be carried out at spatial and temporal scales that would be impossible to tackle in reality.

The behaviour of individual ecologists can be simulated in particular situations and, thus, potential problems arising during data sampling can be extensively explored: limited access to certain areas (e.g. lack of roads, steep slopes); spatial autocorrelation in the samples and in the way ecologists move; interactions with the observation target; varying detection probabilities among other factors. Specific problems can be isolated and thereby better understood. A simulation can help to optimise resources and get an idea of the necessary sampling effort for a desired level of accuracy, given site access, budget constraints, sampling bias, and current knowledge of the system. This becomes particularly important when we are about to spend a large budget in surveying a large area, for example.

VE allows to compare alternative methods and thereby to theoretically circumscribe their application domain. The most appropriate model for any situation can be selected, i.e. the best modelling approach for a given data set, and crucial data needs for the application of more complex descriptive or even mechanistic models may be identified (Hirzel et al. 2001). This has to be seen different from and is more sophisticated than model selection techniques. In model selection the fit of potential models to the data is assessed and models are then ranked according to their predictive power (Burnham and Anderson 2002). For instance, Gotelli et al. (2009) recently proposed a modelling strategy that employs parametric bootstrapping to assess the fit of simulation models and to rank competing models according to their ability to explain large-scale diversity patterns. At first sight, this sounds very similar to VE. However, in model selection the goodness of fit of alternative models can only be evaluated on the given data which might be limited and biased. In contrast, VE allows the models to be evaluated against known (virtual) truth. Thus, in a VE study the question is not about how well the model fits the data but how well the model represents (virtual) reality and under which circumstances it does this.

2.5.1 Limitations

Beside the merits of the virtual ecologist approach, modellers must be aware of possible limitations of VE, which are actually more related to the models used or to the simulation design than with VE itself. Foremost, the benefit of VE depends on the quality of the ecological model, and ignores whatever complexity is not covered by the model. Models by definition simplify; the real world is much more complicated, and conclusions drawn from the virtual data sets might be limited. Wunder et al. (2008) point out that when using VE to identify necessary sample sizes to achieve a desired level of accuracy, these values constitute only lower bounds as they were estimated under the controlled conditions of the virtual reality. In the model of Berger et al. (1999), grasshoppers moved according to a random walk. Deviations from this movement behaviour might lead to a different ranking of the observation errors. However, different movement modes can be implemented and tested in the model, as in the example of Mac Nally (2001). Generally, VE is better at discrediting methods than at corroborating them. If a method fails in the virtual world, chances are that it fails in the real world as well, unless the method’s deficits fortuitously counterbalance the virtual world’s biases. However, if a method works well in the virtual world, this does not guarantee that it works in the real world as well.

In addition, models are prone to errors, and we should never put blind faith in our models (Wissel 1992); this also holds for VE. Numerous limitations can be hidden in the modelling process: uncertainty in input data, in underlying model assumptions, in parameters, and bugs in the simulation program itself (Grimm et al. 1999). Thus, as any other tool, VE needs to be used consciously and cautiously, and it should continuously be scrutinised.

Sometimes, the VE approach may seem a bit circular. For example, Hirzel et al. (2001) sampled from the same statistical modelling type, a logistic regression model that they aimed to test. However, even if one samples from the same (statistical) model, running VE is worthwhile. If the tested method is not able to recover the underlying model, then it will not be worth to further develop this particular method.

2.5.2 The role of mechanistic models

Following the famous words of Albert Einstein one should make the models “as simple as possible, but not simpler”. In good modelling practice this means that both the virtual ecological model and the virtual sampling model should be no more complex than is necessary to answer the scientific question. Of course, this also requires a clear definition of the problem and the target underlying the VE study.

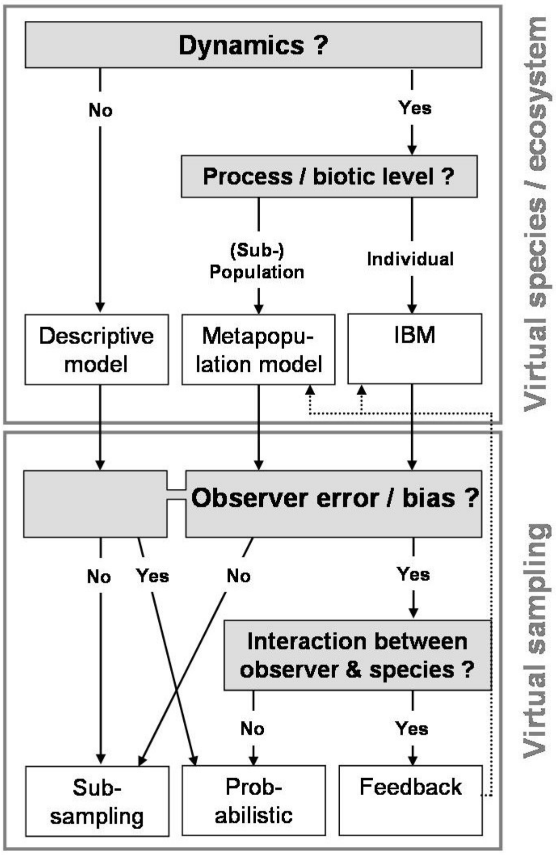


Figure 2.5. Decision tree which methods to use for the virtual ecosystem and the virtual sampling model for which purposes (IBM: Individual-based model).

If the scope of the VE study is to assess whether a pattern may be correctly identified by a particular sampling method or correctly predicted by a model then, in most cases, a descriptive model of the virtual ecosystem will be adequate. In contrast, if the scope is to test whether a specific sampling method is able to identify, or a model is able to predict, for example, certain spatial and temporal dynamics or process rates, then a more mechanistic model of the virtual ecosystem is needed in which the processes are simulated in a “structurally realistic” way (Fig. 2.5; Grimm et al. 2005a, Wiegand et al. 2003). Also, the decision whether the virtual sampling model should be descriptive or mechanistic should be driven by the scope of the VE study; that is questions like: should observer errors or biases be included; are there interactions between the observer and the species (Fig. 2.5)?

Nevertheless, we want to emphasise that a contemporary shift towards generating virtual species/ecosystem and observer from mechanistic models can qualitatively enhance the potential of the VE approach. Mechanistic models can account more realistically for complexity in both ecological and observational processes, including possible interactions. Specific problems or aspects of ecological systems can be incorporated. Data are still controlled, but potentially behave in a non-trivial manner. The exercise becomes one that is equally about understanding complex dynamics and optimising the way we can study them empirically by using mechanistic, “close to nature” simulation models. In mechanistic models of virtual species/ecosystems one has to take care of complicating effects such as coloured noise, stochasticity, and deterministic chaos. We can thus test whether our method under study is working even in the face of such complex inherent interactions, and hence delineate the method’s application domain more accurately.

Individual-based models (IBMs) are the most general mechanistic models as the emergence of metapopulation dynamics is the result of individual interactions in a landscape mosaic (Grimm 1999, Hilker et al. 2006). IBMs differ from descriptive models or mechanistic models on a more aggregated, metapopulation level, in that the ‘true’ values of the population-level parameters we try to estimate are not necessarily known, but rather are an emergent property (Hilker et al. 2006). The parameters can be estimated, however, in the IBM with arbitrary precision because we can produce as many replicates as required (at least if sufficient computer power is available). The efforts of such a complex IBM might be justified if the field study is a non-repeatable project; if a wide-spread sampling method is to be evaluated; or if we want to test how mechanistic models on a more aggregated, metapopulation level converge to more complex (virtual) reality (Hilker et al. 2006). A full-fledged VE approach with the virtual species modelled by means of individual-based modelling and explicit interactions between virtual observer and virtual species (Berger et al. 1999) may be useful in survey planning of highly mobile and sensitive species.

2.5.3 Future directions

We have shown various applications and research fields where the virtual ecologist approach has been successfully employed, and has proven itself as a practical and worthwhile tool. As pointed out throughout this review, the approach is not yet fully explored and many more aspects of ecological surveys and modelling tasks can be addressed with VE.

The ecological community holds enormous stocks of data collected, for example, in herbaria; by voluntary or hobby ornithologists, entomologists; nature conservationists; PhD students etc. Sometimes trust in these data is rather limited because of suspected bias in survey design or observer behaviour. For instance, volunteers monitoring butterflies will often preferentially visit places where they expect to find the most enigmatic and interesting species. Conversely, places where observers do not expect to find many species are likely to not be monitored properly or only very short visits will be paid to such places. Through such unequal observer effort fallacious absences (and also presences) might be induced with unknown effects for subsequent data analyses. Here, VE could help to assess potential effects rigorously and to assess sampling bias if information on the observer effort is available; the data could then be corrected by these estimated values. However, we want to stress that VE is no panacea for flawed survey designs. It can merely be a way to salvage at least some of the information in the data.

Another important research field for which VE holds great potential for the future is global change research. Railsback et al. (2003), Cabral and Schurr (2010) and Zurell et al. (2009, chapter 3) show that VE can help to evaluate models which are intended to project species distributions into the future for different scenarios of environmental change. The effects of many other factors potentially complicating global change projections could be explored with VE: changing biotic interactions or spatially dependent biotic interactions that only take place at the edges of species distributions, behavioural adaptation, evolutionary effects, invasions, climatic extremes or catastrophic events. The VE approach would also allow to assess projections that address the effects of climate change or land use change for individual species with particular species-environment relationships, or to integrate species with different functional characteristics into assessing the effects of global change in whole communities or ecosystems.

In addition to these potential future directions, the virtual ecologist approach could, if it were used more routinely in the future, have more general and perhaps even more important benefits: it could foster the integration of theoretical and empirical work. Empiricists are often unaware of the potentials and limitations of ecological models, and the same holds for theoreticians regarding field work and sampling methods. Working together on the development of sampling methods, designs and efforts by using the VE approach could help overcome this mutual ignorance. It could help practitioners to better plan their work. It could help modellers to increase the practical value of their work. It could also stimulate work that goes far beyond sampling methods. While trying to test sampling methods, new and interesting ecological models and even theories might emerge; and while trying to use existing models for testing sampling methods, ecological models might become more realistic in structure and lead to new questions for empirical research. Also, field work could be oriented more directly towards data needs modellers have for specific modelling tasks. Looking at their models from the perspective of optimising empirical work might make work of theoreticians more valuable, and also it might help to better understand the system.

3 Static species distribution models in dynamically changing systems: how good can predictions really be?[2]

---

[2] An article with equivalent content has been published as:

Zurell, D., Jeltsch, F., Dormann, C.F. and Schröder, B. 2009. Static species distribution models in dynamically changing systems: how good can predictions really be? Ecography 32: 733-744.

3.1 Abstract

It is widely acknowledged that species respond to climate change by range shifts. Robust predictions of such changes in species' distributions are pivotal for conservation planning and policy making, and are thus major challenges in ecological research. Statistical species distribution models (SDMs) have been widely applied in this context, though they remain subject to criticism as they implicitly assume equilibrium, and incorporate neither dispersal, demographic processes nor biotic interactions explicitly. In this study, the effects of transient dynamics and ecological properties and processes on the prediction accuracy of SDMs for climate change projections were tested. A spatially explicit multi-species dynamic population model was built, incorporating species-specific and interspecific ecological processes, environmental stochasticity and climate change. Species distributions were sampled in different scenarios, and SDMs were estimated by applying generalised linear models (GLMs) and boosted regression trees (BRTs). Resulting model performances were related to prevailing ecological processes and temporal dynamics.

SDM performance varied for different range dynamics. Prediction accuracies decreased when abrupt range shifts occurred as species were outpaced by the rate of climate change, and increased again when a new equilibrium situation was realised. When ranges contracted, prediction accuracies increased as the absences were predicted well. Far-dispersing species were faster in tracking climate change, and were predicted more accurately by SDMs than short-dispersing species. BRTs mostly outperformed GLMs. The presence of a predator, and the inclusion of its incidence as an environmental predictor, made BRTs and GLMs perform similarly.

Results are discussed in light of other studies dealing with effects of ecological traits and processes on SDM performance. Perspectives are given on further advancements of SDMs and for possible interfaces with more mechanistic approaches in order to improve predictions under environmental change.

3.2 Introduction

Among the expected consequences of the ongoing climate change are shifts in species' geographic ranges, range expansions and contractions. Robust prediction of these distributional changes are a prerequisite for dynamic and sustainable conservation strategies, and thus constitute a major challenge in present-day ecological research (Guisan and Thuiller 2005; Vaughan and Ormerod 2005).

Statistical species distribution models (SDMs) have been widely used to project species range shifts, and to derive extinction risks for different climate change scenarios (Bakkenes et al. 2002; Midgley et al. 2002; Thomas et al. 2004; Thuiller 2004). These data-driven models relate field observations to environmental predictor variables. They provide an easy-to-use and potentially powerful tool for ecologists and conservationists because simple spatial incidence data can be used to derive the statistical models (Scott et al. 2002). Despite these merits, SDMs also show particular limitations regarding climate change projections (Dormann 2007; Guisan and Thuiller 2005; Pearson and Dawson 2003; Araújo and Rahbek 2006). Foremost, they assume equilibrium between the species and its environment, and aim at predicting a new equilibrium state when extrapolating. Thus, transient dynamics are essentially ignored when projecting into the future. Furthermore, SDMs do not explicitly incorporate demographic processes and biotic interactions, and only few attempts have been made yet to narrow uncertainties due to dispersal assumptions (Midgley et al. 2006). All these issues may lead to substantial uncertainties in climate change projections (Dormann et al. 2008). To date, there is little knowledge of the consequences as the accuracy of SDMs in predicting future species distributions is not easy to evaluate (Araújo et al. 2005; Thuiller 2004). This is mainly because the events we aim to project have not yet occurred, and the future species' geographic ranges are therefore unknown (but see Araújo et al. (2008) for an application for predicting current distributions from historical data).

One way to overcome the data limitations are artificial or virtual experiments (Berger et al. 1999; Austin et al. 2006; Schröder and Seppelt 2006). Such approaches have the further advantages of allowing us perfect knowledge and control over the underlying processes. Previous studies employing virtual experiments and SDMs have tested optimal sampling strategies (Hirzel and Guisan 2002; Reese et al. 2005), compared the performance of different statistical methods, model selection strategies, or threshold criteria for binary predictions (Hirzel and et al. 2001; Reineking and Schröder 2006; Jiménez-Valverde and Lobo 2007), and assessed how good SDMs were at identifying 'source' habitats (Tyre et al. 2001), the effect of diverse occurrence-environment relationships (Austin et al. 2006; Meynard and Quinn 2007) or the use of favourability functions (Albert and Thuiller 2008). To our knowledge, it has not been tested yet how transient dynamics and ecological properties and processes affect SDM accuracy when projecting into the future.

In this study we propose a virtual experiment to test SDM prediction accuracy under ongoing climate change by developing species distribution models on data from a complex, dynamic population model, which is used to model transient responses of a species to climate change.

We therefore built a dynamic, spatially explicit multi-species population model which incorporated species-specific ecological properties and processes such as the ecological niche, dispersal ability and intrinsic growth rate, interspecific interactions such as competition and predation, environmental stochasticity, and climate change. Different scenarios were developed by systematically manipulating model properties. For each modelling scenario SDMs were estimated by applying two different SDM methods, Generalised Linear Models (GLMs) and Boosted Regression Trees (BRTs). Projected species distributions by SDMs were compared to simulated "true" species distributions by the dynamic population model focusing on the following questions: (1) Do transient dynamics lead to a decrease in projection accuracy under climate change? (2) Are modern, flexible statistical modelling techniques (represented in our study by BRT) more capable of projecting future species ranges than long-established, parametric methods (represented here by GLM)? (3) Are these effects confounded by differing ecological properties and processes?

3.3 Methods

3.3.1 Dynamic population model

The purpose of the dynamic population model was to mimic scenarios of real-world situations with a complex virtual world containing a focal species characterised by species-specific properties and processes, and influenced by predation, environmental stochasticity, and climate change. To achieve this, a discrete-generation host-parasitoid system was set in a real environment. Such host-parasitoid systems are well suited for simple population models because they can have a much simpler structure than many other enemy-victim interactions due to the tight link between trophic and reproductive aspects of the parasitoid life history (Hassell 2000; King and Hastings 2003; Nicholson 1933).

The host was the focal species, a holometabolous insect with distinct generations which is henceforth referred to as butterfly. A highly synchronised parasitoid parasitised the butterfly during its larval stage, and thereby caused the death of the butterfly (Mills and Getz 1996). Movement and dispersal were limited to the adult insect stages. In analogy to real systems the model was tritrophic, i.e. the butterfly-parasitoid interaction depended on a host plant, henceforth called plant, which affected the presence and abundance of the butterfly. A coupled-map lattice model was used to link the local and regional dynamics (Bonsall and Hassel 2000; Comins et al. 1992; Hassell et al. 1991). In each cell of a two-dimensional lattice the local butterfly-parasitoid population dynamics were mapped annually. The populations were then connected by dispersal. We thus obtained a spatially explicit multi-species dynamic population model which allowed systematic modifications in several ways.

3.3.1.1 Structure, scales and scheduling

Space was represented by a two-dimensional lattice of 148 × 113 sites with a cell size of 1 km × 1 km. Absorbing boundary conditions were assumed, representing an open system where butterflies and parasitoids were able to leave the habitat, but not to (re-)enter it. One time step represented one year and the whole simulation covered a period of 150 years.

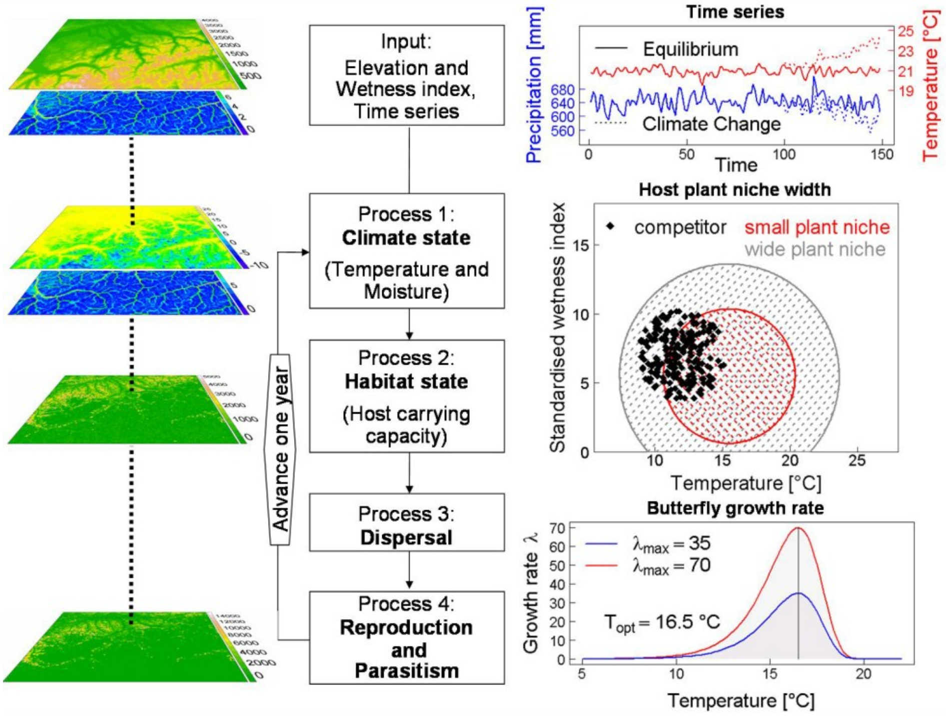


Figure 3.1. Process scheduling of the dynamic model is illustrated in the flowchart in the centre. Each simulation started with the input of elevation and potential moisture distribution (top left) as well as temperature and precipitation time series (top right). After time initiation, four processes were carried out within each time step: Additional ecogeographical information layers were calculated, i.e. actual temperature and moisture distribution (Process 1) as well as local host carrying capacities (Process 2). Then dispersal of hosts and parasitoids was simulated (Process 3) and reproduction and parasitism took place (Process 4). The figure in the centre right depicts the fundamental and realised niche of the host plant. Temperature dependency of host growth rate is shown in the bottom right figure.

During initialisation, the environmental factors elevation and potential moisture were attributed to each cell in the lattice, and the climatic factors temperature and precipitation were assigned to each time step. Butterflies and parasitoids were randomly distributed over the suitable habitat. During simulation, each time step was characterised by four processes (Fig. 3.1). Foremost, climate state and habitat state were updated. Temperature and moisture were assigned to each cell by climatological downscaling. The host plant foliage projective cover was determined by the prevalent temperature and moisture regime, and induced a carrying capacity K for butterflies in each lattice cell. Resource competition at plant level was introduced by adding a second plant species, the competitor, whose fundamental niche overlapped with that of the host plant (Fig. 3.1), and which did not serve as a host plant for the butterfly. At the beginning of each time step, butterflies and parasitoids dispersed throughout the lattice. After colonisation, butterflies reproduced and the offspring could then be parasitised by female parasitoids. Detailed descriptions of the modelled processes are contained in Appendix B, parameter values are given in Table 3.1.

Table 3.1. Constants in the process-based dynamic model. Respective equations are contained in Appendix B.

Function	Symbol	Value	Unit	Description
Grid	w	1	km	Cell width
Climate State	T_{lapse}	7	°C km^{-1}	adiabatic gradient
Habitat State	K_{max}	5000	ind	maximum carrying capacity of a cell
	$\mu_{T,plant}$	15.5	°C	mean of host plant's temperature utilisation function
	$\mu_{W,plant}$	5.5	-	mean of host plant's moisture utilisation function
	$\mu_{T,comp}$	12	°C	mean of competitor's temperature utilisation function
	$\sigma_{T,comp}$	1	°C	standard deviation of competitor's temperature utilisation function
	$\mu_{W,comp}$	7	-	mean of competitor's moisture utilisation function
	$\sigma_{W,comp}$	1	-	standard deviation of competitor's moisture utilisation function
	σ_F	0.008		standard deviation for environmental stochasticity
Dispersal	$\beta_{butterfly}$	1.5	-	butterfly's shape parameter in equation B.4
	$\mu_{butterfly}$	0.75	-	fraction of local butterfly population emigrating
	$\alpha_{parasitoid}$	2	-	parasitoid's scale parameter in equation B.4
	$\beta_{parasitoid}$	1.5	-	parasitoid's shape parameter in equation B.4
	$\mu_{parasitoid}$	0.75	-	fraction of local parasitoid population emigrating
Reproduction & parasitism	$T_{opt,\lambda}$	16.5	°C	optimal temperature for butterfly growth rate, location parameter of Gumbel distribution
	σ_λ	1.4	°C	scale parameter of Gumbel distribution
	N_{crit}	50	ind	critical population size for Allee effect
	c	1	ind	parameter in equation B.5

3.3.1.2 Input

The environmental data employed in the simulations were based on real environmental data derived from a digital terrain model developed by the Swiss Federal Statistical Office, GEOSTAT. The coordinates of the 148 km × 113 km grid are 607,000-754,000 m E / 152,000-264,000 m N (Swiss grid CH1903). Environmental input layers were elevation, drainage area above each cell, slopes and aspects. Altitude in the study region ranged from 269 m to 3854 m a.s.l. Main climate variables in the virtual world were energy and water, in particular mean summer temperatures and mean summer precipitation. Time series were calculated manually by drawing for each time step a random number from a Normal distribution with a characteristic mean (temperature T = 21 °C at 0 m a.s.l.; precipitation $Prec$ = 640 mm) and standard deviation (σ_T = 0.5 °C; σ_{Prec} = 30 mm). A generalised climate change scenario was derived for the period 2001 to 2050. Rates of change approximately followed the projected changes of the IPCC SRES scenario A2 for Central and Northern Europe (Houghton et al. 2001). Mean temperature was increased by 3°C in 50 years, mean precipitation decreased by 50 mm; mean values within the 50 years were linearly interpolated.

3.3.1.3 Scenarios

A standard simulation run lasted 150 years. The model 'spinned up' for 100 years, running with average climate, thereby ensuring a long-term equilibrium between butterfly population and environment which was usually reached after five years. Scenarios were applied over the last 50 model years.

Table 3.2. Range of parameter values in the process-based dynamic model. Please note that low values of $\alpha_{butterfly}$ correspond to long dispersal distances and high values to short dispersal distances. Respective equations are contained in Appendix B.

Function	Symbol	Values		Unit	Description
Habitat State	$\sigma_{T/W,plant}$	1.5	2.5	°C	standard deviations of host plant's temperature and moisture utilisation functions
Dispersal	$\alpha_{butterfly}$	0.5	4	-	butterfly's scale parameter in equation B.4
Reproduction & parasitism	λ_{max}	35	70	ind	maximum butterfly population growth rate
	a	0	0.01	ind	area of discovery in equation B.6

Scenarios were derived in which ecological properties and processes as well as climate were systematically manipulated in a factorial simulation experiment of five factors with two levels each (Table 3.2). Climate change and parasitism were either turned on or off, the latter by adjusting the area of discovery, i.e. the attack rate by the parasitoids. Butterfly growth rate was either low or high through manipulation of the maximum growth rate $\lambda_{max.}$ Plant niche width was either narrow or wide, which was achieved by varying the standard deviation of the plant's resource utilisation functions. Finally, butterfly dispersal distance was either short or long through manipulation of the scale parameter α in Eq. B.4 (Appendix B). A value of $\alpha = 4$ resulted in a maximum dispersal distance of one cell, $\alpha = 0.5$ in a maximum dispersal distance of five cells, while the parasitoids dispersed with a fixed maximum dispersal distance of two cells (α = 2). All possible parameter combinations resulted in $2^5 = 32$ scenarios. For each scenario we ran 10 replicate simulations.

3.3.2 Sampling by virtual ecologist

Similar to real field studies, a virtual ecologist sampled the butterfly population with the same strategy as an ecologist might choose in reality. A random stratified sampling strategy was applied (Hirzel and Guisan 2002), with temperature as the stratifying variable. The quantiles (0.2-, 0.4-, 0.6- and 0.8-quantiles) of the temperature distribution were taken to split the data into five ordinal classes, generating five homogenous environmental strata with respect to temperature. An equal number of cells (replicates) were chosen in each stratum. In a selected cell, the incidence of the butterfly and the prevailing environmental conditions were recorded. In order to reduce spatial autocorrelation in the response variable, samples were not taken in adjacent cells. The virtual ecologist made no errors in detection, i.e. butterfly occurrence and environmental conditions were recorded exactly as given in the dynamic model. This way, the performance of the statistical model could be directly related to the underlying demographic and stochastic processes (Tyre et al. 2001). Training data were sampled directly after ‘spin up’, i.e. after 100 model years, with a sample size of 1000. For each simulation run, five training data sets were sampled to capture the variability introduced by snapshot data; SDM accuracies for these five training data sets were averaged later. Independent (test) data sets (sample size = 1000) were sampled in the year 100, and in every subsequent 10 years until year 150.

3.3.3 Statistical modelling

3.3.3.1 Model formulation

Butterfly occurrences were analysed by Generalised Linear Models (GLMs) and Boosted Regression Trees (BRTs) using a binomial error distribution and a logistic link function. GLMs have been traditionally used in species distribution modelling, and fit parametric terms. BRTs were developed within the machine-learning community, and are an ensemble-prediction method combining regression trees and boosting. They are very flexible, but at the same time resistant to overfitting, and are able to automatically model complex interactions between predictor variables (Ridgeway 1999; Leathwick et al. 2006; Thuiller et al. 2006; Elith et al. 2008).

Before the application of GLMs and BRTs, the predictor variables were tested for multicollinearity by calculating Spearman’s rank correlation coefficient ρ_S. Following

Fielding and Haworth (1995), if two variables had a correlation $\rho_S > 0.7$ the predictor with less ecological importance in respect to butterfly occurrence was removed. GLMs were estimated for the remaining predictor variables by applying an Akaike Information Criterion (AIC)-based stepwise variable selection procedure (Akaike 1974; Harrell 2006). According to the ecological knowledge we had (from the 'virtual' reality), we included linear (e.g. host plant cover) and quadratic terms (e.g. temperature and soil moisture) in the GLMs as well as an interaction term between temperature and soil moisture. The linear term was forced into the model each time the quadratic term or the interaction term was selected in the final model. BRTs were estimated with a tree complexity of 2, a bag fraction of 0.75 and a learning rate of 0.005 which ensured that the models were fitted with at least 1000 trees (cf. Elith et al. 2008).

3.3.3.2 Extrapolation in space and time

The resulting SDMs were used to make predictions to independent (test) data sets (sample size = 1000) for the year 100, in which the models were fitted, and for every subsequent 10 years until year 150 where the simulation ended. Thus, SDMs were fitted under average climate where the butterfly population was in long-term equilibrium with its environment, and, in the case of climate change, the occurrence of butterflies was projected to differing time slices under gradually ongoing climate change.

3.3.3.3 Model transferability: Validation

For each prediction in space and in time, three different measures of accuracy were calculated in order to get a multi-facetted view of how good the SDM predictions were. The proportion of deviance explained by the final models was quantified by the explained deviance r^2_L, a logistic regression equivalent to the coefficient of determination r^2 (Menard 2000). We derived the deviance by applying Equation 1.10 in Hosmer and Lemeshow (2000). The models' ability to discriminate between occupied and non-occupied sites was assessed by calculating AUC, the area under the ROC-curve (Fielding and Bell 1997). AUC is independent of classification thresholds and typically assumes values between 0.5 and 1, with AUC = 0.5 for models with predictive ability no better than the null model and AUC = 1 for perfectly discriminating models. Values of AUC > 0.7 indicate useful predictions according to Hosmer and Lemeshow (2000). Additionally, the calibration curve was calculated, to determine the agreement between observations and predicted values, i.e. the goodness-of-fit (Pearce and Ferrier 2000). It was derived from a logistic regression of the observed values on the logit of the predicted values (Harrell 2001; Reineking and Schröder 2006). A perfectly calibrated model would exhibit a calibration curve with a slope of one and an intercept of zero. Departures from these values indicate bias and spread, respectively, in the predicted values.

3.4 Results

3.4.1 Dynamic population model

Not all suitable cells were occupied by butterflies. This was a consequence of local extinctions caused by predation or stochastic processes, or due to dispersal limitation. The relative proportion of occupied habitat, the prevalence, became greater when the plants had wider niches resulting in more available habitat for the butterflies, and when the butterflies were able to travel farther distances which allowed them to spread throughout more of their geographical niche and to reach even more distant patches (Fig. 3.2). Prevalence was also greater for scenarios without parasitism, as extinction then only occurred due to stochastic processes in the environment. Although high butterfly growth rates caused higher butterfly abundances, prevalence was not affected, and did not differ considerably between scenarios of high and low butterfly growth rates.

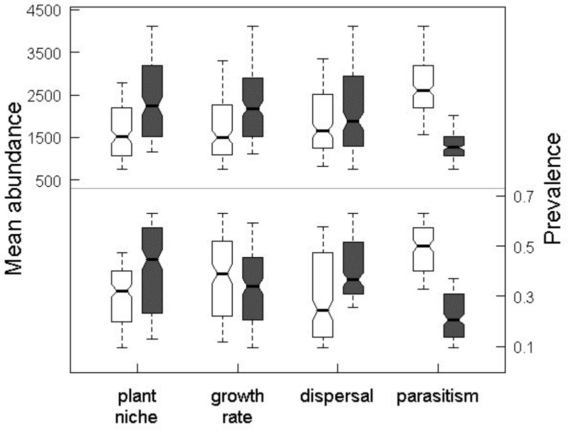


Figure 3.2. Effects of ecological properties on mean abundances and prevalences of butterflies in the virtual world in year 100 when butterflies were in long-term equilibrium with their environment. Open and filled boxes indicate low and high values for a given ecological parameter, respectively (Table 3.2). Sample size is n = 160.

In all scenarios under climate change the butterfly population moved southwards, not gradually, but rather in distinct steps which corresponded to distinct steps in the temperature trajectory (Fig. 3.3). After 115 years, the butterflies started to shift their geographical range southwards which was accompanied by a small range contraction. Then after 135 years, distinct range contractions took place accompanied by ongoing southwards movements. The northernmost patches which formerly supported intermediate relative butterfly abundances became unoccupied after year 140.

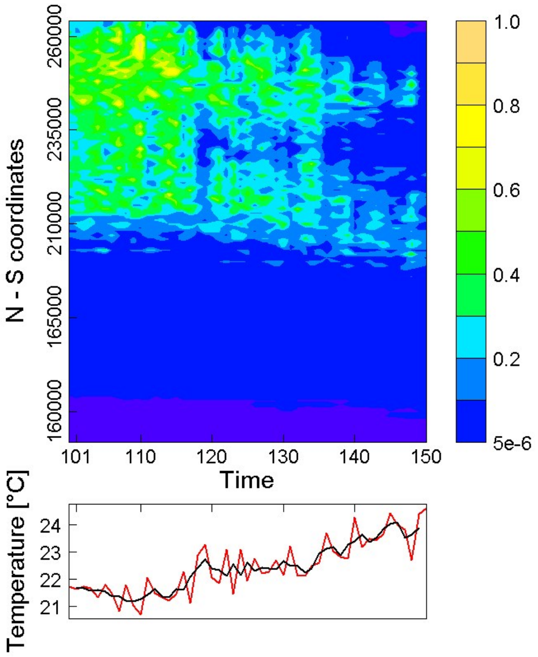


Figure 3.3. Range dynamics under climate change. The shift in relative butterfly abundances in north (N) -south (S) direction is depicted in the top panel. It is the average butterfly abundance of all (16) scenarios and replicate runs under climate change, and in each 1-km wide N-S transect in years 100 to 150, when climate change took place. The bottom panel shows the temperature trajectory under climate change for the years 100 to 150 (red) and the 3-year moving average (black). Range shifts took place after year 115, after year 135 distinct range contractions occurred. These steps coincided with steps in the temperature trajectory.

3.4.2 Statistical models

Under average climate, both BRTs and GLMs achieved high prediction accuracies. According to the rules of thumb given by Hosmer and Lemeshow (2000) the average discrimination ability could be considered as outstanding with (mean and median) AUC > 0.9. Furthermore, models were transferable in space without noticeable loss in predictive power (Fig. 3.4a). Under climate change, the distinct steps in the range dynamics were reflected in the prediction accuracies achieved for the different time slices (Fig. 3.4b). The range shift after year 115 caused only a slight difference, namely a wider range of prediction accuracies for the year 120 while for the year 130 the pattern seen in Fig. 3.4a was retrieved. Thus, abrupt range shifts caused a loss in predictive power in some scenarios, but, after a small time lag, predictive power was resumed. After year 140 which corresponded to the distinct range contractions, there was a profound difference between the prediction accuracies achieved by BRTs and GLMs. While the mean discriminatory power of BRTs even increased and the range decreased, the opposite was true for prediction accuracies of GLMs with a decrease in mean performance and a much wider range. Still, all scenarios yielded AUC > 0.7 indicating that for all scenarios both BRTs and GLMs were able to make useful predictions.

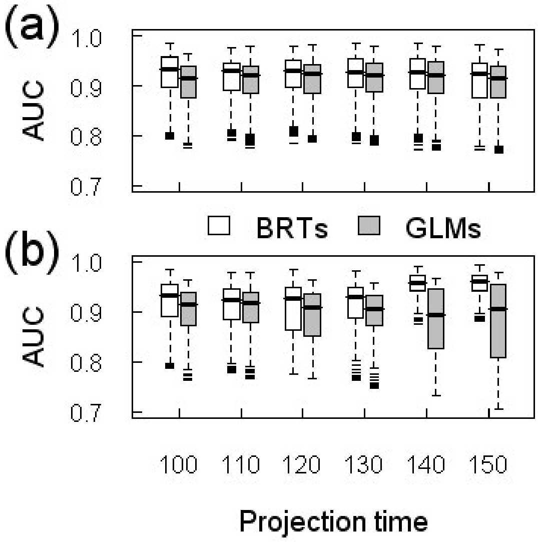


Figure 3.4. Boxplots of AUC values for scenarios under average climate (a) and climate change (b). SDMs were fitted in year 100; predictions were made on independent data for year 100 and every subsequent 10 years. The AUC values achieved for BRTs and GLMs, respectively, for the different climate regimes in the respective years are depicted in the boxplots; *n* = 160.

The effects of different ecological properties on the mean prediction accuracies achieved under climate change are shown in Fig. 3.5. Accuracies for the year 100 correspond to accuracies the SDMs would achieve under average climate. When the butterflies were not influenced by a parasitoid-interaction (Fig. 3.5a-c) differing butterfly population growth rates caused the only considerable effect on prediction accuracies, with higher AUCs for lower growth rates. There were trends that long butterfly dispersal distances and wide plant niche widths led to higher prediction accuracies. BRT prediction accuracies slightly decreased for year 120, except for scenarios with far butterfly dispersal distances where mean AUCs remained constant, and then increased and achieved even higher values in the year 150 than at the time of model estimation. GLM prediction accuracies exhibited the same pattern up to the year 130 but then strongly decreased for the years 140 and 150 where the distinct range contractions occurred. The exception were the scenarios with wide plant niche widths which only showed slight decreases in prediction accuracies under range contractions. Both BRT and GLM prediction accuracies for the year 120 only decreased for scenarios with short butterfly dispersal distances and there was this aforementioned time lag until predictive power was retrieved. Thus, butterflies with short dispersal distances did not track the range shift instantaneously but with some time lag.

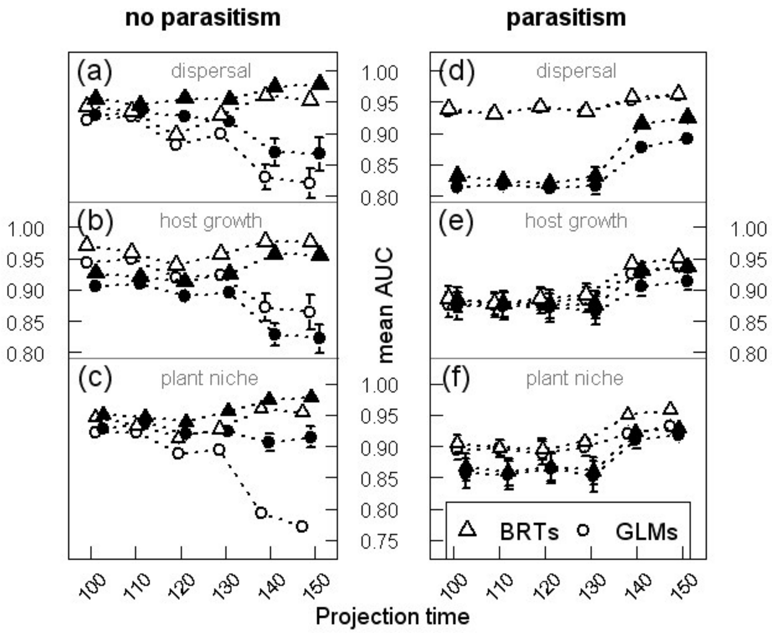


Figure 3.5. Effects of ecological properties on mean prediction accuracies (AUCs) of BRTs and GLMs achieved under climate change for all time slices, and for cases without parasitism (a-c) and with parasitism (d-f), respectively. Open and filled symbols indicate low and high values for a given ecological parameter, respectively (Table 3.2). Error bars indicate 95%-confidence intervals. Sample size is *n* = 40.

When parasitoids attacked the butterflies, the resulting prediction accuracies for the different time slices looked completely different (Fig. 3.5d-f). There were only minimal differences between BRTs and GLMs, and when the BRT prediction accuracies increased with range contractions, those of GLMs did as well. The virtual ecologist had perfect knowledge of the occurrence of parasitoids at all times. In the presence of a parasitoid-interaction the inclusion of this parasitoid incidence as predictor in the SDMs put GLMs on a par with BRTs. In contrast to scenarios without parasitism, butterfly population growth rates now did not show a remarkable effect on prediction accuracies anymore, and the effects of plant niche widths and butterfly dispersal distances were reversed. Butterfly dispersal ability exhibited the most pronounced effect with much higher prediction accuracies for short dispersal distances up to the year 130. When range contractions occurred this effect was smaller but still noticeable.

While for the year 150 under climate change even the lowest prediction accuracies achieved by GLMs still indicated useful predictions, they had alarmingly low explanatory power in some scenarios (Fig. 3.6). Without any parasitoid-interaction BRTs explained at least 50% of the deviance and achieved even values up to 90%. GLMs, on the other hand, did not even explain 20% of the deviance in five out of eight cases. Only in scenarios with wide plant niche widths and low butterfly population growth rates and in the scenario with high plant niche width, high butterfly population growth rate and far butterfly dispersal distance did

GLMs have explanatory power above 40% up to 60% explained deviance. Explained deviances achieved intermediate values between 30% and 70% in scenarios with parasitism assumed, and were similar for BRTs and GLMs.

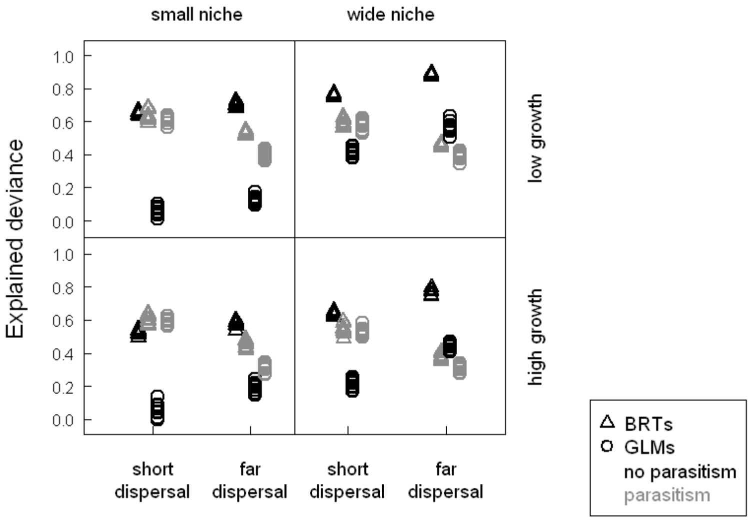


Figure 3.6. Effects of ecological properties on explained deviance achieved by BRTs and GLMs under climate change for year 150.

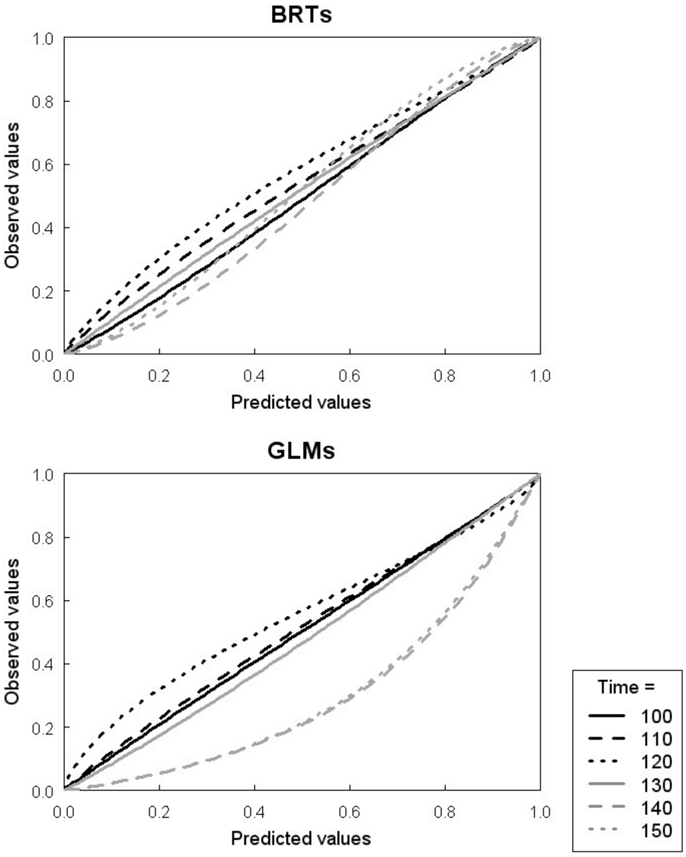


Figure 3.7. The mean calibration curves achieved by BRTs and GLMs under climate change without parasitism for all time slices. Sample sizes are *n* = 80.

Calibration statistics allowed us to judge the bias and spread in the predicted probabilities of occurrence compared to observed occurrences. The calibration curves obtained for BRTs and GLMs under climate change and without parasitism are shown in Fig. 3.7. Both BRTs and GLMs slightly underestimated the probability of butterfly occurrence in the year 120 when the butterflies started to shift their geographical range. This was true for all scenarios regardless of dispersal ability, indicating that the butterflies persisted at the trailing edge of the range shift for some time whereas the SDMs predicted unsuitable habitat. When range contractions took place, the probability of occurrence was overestimated, only slightly by BRTs but consistently by GLMs which showed a strong bias in their predictions (Fig. 3.8).

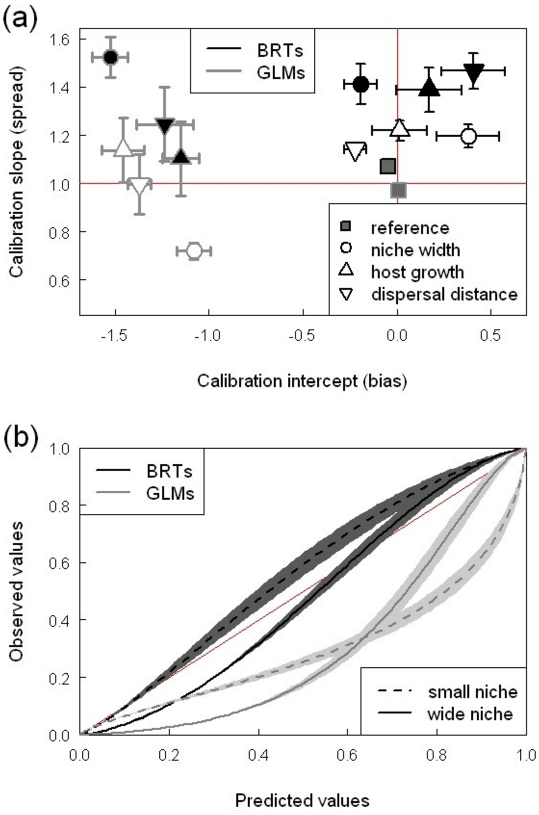


Figure 3.8. Effects of ecological properties on calibration statistics of BRTs and GLMs under climate change without parasitism for the year 150. (a) Open and filled symbols indicate low and high magnitudes, respectively (Table 3.2). The reference is the fit in year 100. Error bars (a) and shading lines (b) present the 95%-confidence interval. Sample sizes are *n* = 40, respectively *n* = 80 for the reference (a).

Overall, predictions made by BRTs fitted the observations well even under ongoing climate change. Bias and spread in the predictions differed for the different scenarios, i.e. for different ecological properties (Fig. 3.8). For instance for the year 150, short butterfly dispersal distances and wide plant niche widths caused BRTs to be slightly biased towards overestimating the probability of butterfly occurrence while low butterfly population growth rates caused no bias, and all other scenarios caused bias towards underestimating the probabilities of occurrence. All scenarios resulted in calibration slopes greater than one indicating that higher predicted values were underestimating the occurrence of butterflies while lower predicted values were overestimating the occurrence of butterflies. Nevertheless, for BRTs differences to the ideal calibration curve were small and in no way alarming. The strong bias in GLM predictions led to consistent overestimation of butterfly occurrence for all scenarios (Fig. 3.8a). Here, differing calibration slopes only determined whether this overestimation was more extreme for very low or very high predicted values (Fig. 3.8b). Overall, due to consistent overestimation GLMs were not able to accurately predict the absences under range contraction which, in contrast, was the major strength of the BRTs.

3.5 Discussion

3.5.1 Prediction accuracies under climate change

The main outcome of this study was that the ways in which species respond to climate change lead to quite different projection accuracies achieved by SDMs. As one might expect, prediction accuracies initially decreased when species started to shift their geographic range due to climate change. The calibration statistics helped to explain how this mismatch between simulated true species distribution and forecasts made by SDMs was determined on one hand by the dispersal ability of the species and on the other hand by the ability of the species to endure, at least for some time, suboptimal conditions at the trailing edge of the range shift where habitat became gradually unsuitable (Morin and Thuiller 2009). Both mechanisms led to a time lag after the range shift where the predictive performance of SDMs was decreased, although the mechanisms at the trailing edge were of minor importance. The uncertainty in prediction accuracies introduced by the unlimited dispersal assumption strongly depended on the dispersal ability of the species (Midgley et al. 2006; Thuiller et al. 2005). As soon as the species' potential geographic range remained static long enough for the species to fill its entire range, i.e. as a new equilibrium situation was realised, prediction accuracies increased again to values the SDMs would achieve under average climate. This also implied that rates and intensity of climate change are of utmost importance for the predictive performance of SDMs. If the potential geographic range of the species were to shift continuously, or if climate change were accelerated for periods of time, this would cause greater discrepancies between predicted and true species occurrences. Somewhat counterintuitively at first sight, the predictive performance of SDMs increased when species geographic ranges contracted. At second sight however, we saw that this happened because the absences were predicted more accurately. Thus, range contractions and consequently refugia could be modelled quite accurately by SDMs, and thus may allow identification of core areas for nature conservation. The results also highlight the benefit and importance of using different performance measures for SDMs. Models performing well in terms of predicting climate-change induced distributional shifts from a discrimination perspective (measured using the popular AUC statistic) may nevertheless perform poorly in terms of calibration, with significant implications for estimates of extinction risk and colonisation success.

3.5.2 Model comparison

As one might have expected, BRTs outperformed GLMs both when making predictions under both average climate and climate change. The high flexibility of BRTs and their ability to model thresholds in species' occurrence made them superior to GLMs. Surprisingly, in the presence of a parasitoid interacting with the butterfly this effect vanished and BRTs and GLMs were equivalent, highlighting the importance to include biotic interactions as predictors. It was striking that the mean discriminatory power of BRTs increased when range contractions took place while the mean performance of GLMs decreased. But can we generalise these results and, thus, can we expect BRTs to generally better perform under climate change than GLMs? The answer is no, because attention should be paid to the circumstances where the models were estimated. As BRTs model thresholds in species' occurrences and extrapolate beyond the parameter range by predicting the mean response of the parameter region closest to the newly encountered parameter space, the prediction accuracy strongly depends on the extent to which the recorded occurrences correspond to the entire niche of the species. Ideally, the full range of a species should be used for estimating SDMs because then the probability is reduced to extrapolate to environmental conditions the species has never encountered before (Dormann 2007; Thuiller et al. 2004); examples are given by del Barrio et al. (2006) and Pearson et al. (2002). If this is met, then BRTs will probably always outperform parametric methods as GLMs, simply because they allow a highly non-linear threshold-like fitting of presence-absence data, rather than relying on monotone approximations such as the logistic curves of binomial GLMs.

3.5.3 Effects of ecological properties and processes

Several studies reported decreasing spatial prediction accuracies with increasing range sizes and niche breadth, i.e. more accurate predictions could be made for specialists than for generalists (Brotons et al. 2007; Hernandez et al. 2006; McPherson and Jetz 2007; Pearce et al. 2001; Segurado and Araújo 2004; Seoane et al. 2005; Stockwell and Peterson 2002). This however, is not beyond controversy as e.g. Garrison and Lupo (2002) reported better model performances for species with larger range sizes. We encountered both effects: when butterflies were interacting with a parasitoid, specialists were modelled more accurately. In contrast, when no parasitoid-interaction was present there was no considerable effect for spatial predictions but under ongoing climate change the distributions of generalists were modelled more accurately than of specialists. There is no easy biological explanation for this. To explain why specialists can be modelled more accurately than generalists Stockwell and Peterson (2002) suggested that widespread species may show local ecological adaptations. Modelling all these subpopulations together would effectively overestimate the species' niche, and therefore reduce model performance. However, our dynamic model did not incorporate any local adaptation and we may thus rule out this explanation. A likely explanation why in the presence of a parasitoid-interaction SDMs performed better for specialists than for generalists is that the relationship between butterfly and parasitoid occurrence might be noisier for wide-ranging butterflies. Without parasitism a remarkable difference between model performances for generalists and specialists only occurred when the species started to shift their geographic range and in the case of GLMs increased noticeably when range contractions occurred. A reason might be that suitable habitat became more isolated with ongoing range shifts and contractions, and that this isolating effect was severer for specialists. Thus, butterflies were not able to reach all suitable habitat patches, this effect being more pronounced for narrow-ranging than for wide-ranging butterflies.

Without parasitism lower butterfly population growth rates led to higher predictive performances of both BRTs and GLMs under average climate and for range shifts. There was no considerable effect when range contractions occurred and when the butterflies were interacting with parasitoids. Higher growth rates caused higher abundances and because of local dispersal also higher prevalences, but only in particular regions where the temperature was near the optimum growing temperature. This may have resulted in biased habitat selection patterns and therefore response surfaces, obscuring the true species-habitat relationship. These findings are in contrast to the results of Seoane et al. (2005) who obtained better models for species that can reach high densities. They, however, predicted abundances instead of probabilities of occurrence, and for accurate predictions of species abundances other ecological factors may be of importance.

Under average climate and without parasitism, model performances did not differ between short and far-dispersing butterflies. This is consistent with results found by Garrison and Lupo (2002) and Stockwell and Peterson (2002). Pearce et al. (2001) on the other hand reported poorer prediction accuracies for mobile species though this effect was not significant. As mentioned before, when the species started to shift their geographic range due to climate change short-dispersing butterflies were initially outpaced by climate change. When butterflies were interacting with parasitoids prediction accuracies were much better for short-dispersing butterflies. This is an effect of parasitoids' dispersal ability. When parasitoids were worse dispersers than the butterflies then the relationship between butterfly and parasitoid occurrences was much noisier. Thus, not only the dispersal ability of the focal species is of importance but also the dispersal behaviour of species it is interacting with.

3.5.4 Limitations and extensions

Creating a virtual world is fraught with difficulties. Our spatially explicit tritrophic system and companion virtual ecologist represent only one possible implementation, but it enabled us to manipulate important biotic interaction and dispersal effects on SDM accuracy.

One caveat of our study is the assumption that our virtual ecologist acts flawlessly and under optimum conditions: the virtual species is detected perfectly and the spatial samples are complete in coverage and instantaneous in time. In studies of real data ecologists have to deal with false negatives in the data, incomplete coverage of environmental predictors, more complex species-habitat relationships, etc., the effects of which clearly remain to be explored by future extensions of our approach.

Additionally, several other effects can be explored with this approach, which lie outside experimental manipulation in the real world. First the effect of other types of ecological processes can be investigated, such as spatial dependency of biotic interactions (i.e. some taking place only at the edge of a species distribution) or changing biotic interactions under environmental change, the effects of changing disturbance regimes or local ecological adaptation. Secondly, several statistical and sampling issues can be addressed, such as the usefulness of proxies (e.g. NDVI as surrogate for host plant abundance); effect of missing important variables (e.g. omitting incidence of parasitoids from SDMs); or density-dependence in detection probability of the focal species (a problem that underlies the development of efficient survey designs).

3.5.5 Perspectives and research needs in species distribution modelling

Several steps must be taken in order to improve predictions of species distributions under scenarios of environmental change. Distributional patterns of species in space and time are determined by environmental variability, and processes acting at specific spatial scales and times may be crucial for the occurrence of a species. Climate change may even increase variability in the environment both spatially and temporally, and thus this variability must be accounted for in species distribution modelling. The importance of spatial scale and hierarchical structure in ecological processes has long been recognised (Mackey and Lindenmayer 2001), but only very few studies have so far explicitly dealt with multiple spatial scales in a hierarchical manner (Graf et al. 2005; Diez and Pulliam 2007; McMahon and Diez 2007; Albert et al. 2008). Ignoring hierarchical structure in processes may be fallacious and result in erroneous projections of future species distributions under environmental change (Davis et al. 1998; Diez and Pulliam 2007; Dormann 2007). In real world studies, the underlying processes are rarely known, making, in our opinion, consideration of hierarchy in scales and processes indispensable, for example by means of multilevel modelling (Gelman and Hill 2007). Our results showed that temporal patterns of climate change and transient dynamics greatly affect SDM prediction accuracies, and other studies have suggested that temporal variability increases the probability of population extinction (cf. Thuiller et al. 2008). Midgley et al. (2006) showed that even a simple ‘time-slice’ approach may reveal transient range dynamics which are obscured by ‘one-step’ projections as commonly applied when projecting future species ranges by SDMs. We recommend the use of ‘time-continuous’ approaches with discrete time steps in which step lengths should be as small as possible or should at least be determined by temporal patterns and rates of expected environmental change (cf. Schröder et al. 2008 for an example on landscape-scale). Overlaying the resulting habitat suitability maps of the different time steps or years may allow the identification of core areas within a species’ range (cf. Osborne and Suarez-Seoane 2007) and thus core areas for nature conservation.

Our study showed that the performance of SDMs predicting species which experienced range shifts strongly depended on two processes: dispersal at the leading edge and extinction or persistence at the trailing edge of the range shift. The incorporation of these processes into species distribution modelling is thus of major importance. Several strategies have already been tested to incorporate animal dispersal or animal dispersed pollen and seeds into SDMs, including the simple assumption of maximum dispersal rates (Midgley et al. 2006), and connectivity analyses (del Barrio et al. 2006; Graf et al. 2005). More complex approaches mechanistically modelling dispersal rely on dispersal kernels (e.g. del Barrio et al. 2006) or individual-based models (e.g. Graf et al. 2005). Applying such mechanistic approaches to range projections under climate change additionally requires integrated modelling of local population dynamics. The choice of approach to use depends on the specific aims of the study in question. However, for the prediction of species’ responses to climate change an integration of dispersal and local population dynamics in a mechanistic manner seems promising (del Barrio et al. 2006; Keith et al. 2008), on the one hand because knowledge of local population dynamics is needed for the prediction of persistence at the trailing edge and local extinctions within the species' range. On the other hand, incorporation of local population dynamics may help to predict species' responses to, for example, seasonally asymmetric climate change or extreme events. Explicit consideration of dynamic species' responses may provide the basis for dynamic and integrated conservation strategies.

Biotic interactions must be included in SDMs. But then, future projections of species' distribution then also require knowledge and thus prediction of the distribution of interacting organisms (Hawkins and Porter 2003, Schweiger et al. 2008). In cases where the link between predator and prey is as tight as in our virtual world, where the parasitoid only foraged on the butterflies and was directly dependent on them, the temporal distribution of the predator may be approximated by a simple dispersal model simulating movement between patches exhibiting a probability of prey occurrence above a certain threshold. Also, the distribution of lower trophic levels on which the focal species forages must be known or predicted at all projection times introducing further uncertainties in range projections. There is no simple solution to that, and for now we must be content with making projections under specific assumptions regarding the distribution of any interacting organisms.

3.5.6 Conclusion

Different range dynamics may lead to quite different prediction accuracies of SDMs under climate change. A species' ability to track climate change, determined by dispersal ability and the rate of change, is decisive for SDM performance when species shift their geographic range. Range contractions may be predicted quite accurately as the absences are predicted well. Flexible methods as BRTs will probably always outperform parametric methods due to their ability to fit non-monotone relationships. The study demonstrates the benefits and capabilities of integrating dynamic and statistical modelling approaches in different ways. On the one hand, dynamic population modelling as virtual playground for testing statistical models allows the extensive exploration of specific questions. On the other hand, the integration of dynamic processes into species distribution modelling may help to improve predictions of species distributions under environmental change. Here, the present study provides valuable insights which processes are of relevance when species undergo transient dynamics and should hence be incorporated in species distribution models.

4 Uncertainty in predictions of range dynamics: black grouse climbing the Swiss Alps[3]

---

[3] A manuscript with equivalent content has been published as:

Zurell, D., Grimm, V., Rossmanith, E., Zbinden, N., Zimmermann, N.E. and Schröder, B. (2011). Uncertainty in predictions of range dynamics: black grouse climbing the Swiss Alps. Ecography. doi: 10.1111/j.1600-0587.2011.07200.x

4.1 Abstract

Empirical species distribution models (SDMs) constitute often the tool of choice for the assessment of rapid climate change effects on species' vulnerability. Conclusions regarding extinction risks might be misleading, however, because SDMs do not explicitly incorporate dispersal or other demographic processes. Here, we supplement SDMs with a dynamic population model (i) to predict climate-induced range dynamics for black grouse in Switzerland, (ii) to compare direct and indirect measures of extinction risks, and (3) to quantify uncertainty in predictions as well as the sources of that uncertainty. To this end, we linked models of habitat suitability to a spatially explicit, individual-based model. In an extensive sensitivity analysis, we quantified uncertainty in various model outputs introduced by different SDM algorithms, by different climate scenarios and by demographic model parameters. Potentially suitable habitats were predicted to shift uphill and eastwards. By the end of the 21st century, abrupt habitat losses were predicted in the western Prealps for some climate scenarios. In contrast, population size and occupied area were primarily controlled by currently negative population growth and gradually declined from the beginning of the century across all climate scenarios and SDM algorithms. However, predictions of population dynamic features were highly variable across simulations. Results indicate that inferring extinction probabilities simply from the quantity of suitable habitat may underestimate extinction risks because this may ignore important interactions between life history traits and available habitat. Also, in dynamic range predictions uncertainty in SDM algorithms and climate scenarios can become secondary to uncertainty in dynamic model components. Our study emphasises the need for principal evaluation tools like sensitivity analysis in order to assess uncertainty and robustness in dynamic range predictions. A more direct benefit of such robustness analysis is an improved mechanistic understanding of dynamic species' responses to climate change.

4.2 Introduction

Recent studies in biogeography and macroecology resulted in growing concerns about species' range shifts driven by ongoing climate and land use change. Species dynamically adjust their ranges in response to the complex interplay of environmental forces, changing biotic interactions, and their interactions with key demographic traits (Araújo and Luoto 2007, Thuiller et al. 2008, Walther et al. 2002). To date, a substantial body of literature has amassed on predicting potential range dynamics as well as extinction risks in order to derive mitigation strategies for global change impacts (Midgley et al. 2002, Thomas et al. 2004, Thuiller 2004).

Many, if not most, recent climate impact studies rely on correlative, phenomenological species distribution models (SDMs). These derive statistical relationships between the species' occurrence (or abundance) and prevailing environmental (biotic and abiotic) factors to characterise the environmental niche (Guisan and Zimmermann 2000). Potential future ranges of species are projected by transferring this relationship to future environmental conditions, thus allowing for rapid assessment of potential threats. SDMs require comparably simple species location data such as presence-absence and do not rely on profound prior knowledge on the species' biology. Therefore, they constitute one of few practical approaches to study environmental change impacts on a wide range of species quickly (Elith and Leathwick 2009, Huntley et al. 2004) and have spurred hundreds of applications and publications on these issues (Zimmermann et al. 2010).

However, SDMs are not intended for making transient predictions under environmental change. Many recent publications have tried to raise awareness to the inherent fundamental as well as methodological limitations accompanying SDMs (Buckley and Roughgarden 2004, Dormann 2007, Guisan and Thuiller 2005, Hampe 2004). Some principal limits for SDMs arise from their conceptual underpinning. Foremost, they assume that species are in equilibrium with their environment, which may not even be the case for many post-glacial distributional ranges (e.g. Svenning and Skov 2004). Correspondingly, when extrapolating to new times and places, SDMs implicitly assume an instantaneous realisation of a new equilibrium situation. Thereby, transient population dynamics and important life history traits such as dispersal capacity and local persistence ability that shape a species' response to environmental change are essentially ignored (Thuiller et al. 2008, Zurell et al. 2009, chapter 3). This may lead to biased estimates of extinction risks. In addition, discussions about methodological issues prevail. Different SDM algorithms, for instance, have led to divergent predictions of habitat suitability for scenarios of climate change (Buisson et al. 2010, Pearson et al. 2006, Thuiller 2004). Among others, model predictions can be expected to be sensitive to model building steps and data characteristics including uncertainty in future climate scenarios (Araújo and Guisan 2006, Dormann et al. 2008, Heikkinen et al. 2006).

Challenges for SDM predictions under environmental change are manifold and, therefore, several steps have been proposed to improve SDMs and to yield more robust predictions. One solution is to make use of multiple models within an ensemble framework which allows analysing the range of uncertainty introduced, for example, by different SDM algorithms and different climate scenarios (Araújo and New 2007, Thuiller et al. 2009). To overcome fundamental limitations of SDMs that are related to their static nature, several authors have urged to supplement SDMs by more mechanistic, stochastic population models that incorporate key demographic processes determining range dynamics (Araújo and Guisan 2006, Guisan and Thuiller 2005, Thuiller et al. 2008, Schröder 2008, Zurell et al. 2009, chapter 3). Stochastic population models explicitly describe demographic processes such as mortality, reproduction and dispersal while taking into account environmental and demographic stochasticity. They allow the assessment of species vulnerability or extinction risks via population viability analyses (PVA, Burgman et al. 1993, Brook et al. 2000) and may help to uncover 'tipping points' that lead to rapid and potentially irreversible species' responses to environmental change (Pereira et al. 2010). However, these models are also highly data demanding, usually involve more complex model structures, and rely on extensive knowledge on species' biology and population processes which often constrains the spatial scale of the studies, the number of species or the generality of results (Jeltsch et al. 2008).

Attempts have been made to make use of both phenomenological and population dynamic approaches when predicting climate change-induced range shifts (Anderson et al. 2009, Cheung et al. 2009, Keith et al. 2008). Thereby, SDMs and comparably simple, spatially explicit population models are integrated by constraining basic demographic parameters of the dynamic model (e.g. carrying capacity) by SDM output (e.g. habitat suitability). As such, the predictive accuracy of SDMs at large spatial scales is retained while being able to capture transient population dynamics in response to climate change (Gallien et al. 2010, Keith et al. 2008). Another simple way is to run a dynamic, multi-species population model under a range of environmental and landscape contextual conditions, and then to fit the major outcome of these simulations, namely migration rate, against climate and competition as predictors, and to combine this information in a simple GIS time-step model to predict transient responses of the target species to changing land use and climates (Meier et al. 2011).

The goal of all these considerations and efforts is to increase robustness of model predictions under environmental change. Quantitative predictions of models typically carry substantial error margins due to structural (model specification) uncertainty and parameter (data) uncertainty as well as inherent (natural) stochasticity of ecological dynamics (Barry and Elith 2006, Jeltsch et al. 2008). Conclusions regarding the robustness of predictions can only be made conditional on explicit simulation runs. When integrating SDMs and dynamic population models in order to predict range dynamics for scenarios of environmental change final predictions essentially carry errors of three different models (SDM, population model and climate model; Beaumont et al. 2008, Wiens et al. 2009). These uncertainties need to be quantified in order to draw inferences about the robustness of model results.

In this context, the objectives of our study were threefold: (1) to predict climate-induced range dynamics for black grouse in Switzerland, (2) to compare direct and indirect measures of extinction risks, and (3) to quantify uncertainty and robustness of predictions and assess relative contribution of different modelling components to overall uncertainty. To achieve this, habitat suitability maps obtained from spatio-temporal SDM predictions were linked to a spatially explicit individual-based model that described key demographic processes of black grouse. Predictions were derived and compared for multiple key model outputs (population and occupied area size, probability of extinction, mean elevation and mean population centre). Uncertainty in predictions was quantified by extensive sensitivity analysis. Thereby, we focused on three different uncertainty components: climate scenarios, SDM algorithms, and demographic model parameters. Furthermore, sensitivity was evaluated for each key model output to delineate more or less robust features of dynamic range predictions.

4.3 Methods

4.3.1 Species data

In the Swiss Alps, black grouse (*Tetrao tetrix*) mainly occurs in treeline habitats, in dwarf-shrub-rich transition zones between forests and alpine meadows at an altitude of up to 2500 m above sea level (Zbinden and Salvioni 2003). Swiss black grouse populations were judged as stable by comparisons between the two observation periods of the Swiss Breeding Bird Atlases 1972-1976 and 1993-1996 (Schifferli et al. 1980, Schmid et al. 1998). However, population sizes are known to fluctuate strongly and, thus, estimates on population status derived from such short time periods may be imprecise. For example, local declines were reported for the northern as well as southern Prealps caused by habitat loss and fragmentation (Schmid et al. 1998, Zbinden and Salvioni 2003).

Species distribution data at 1 km resolution were obtained from the Swiss Breeding Bird Atlas (Schmid et al. 1998). Count data for assessing reproductive success were obtained from a time series observed between 1981-2007 in Ticino, Switzerland, where the numbers of chick-rearing hens and juveniles were recorded annually in the second half of August (Zbinden and Salvioni 2003).

4.3.2 Environmental predictors

Environmental predictors included climatic variables as well as land use and vegetation data at 1 km resolution. Climate data were derived from the BIOCLIM database (Swiss Federal Research Institute WSL) including long-term averages from the period 1961-1990 on summer

(June-August), winter (December-February) and annual values for the variables: precipitation sum; mean temperature; potential solar radiation; mean summer moisture index (precipitation – potential evapotranspiration); and growing degree days above 0 °C. Details for the derivation of these climate layers are given in Zimmermann and Kienast (1999) and in Guisan et al. (2007). Land use and vegetation data were compiled from the land use and land cover database GEOSTAT (Swiss Federal Statistical Office). From these, we chose five land use categories that we deemed sensible to explain black grouse presences and absences, based on the ecology of the species: scattered forest, bushy forest, grassland and arable land, unproductive vegetation, and residential and infrastructural areas.

4.3.3 Climate change scenarios

Climate change scenarios were obtained from the ENSEMBLES Project (http://www.ensembles-eu.org/). Five scenarios were obtained from three regional circulation models with three different underlying general circulation models and three different emission scenarios (A1B, B1, B2, see Table 4.1). These scenarios were chosen to reflect a range of predictions for the Central European Alps that were both realistic and reached from pessimistic to optimistic. Scenarios were downscaled to a 1 km spatial resolution according to the procedure described in Engler et al. (2011). Climate scenarios were available as 10 year time slices which we interpolated to obtain annual changes in climate. The general climate trend over the 21st Century is illustrated in Appendix C, Fig. C.1.

Table 4.1. Regional circulation models (RCM) used in the ensemble simulations of this study. Each RCM was based on the boundary inputs from a General Circulation Model (GCM). We used three different SRES scenarios, which translate for the Swiss case study to tabulated climate anomalies by the end of the 21st century (ΔT, ΔP). HC: Hadley Center; MPI: Max Plank Institute; SMHI: Swedish Meteorological and Hydrological Institute.

Short	RCM	GCM	Institute	SRES	ΔT	ΔP
H-a1	HadRM3q0	HadCM3	HC	A1B	+5.26°C	+4.67mm
M-a1	CLM	ECHAM5	MPI	A1B	+4.51°C	+5.96mm
M-b1	CLM	ECHAM5	MPI	B1	+3.07°C	+10.51mm
S-a1	RCA30	CCSM3	SMHI	A1B	+2.71°C	+0.70mm
S-b2	RCA30	CCSM3	SMHI	B2	+2.89°C	+1.55mm

4.3.4 Species distribution model

Black grouse potential distribution was predicted using three different statistical algorithms that take presence-absence input data, are widely used in species distribution modelling and that present different levels of flexibility (Elith et al. 2006, Heikkinen et al. 2006), namely:

generalised linear models (GLM), generalised additive models (GAM) and boosted regression trees (BRT).

In order to minimise multicollinearity problems, we pre-selected the final predictors prior to modelling so that bivariate Spearman correlations were below |r|=0.7 (Fielding and Haworth 1995). Thereby, we gave preference to land use variables as we regard these as more proximal predictors for black grouse occurrence and, hence, retained only those climate variables that we expected to have a direct effect on black grouse occurrence. Our final predictor set included five land use variables (see above), two climate variables (mean annual temperature, winter precipitation), and potential solar radiation describing topographic effects.

We allowed second-order polynomials in GLM, and non-parametric cubic smoothing splines with up to four degrees of freedom in GAM. BRT was estimated with a tree complexity of 2, a bag fraction of 0.75 and a learning rate of 0.01 which ensured that the model was fitted with at least 1000 trees (cf. Elith et al. 2008).

A split-sample approach was used to validate SDM performance (Araújo et al. 2005). Models were calibrated on a randomly selected sample of 70 % of the data and validated against the remaining 30 %. Data splitting was repeated 100 times and evaluation statistics were averaged to yield a final evaluation that is quasi-independent of initial conditions (Thuiller et al. 2009). Several measures of accuracy were calculated: explained deviance R2 (Menard 2000), the area under ROC curve (AUC; Fielding and Bell 1997), the true skill statistic (TSS) (Allouche et al. 2006), sensitivity (true presences) and specificity (true absences) as well as slope and intercept of the calibration curve which describe spread and bias in the predictions (Reineking and Schröder 2006, Zurell et al. 2009, chapter 3). We derived the deviance by applying eq. 1.10 in Hosmer and Lemeshow (2000). As TSS, sensitivity and specificity require binary predictions we converted the predicted occurrence probabilities into presence-absence maps by applying the prevalence threshold (Liu et al. 2005). All SDMs with accompanying analysis of their performance were built in R version 2.12.1 (R Development Core Team 2010).

The resulting SDMs estimated black grouse occurrence probabilities for entire Switzerland. High occurrence probabilities were interpreted as indicating environmental conditions that define highly suitable habitat for black grouse (Araújo et al. 2002, Söndgerath and Schröder 2002).

4.3.5 Individual-based model

We simulated population dynamics of black grouse by a stochastic, spatially-explicit individual-based model (IBM) that followed the fate of individual birds from birth to death. The subsequent model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual-/agent-based models (Grimm et al. 2006, Grimm et al. 2010).

Purpose: The main purpose of the model is population viability analysis.

Entities, state variables and scale: Female birds constituted the biological entity in our model. In black grouse, females are the limiting sex regarding not only reproduction but also dispersal as the latter is restricted predominantly to first-year hens while first-year cocks affiliate to the nearest lek (mating arena for competitive courtship display), and adults are rather sedentary (movements within the home ranges were ignored, Caizergues and Ellison 2002). Individuals were characterised by the state variables location and age. The model landscape represented entire Switzerland and consisted of a grid of 42181 cells of 1 km resolution. Each grid cell was characterised by its carrying capacity K. Boundary conditions were reflecting so that emigration from the study area equalled immigration. The model proceeded in annual time steps (from spring to spring).

Process overview and scheduling: At the beginning of each time step, carrying capacity *K* of all cells was determined from habitat suitability as estimated by SDMs. In summer, hens reproduce and raise juveniles that survive until first autumn with the probability *pleadYoung* (see Table 4.2 for IBM parameters). Thus, *pleadYoung* subsumes the processes of clutch survival, hatching rate and early chick survival. The probability of a hen to lead a certain number of juveniles is *p(x)Fledglings*. The probability for a fledgling to be female is *pFemale*, otherwise it is a male and is subsequently ignored. In autumn, first-year hens disperse from their natal patch with a probability *pDispersal*. Individual birds perceive the environment as heterogeneous and avoid to settle in or to traverse wide stretches of unsuitable habitat (Graf et al. 2007). All sources of mortality are subsumed under an annual survival probability *pSurv*, the probability of an individual hen to survive until early spring. Mortality and emigration may increase with density due to increased predation risk or simply due to shortage of resources. At the end of the simulation year (early spring), the age of all individuals is incremented by one year. Individuals growing older than *MaxAge* are removed.

Design concepts: The model follows a bottom-up approach, and population dynamics and spatial distribution of black grouse emerge from individual behaviour. Life cycle, reproduction, and survival rates are imposed by empirical rules and parameters. Dispersal includes the basic adaptive decision to avoid unsuitable and over-crowded habitat. Demographic stochasticity is included to mimic individual-level variability by interpreting all demographic parameters as probabilities (Burgman et al. 1993). Environmental stochasticity is considered by drawing *pleadYoung* (probability of hen to reproduce and raise juveniles that survive until first autumn) from a normal distribution. This parameter subsumes the processes of nest predation, hatch rate and early chick survival that are most strongly influenced by environmental fluctuations between years. The normal distribution was defined by the mean and SD derived from empirical data, cut at minimum and maximum of empirically observed values (Table 4.2). Key outputs monitored from the model are population size, probability of extinction by time t (proportion of replicate runs that went extinct), area size, mean elevation, and mean population centre (lon/lat).

Table 4.2. IBM parameters.

Parameter	Value	Description
pleadYoung (min, max)	0.6 ± 0.09 (0.39, 0.77)	probability of a hen to lead young during simulation year
p(x)Fledglings	0.103/1, 0.198/2, 0.270/3, 0.249/4, 0.124/5, 0.037/6, 0.013/7, 0.004/8, 0.002/9	probability to produce *x* fledglings (given as probability/clutch size)
pFemale	0.5	probability to be female at birth
pDispersal	0.81	probability of juveniles to emigrate
meanDist	8	mean dispersal distance [km]
rangeDist	1.0-29.0	range dispersal distance [km]
pSurv	0.5	probability to survive the simulation year
Kmax	10	maximum carrying capacity [km^{-2}]
MaxAge	10	maximum age

Initialisation: Initially, 8000 individuals were randomly distributed in suitable habitat, and were assigned a random age (between 1 and 3 years), which is in accordance with data from the Swiss Breeding Bird Atlas (Schmid et al. 1998). The initial habitat suitability map is obtained from the species distribution model run with current climate. The model 'spinned up' for 25 years to exclude initialisation effects (Rossmanith et al. 2007). After this 'spin-up' climate change was initiated with annual timesteps.

Input data: For each time step, a habitat suitability map is derived from the species distribution model described above given the environmental input layers (climate and land cover).

Submodels: Detailed descriptions of submodels implementing the modelled processes are provided in Supplementary material Text S1. The entire IBM was implemented in C++.

4.3.6 Sensitivity analysis

We evaluated three major sources of uncertainty in range predictions: underlying species distribution models (SDM), climate scenarios (RCM), and demographic parameters of the individual-based model. In a preliminary local sensitivity analysis we found that IBM parameters affecting survival and reproduction, namely survival probability (*pSurv*), the probability to be female at birth (*pFemale*) and the probability of a hen to lead young (*pleadYoung*), were the most sensitive parameters for range predictions while others such as dispersal parameters had little effect on population fate. This is not unexpected because as black grouse range contracts and retrieves to higher elevations of the Swiss Alps in response to warmer regional temperatures the species' fate is more restricted by local persistence ability and successful establishment at higher elevations than by dispersal. Thus, in subsequent sensitivity analysis we concentrated on the three above-mentioned survival and reproduction parameters and varied them in a 3k factorial design (low, intermediate, and high values given by default parameters in Table 4.2 ± 5%). As *pleadYoung* is drawn from a normal distribution we manipulated both position and shape of this distribution by shifting the entire distribution by ± 5% and by varying the standard deviation of this distribution by ± 5% (resulting in a more peaked or more flattened distribution). Our sensitivity analysis thus crossed three different SDM techniques, five different climate scenarios, and four different demographic parameters (note that *pleadYoung* counts twice) with three levels each resulting in a total of 1215 different model configurations. For each of these we performed 35 replicates (McCarthy et al. 1995). We quantified the sensitivity in the years 2001, 2050 and 2100 for five different model outputs (population size, probability of extinction by year t, area size, mean elevation, and mean population centre). First, for each parameter combination we calculated the mean values of the five key model outputs from the 35 replicate simulations. Then, for each model output and for each uncertainty component we performed univariate linear regressions with the respective model output as dependent variable and the respective uncertainty component as independent variable (cf. Dormann et al. 2008). The relative contribution of each uncertainty component to variability in predictions was then given by the explained variance R2 of the linear regression models. Additionally, we ran 'control' simulations with default IBM parameterisation across the different SDM algorithms and climate scenarios with 100 replicates each to obtain an estimate of variation in model outputs due to stochasticity. All analyses of IBM output were carried out in R version 2.12.1 (R Development Core Team 2010).

4.4 Results

4.4.1 Statistical modelling and range predictions

All three SDM techniques fitted consistent relationships between black grouse occurrence and environmental predictors (Fig. 4.1) although differences were also apparent, mainly in areas of the environmental space with lower data coverage. Mean annual temperature was by far the most important variable (Fig. C.2), followed by grassland cover type which mainly described species absences, and followed by bushy and scattered forest and unproductive vegetation which were more important for describing species presence. In the split-sample validation (n=100) we found only slight differences in model performance between methods. All three SDMs showed excellent discrimination in terms of AUC (approx. 0.95), very good accuracy in terms of TSS (approx. 0.78), high rates of correctly predicted presences (sensitivity: 0.93-0.95) and absences (specificity: 0.84-0.86), and excellent calibration (calibration slope and intercept near one and zero; Table C.1). BRT showed highest scores for all measures except for sensitivity, which was highest for GLM (although differences were not pronounced). Overall, SDMs explained between 57.2 and 59 % of the deviance in black grouse occurrence (Table C.1).

Table 4.3. Model output for Default IBM parameterisation, averaged across different SDM algorithms and climate scenarios.

Output	Year	Mean	SE	Median
Population size	2001	5,508	56	5,144
	2050	2,318	36	1,998
	2100	974	21	703
Area size [km2]	2001	3,221	27	3,090
	2050	1,478	20	1,323
	2100	662	14	504
Mean elevation [m]	2001	1,791	1	1,791
	2050	2,039	15	2,026
	2100	2,217	32	2,171

GLM predicted greatest total area size of potentially suitable habitat for black grouse under current environmental conditions, BRT smallest (Year 2001; GLM 11,690 km2, GAM 11,240 km2, BRT 10,590 km2). Predictions of habitat suitability changes under climate change were very similar across all three SDMs. Differences did not emerge until the end of the 21st century when predictions varied considerably across climate change scenarios with great and abrupt habitat losses under the more extreme scenarios H-a1 and M-a1 (Fig. C.3). For these extreme cases, also differences between SDMs became more apparent with greatest losses predicted by GAM, lowest by GLM. Altitudinal ranges were predicted to shift uphill from mean elevations of approx. 1,800 m a.s.l. in 2001 to mean elevations of approx. 2,200 m a.s.l.

by 2100 (Fig. 4.2 and Table 4.3). BRT predicted accompanying range contractions while GLM and GAM predicted an eastward shift in suitable habitat. Range contractions were predicted in the western Prealps primarily due to elevational limits (Fig. 4.3). Consensus on black grouse presence was high for the Central and Eastern Swiss Alps (Fig. C.4).

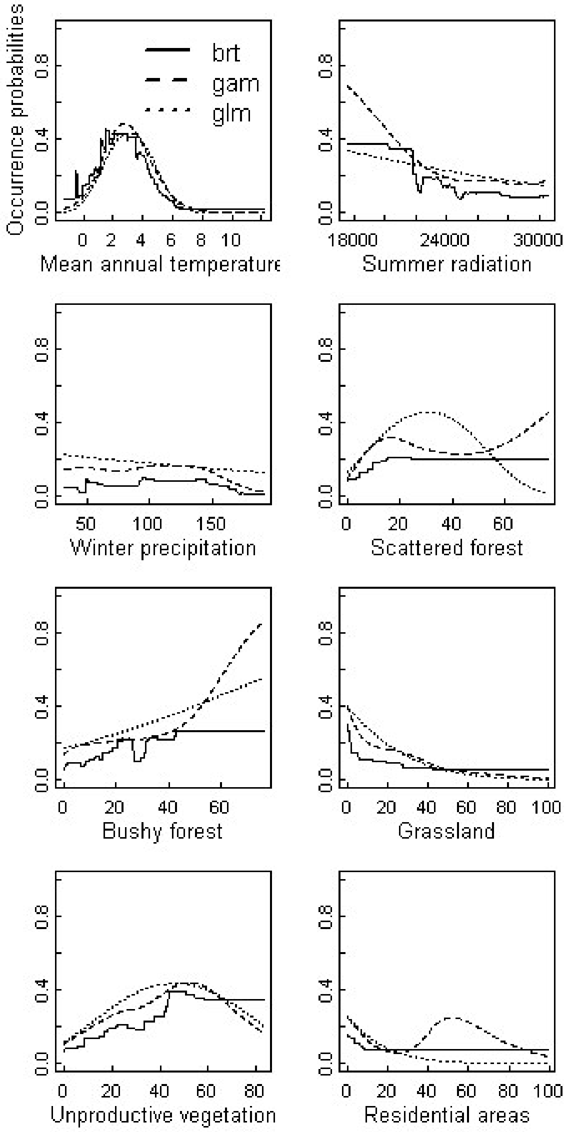


Figure 4.1. Partial dependence plots for all eight environmental predictors and for the three different SDM algorithms (BRT, GAM, GLM).

4.4.2 Population dynamics

The IBM predicted mean population sizes of ca. 5,500 female black grouse for current environmental conditions and for default IBM parameterisation (Fig. 4.4 and Table 4.3). Population size was predicted to gradually decline over the century (Fig. 4.4). By the end of the century, black grouse population sizes were predicted to drop to 12 – 22 % of their initial size. The strong population decline mainly resulted from a negative population growth rate given the demographic rates (Table 4.2). For comparison, we manipulated the parameter survival probability so that current population trend was stable (*pSurv* = 0.51). This resulted in higher predicted population sizes and moderate declines which were similar in trend yet not identical in shape to habitat trajectory (Fig. C.5).

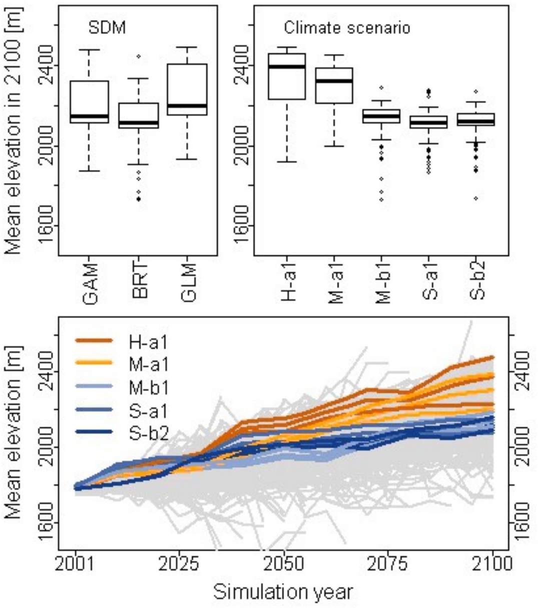


Figure 4.2. Mean elevation occupied by black grouse for scenarios of climate change. Bottom: Grey lines show mean elevations across all simulations, coloured lines those for default IBM parameterisation (cf. Table 4.2) across different SDMs and climate scenarios. Top: Boxplots depict variation of mean elevations predicted for the end of 21st century (2100) and for different SDMs and climate scenarios.

4.4.3 Sensitivity analysis

The relative contribution of each uncertainty component to variation in predictions differed for the different time slices considered and for the different model outputs. Great variations across simulations were found in predictions of population dynamic features such as population and occupied area sizes as well as for probabilities of extinction. Variation in predicted population size due to uncertainty in demographic parameters was approximately one order of magnitude greater than variation due to environmental and demographic stochasticity and due to uncertainty in SDMs and climate scenarios (Tables 4.3 and 4.4). On the other hand, geographic features like mean population centre, range extent, and mean elevation showed comparably low variation across simulations. Different climate scenarios had no considerable effect on population dynamic features, yet they were the most important uncertainty component for geographic features. Specifically, the variation in mean elevation was best explained by climate scenarios (Table 4.4 and Fig. 4.2). Also, the choice of SDM algorithms had no effect on population dynamic features, but explained a considerable amount of variance in mean population centres and in mean elevation. Probability of survival proved to be the most crucial demographic parameter (Table 4.4). For example, the linear models fitted to the results of the sensitivity analysis estimated that an increase in survival probability of 0.01 would cause an increase in population size of 3,000 to 4,000 individuals (compare Fig. C.5).

Table 4.4. Sensitivity analysis of model outputs based on *n*=1,215 model configurations.

						Explained variance R^2 by uncertainty components and direction of influence (in parentheses)				
Output	Year	Mean	SE	Median	*N*	SDM	RCM	*pSurv*	*pFemale*	*pleadYoung mean*
Population size	2001	15,430	558	5,127	1,215	0	0	0.55 (+)	0.14 (+)	0.10 (+)
	2050	17,330	618	2,207	1,215	0	0	0.60 (+)	0.11 (+)	0.08 (+)
	2100	13,770	521	856	1,215	0	0.04	0.52 (+)	0.09 (+)	0.07 (+)
Probability of extinction	2001	0	0	0	1,215					
	2050	0.23	0.01	0	1,215	0	0	0.44 (-)	0.10 (-)	0.08 (-)
	2100	0.38	0.01	0	1,215	0	0	0.59 (-)	0.08 (-)	0.07 (-)
Area size [km^2]	2001	4,462	120	3,022	1,215	0	0	0.68 (+)	0.12 (+)	0.09 (+)
	2050	4,339	138	1,389	1,215	0	0	0.63 (+)	0.09 (+)	0.07 (+)
	2100	3,685	126	585	1,215	0	0.02	0.56 (+)	0.08 (+)	0.07 (+)
Mean elevation [m]	2001	1,788	0.19	1,790	1,215	0.18	0.13	0.14 (+)	0.05 (+)	0.03 (+)
	2050	2,014	2.33	2,013	1,102	0.08	0.40	0.11 (+)	0.01 (+)	0.01 (+)
	2100	2,199	4.39	2,159	900	0.14	0.63	0.03 (+)	0	0
Mean population centre	2001 Easting	683,600	57	684,000	1,215	0.18	0	0.21 (+)	0.05 (+)	0.03 (+)
	2001 Northing	160,000	20	159,800	1,215	0.50	0	0	0	0
	2050 Easting	694,800	422	697,000	1,102	0.01	0.01	0.10 (+)	0	0
	2050 Northing	158,400	176	158,200	1,102	0.01	0.01	0.01 (-)	0	0
	2100 Easting	707,200	581	706,700	900	0.05	0.13	0.01 (+)	0	0
	2100 Northing	157,400	187	157,200	900	0.06	0	0.02 (-)	0	0

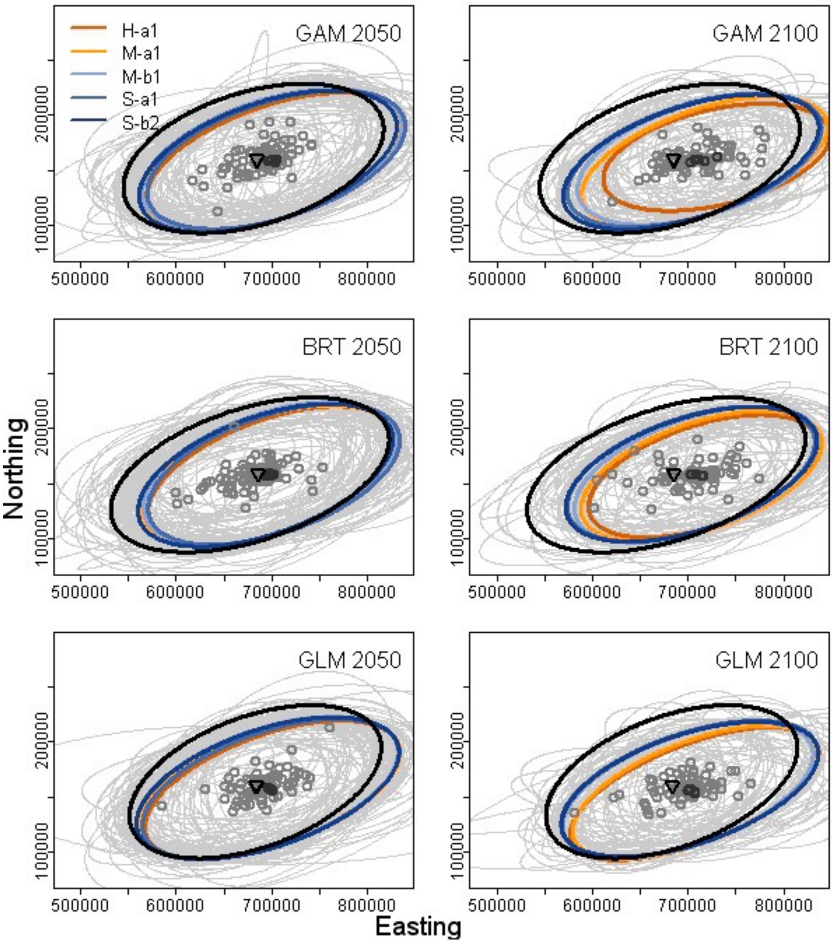


Figure 4.3. Mean population centres of black grouse for scenarios of climate change. Small symbols show mean population centres predicted for different SDMs (from top to bottom) and for the years 2050 (left) and 2100 (right) across different climate scenarios and model parameterisations. Thereby, dark triangles depict current population centre, dark circles depict default IBM parameterisation (cf. Table 4.2), light circles depict all simulated population centres for the respective time slice. Ellipses depict 1.5 directional standard deviation. Black ellipses depict current black grouse range; coloured ellipses depict default IBM parameterisation grey ellipses depict all simulated ranges for the respective time slice.

Under current climate, survival probability alone represented 55 % of variation in population size and even 68 % of variation in occupied area size. While probability of extinction by 2100 was zero for the default IBM parameterisation, decreases in the demographic parameters especially survival probability led to black grouse extinction in up to 90% of the simulations on average (Fig. 4.5). Conversely, increases in the demographic parameters reversed climate-induced population declines and even led to temporarily increasing population sizes (Fig. 4.4). The shape of the probability distribution of *pleadYoung* (more flattened or more peaked; determined by standard deviation of the Gaussian distribution, see Table 4.2) and, thus, the magnitude of environmental stochasticity, had no effect on the mean predictions but only resulted in slightly increased variability between replicates of simulations. We calculated a consensus map across all simulations as the fraction of simulations (n = 1,215) that predicted black grouse to be present at a site (Fig. 4.6). Under current climate, consensus about black grouse presence was very high (> 80 %) in the Swiss Alps and intermediate (20 - 60 %) for most parts of the Jura mountains where black grouse are in fact absent (Schmid et al. 1998). With ongoing climate change, consensus on presence sites decreased considerably as extinction probability increased for many model configurations.

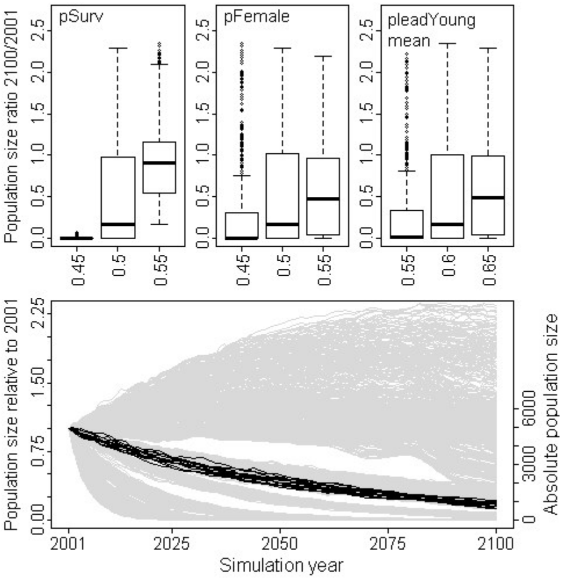


Figure 4.4. Population size relative to 2001 (current climate). Bottom: Grey lines show relative population trajectories across all simulations, black lines those for Default IBM parameterisation (cf. Table 4.2) across different SDMs and climate scenarios. Top: Boxplots depict population size ratio of year 2100 relative to 2001 for different demographic parameters.

4.5 Discussion

In this study, we integrated correlative species distribution models and a simple, spatially explicit individual-based model to predict climate-induced range dynamics of black grouse in the Swiss Alps and evaluated variability introduced by different uncertainty components. By this, we were able to better understand important features of range predictions and current as well as transient population dynamics. Our results clearly show that extinction risks cannot simply be approximated by expected changes in suitable habitat (Akçakaya et al. 2006, Brook et al. 2009, Keith et al. 2008). Rather, the expected population trajectory seems to result from a complex interplay between available habitat and demographic processes. Our study also underscores the necessity of sensitivity analyses in dynamic range predictions. Predicted population response to environmental change may be highly variable, both quantitatively as well as qualitatively. Thus, robustness of modelling results can only be assessed if the inherent uncertainty is explicitly considered.

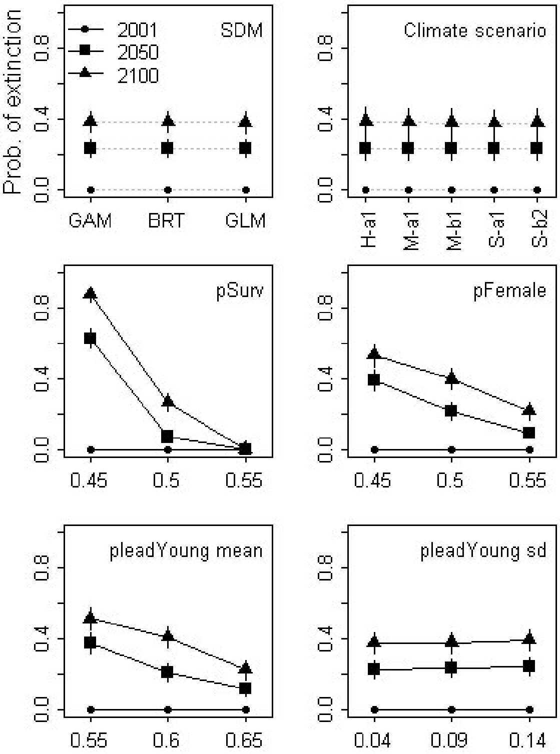


Figure 4.5. Effects of different uncertainty components on probability of extinction for the years 2001 (current climate), 2050 and 2100. Symbols indicate mean values; errors bars show 99 percent confidence interval.

4.5.1 Black grouse population and range dynamics

We were very careful in choosing SDM algorithms and climate scenarios that were both realistic and reflected a range of predictions reaching from pessimistic to optimistic. Overall, all three SDMs produced congruent predictions of habitat change (Fig. C.3). Absolute area size of suitable habitat, however, differed slightly and differences became more pronounced with ongoing climate change. This both corroborates and contradicts findings of previous studies. On the one hand, differences between predictions become more pronounced the further we project into the future which is in line with earlier findings (Buisson et al. 2010, Pearson et al. 2006, Thuiller 2004). Consensus between SDM predictions was still remarkably high though (Fig. C.4) while earlier studies partially reported highly contrasting predictions (e.g. Buisson et al. 2010). Nevertheless, further research is needed regarding why method performance and predictions differ (Elith and Graham 2009) and to provide general guidelines on appropriate model choice.

By the end of the 21st century, differences in suitable area were larger between climate scenarios than between SDMs. Considerable loss in suitable habitat was predicted for two out of five climate scenarios, namely for the more extreme climate scenarios with mean temperature increases between 4°C and 5°C. Current trends in CO2 emissions and global air temperature indicate that expected increases in temperature may be at the upper end of current climate projections or even above (Rahmstorf et al. 2007). Thus, while absolute area size of suitable habitat is predicted to remain more or less unchanged until the middle of the century, in the second half of the century abrupt losses in suitable area of 40 % are not unlikely to expect. However, our results also clearly demonstrate that suitable and actual habitat are not directly related and, thus, population trajectory may take a different course than suitable habitat (Fig. C.5).

In the dynamic model runs, the area of suitable habitat was not completely occupied by black grouse. Under current environmental conditions, the high sensitivity of occupied area size to survival probability indicated high site turnover where suitable habitat frequently became unoccupied. Higher survival probabilities and, thus, higher local persistence ability led to lower site turnover, more complete range filling, and consequently to greater area occupied and less fragmented ranges. Although the model predicted only small declines and shifts in suitable habitat early in the 21st century, gradual declines in black grouse population and occupied area sizes were predicted across all climate scenarios and underlying SDMs. This primarily resulted from a negative trend in population growth given the observed demographic rates (Fig. 4.4). On the other hand, Schmid et al. (1998) judged the population to be stable but these estimates rely only on rather short time periods. The strong fluctuation and high site turnover predicted by our model suggest that longer observation periods are needed to accurately assess black grouse population status. Reassuringly, however, even with the negative trend in current population growth rate, population size is predicted to not fall below 1000 hens by 2100 which is a decent population size especially as that population is predicted to strive in continuous areas (Fig. 4.6).

Our results underscore that inferring extinction risks simply from quantity of suitable habitat might be misleading (Fig. C.5; Akçakaya et al. 2006, Brook et al. 2009, Keith et al. 2008). A non-dynamic approach might considerably underestimate extinction risks because important interactions between life history traits and habitat suitability would be ignored. Expected mean abundance is only indirectly related to habitat suitability through demographic functions which determine site turnover and, thus, how much of available habitat is maximally occupied at the time (Table 4.4). Considering the differences between habitat suitability predictions by different SDM algorithms and the associated population dynamics (Fig. C.5), expected mean abundance also depends on spatial distribution of available habitat and on the degree of fragmentation.

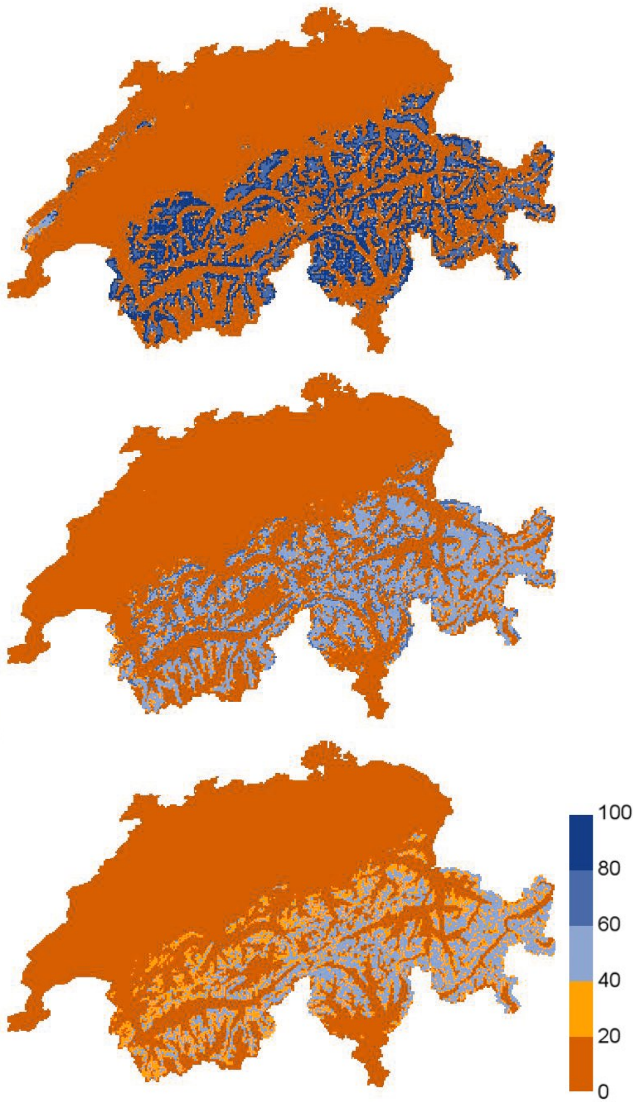


Figure 4.6. Consensus on black grouse presence for years 2001 (top), 2050 (centre) and 2100 (bottom); calculated as the fraction of all simulations (*n*=1212) predicting black grouse to be present. (Note that zero percent consensus on presence equal 100 percent consensus on black grouse absence.)

4.5.2 Robustness of range predictions

Our study not only highlights the benefits of a dynamic approach to range predictions but also underlines that we have to deal with immense additional prediction uncertainty when modelling population dynamics and that robustness of model results needs to be explicitly assessed. Here, quantitative predictions of absolute population and occupied area size as well as probability of extinction showed great variations across simulations (Table 4.4). This is in accordance with previous criticism on spatially explicit simulation models (SEPM, Dunning et al. 1995) and related population viability analysis (PVA) expressing concerns about taking predictions, for example probabilities of extinction, at face value (Beissinger and Westphal 1998, McCarthy et al. 2003). Alternatively, we could have made qualitative predictions by evaluating relative differences among model outputs. However, previous SEPM and PVA discussions focused on equilibrium population dynamics opposed to transient dynamics as expected under environmental change. In our black grouse system, also predictions of relative population size were fragile across parameter space and rather sensitive to demographic parameters and available habitat (Fig. 4.4). We believe this is a symptom of two general problems when using such simple SEPMs in combination with SDMs in environmental change context. First, it is difficult to determine reasonable error margins for the highly aggregated demographic parameters to be used in robustness analysis of model predictions. Second, if the structure of the demographic model is very simple this may lead to high parameter sensitivity and thus large prediction uncertainty.

For the sensitivity analysis of the demographic parameters, we chose a heuristic rather than applied view by perturbing the parameters in fixed intervals of ±5 % instead of choosing error margins that could be expected in the field. One reason for this was simply because such error margins were difficult to evaluate for Swiss black grouse, which probably holds for the majority of populations/species. On the other hand, longer-term predictions are inherently risky for example due to unforeseeable fluctuations induced by the environment and that way current error margins for demographic parameters might not be very meaningful under climate change. In this respect, we find it reasonable to heuristically choose the parameter space as it allows theoretically circumscribing possible population outcomes given these boundary conditions. Although, we believe that the fixed interval of ±5 % of the respective demographic rate is greater than the error range that could reasonably be expected in Switzerland for these highly aggregated parameters, for example survival probability.

It is known from PVA that very simple population models generally exhibit high parameter sensitivity and thus large prediction uncertainty (Beissinger and Westphal 1998, Grimm and Storch 2000). Arguably, combined population – SDM models should be as simple as possible because they have to cover a wide range of habitat types and environmental conditions. Due to its simplicity the model presented here is also highly general and - especially in conjunction with extensive sensitivity analysis - it provides valuable insights into possible population outcomes for Swiss black grouse. However, the large parameter sensitivity in the demographic model may in part arise because important mechanisms shaping population response are missing or inadequately represented in the model structure. For example, Grimm et al. (2005b) suggested that simple population models may overestimate extinction risk because they lack certain buffer mechanisms that reduce environmental stochasticity. Thereby, the most simple and general buffer mechanism that could be considered is individual variability such that individuals differing in fitness are not equally affected by environmental fluctuations (Rossmanith et al. 2006). Also, the exact form of density dependence and carrying capacity may strongly affect predicted extinction risks (Beissinger and Westphal 1998). Although assuming a linear link between demographic parameters (here, carrying capacity) and predicted habitat suitability is the only practicable approach given general data limitations, this is not fully supported by empirical findings and further research is required in this field (Gallien et al. 2010).

4.5.3 Challenges in species distribution modelling

By integrating predictions of habitat suitability made by correlative species distribution models with spatially explicit, dynamic population models we are able to overcome some limitations associated with SDMs. For example, by relaxing the equilibrium assumption such combined models allow the prediction of transient population response to environmental change. However, spatially explicit population models do not solve all problems associated with correlative SDMs in global change context. Most importantly, we still assume constant species-environment relationships (niche conservatism, Pearman et al. 2008). This assumption underlies both the correlative model producing habitat suitability maps and it also underlies the constant demographic rates in the population model. Thus, spatially explicit population models like our black grouse IBM are only valid as long as environmental change only shifts the environmental conditions in space. Changes in biotic interactions as well as ecological and behavioural adaptations will violate this assumption of niche conservatism. Also, demographic rates might change in response to changing environmental conditions, for example if environmental stress regimes change. As we have shown, possible population outcomes for changing boundary conditions (e.g. demographic rates) can be assessed via sensitivity analyses.

More realistic model assumptions can be achieved by including demographic rates and behavioural adaptations that are ecophysiologically informed and based on first principles. For example, biophysical or mechanistic SDMs could provide biophysical calculations as key input data for dynamic population models and include e.g. climate-dependent vital rates, movement potential and sex ratios (Kearney and Porter 2009). Moreover, the individual-based perspective taken here allows easy implementation of diverse behavioural responses such as feeding location or prey selection (e.g. Railback and Harvey 2002, Stillman and Goss-Custard 2010), consideration of spatial characteristics such as resource heterogeneity and direct interactions between these two, for example through resource depletion (Grimm and Railsback 2005). Also, selective pressures and genetic adaptation can easily be incorporated (e.g. Burton et al. 2010). Thus, various processes could be included in our model framework potentially increasing realism in the model. Dynamic models that are based on first principles can be designed to predict the response of demographic parameters to the full range of environmental conditions of concern, even including conditions for which no demographic data exist (e.g. Goss-Custard et al. 2008). Such models require considerable resources for development and testing, and certainly cannot be developed for all species. However, once such a model exists, it can be relatively straightforward to adopt its design to similar species (Stillman 2008). Both simple and more complex population models can be valuable for predicting species distributions. The right choice depends on how important model predictions are for supporting decision making, and on how much resources one is able, or willing, to invest.

A crucial issue for mechanistic range predictions is the availability of data for model parameterisation as well as validation. For making sensitivity analyses of range predictions, a standard tool has the benefit that also indirect sources can be utilised for model parameterisation without sacrificing robustness or reliability of model results. Indirect sources may include life history data obtained from different subpopulations or from related species (Keith et al. 2008) or demographic parameters derived from allometric relationships (Cheung et al. 2009). Pattern-oriented modelling is a general strategy for systematically exploiting the information contained in such multiple, often qualitative, patterns observed at different scales and levels of organization (Grimm et al. 2005a, Wiegand et al. 2003). One important element of this approach, parameterisation by Monte-Carlo filtering of parameter combinations, can be complemented by Bayesian parameterisation methods (Martinez et al. 2011, Hartig et al. 2011).

One source of uncertainty that we did not include in our case study is land use and land cover change. Further investigations are needed to understand the role land use change may play for the persistence of black grouse in the Swiss Alps. For example, black grouse are known to respond sensitively to abandonment of alpine summer pastures with accompanying shrub encroachment and reforestation. Here, we included land use variables as static predictors only. In future studies, the interactions of land use and climate change should be evaluated.

4.5.4 Conclusions

Integrating correlative species distribution models into spatially explicit population models for predictions of large-scale range dynamics allows for a more direct, multi-faceted view of complex, spatiotemporal species' response to environmental change and related extinction risks. However, without explicit assessment of robustness of predictions, for example by means of sensitivity analysis, the task remains of more theoretical nature. The merit of developing dynamic population models for climate impact studies only becomes apparent and the effort justified when this undertaking is accompanied by explicit investigation of sensitivity and robustness of the results. This substantially increases the confidence in range predictions and, as a more direct benefit, increases our mechanistic understanding of the studied ecological system and the expected population response. Further research is needed to provide general guidelines for models predicting climate-induced range dynamics. Thereby, challenges remain for both static and dynamic modelling components and include, for example, the choice of appropriate SDM algorithms, the role of land use and climate change, model structure and complexity, or the design of robustness analysis. Addressing these challenges will help to establish this comparably new avenue of climate impact assessment as a feasible and reliable tool.

5 Predicting to new environments: tools for visualising model behaviour and impacts on mapped distributions[4]

---

[4] A manuscript with equivalent content has been conditionally accepted in *Diversity and Distributions*:
Zurell, D., Elith, J. and Schröder, B. conditionally accepted. Predicting to new environments: tools for visualising model behaviour and impacts on mapped distributions.

5.1 Abstract

Data limitations can lead to unrealistic fits of predictive species distribution models (SDMs) and spurious extrapolation to novel environments. Here, we want to draw attention to novel combinations of environmental predictors that are within the sampled range of the individual predictors but are nevertheless outside the sample space. These tend to be overlooked when visualising model behaviour. They may be a cause of differing model transferability and environmental change predictions between methods, a problem described in some studies but generally not well understood. We here use a simple simulated data example to illustrate the problem and provide new and complementary visualisation techniques to explore model behaviour and predictions to novel environments. We then apply these in a more complex real world example. Our results underscore the necessity of scrutinising model fits, ecological theory and environmental novelty.

5.2 Introduction

Predictive species distribution models (SDMs, Guisan and Zimmermann 2000, Elith and Leathwick 2009) have become a prominent technique in conservation biogeography and are increasingly used as prediction tools for environmental change forecasts and invasive species research (Franklin 2010). Numerous SDM algorithms exist with varying degrees of model complexity (Elith et al. 2006, Heikkinen et al. 2006). Several studies have shown that these algorithms can predict substantially different future potential ranges even if current predictions are largely congruent (Thuiller 2004, Buisson et al. 2010). Explanations for varying behaviour usually point to the extent to which the environmental range was covered by the training data and to the specific assumptions made by each algorithm when extrapolating beyond that range (Thuiller et al. 2004, Pearson et al. 2006, Elith and Graham 2009). Williams and Jackson (2007) argued that data limitations may impede extrapolation to novel environments because the species' niche may not be fully represented by data (here, termed 'truncated niches') and, depending on the direction of environmental change, currently unobserved portions of the niche may open up. Fitzpatrick and Hargrove (2009) contended that predictions should not be attempted to environmental conditions without analogues to the combinations under which the model was calibrated, or at least that maps should indicate where extrapolation has occurred.

Useful ideas are emerging for probing models and predictions, enabling users to understand model behaviour in novel space. For instance environmental spaces have been compared using principal component analyses and metrics summarising differences between niches

(Broennimann et al. 2007, Warren et al. 2008, Medley 2010), impacts of sample design on environmental and niche coverage have been explored and related to models and their predictions (Albert et al. 2010), and methods for mapping novel environments in geographic space have been suggested (Williams et al. 2007, Platts et al. 2008, Elith et al. 2010). Here we add to these by focussing on the issue of combinations of variables that are within the sampled range of each predictor treated individually, but are nevertheless outside of the sampled environmental space (Fig. 5.1, hatched areas). These tend to be overlooked in visualisation methods (cf. Fitzpatrick and Hargrove 2009).

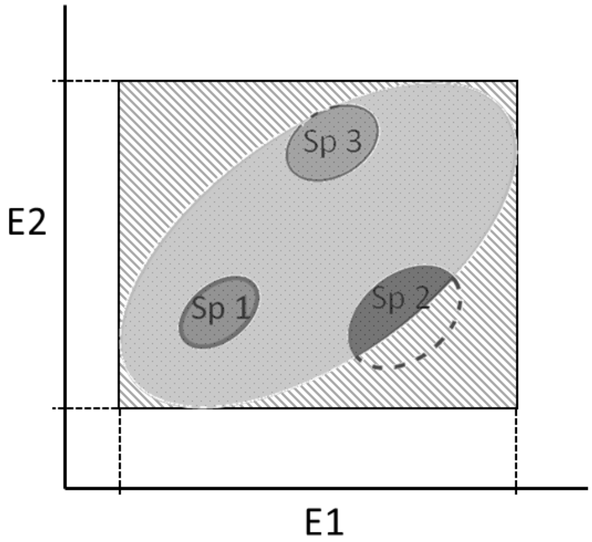


Figure 5.1. Conceptual diagram illustrating three situations how species niche may be represented in sampled environmental space (dotted ellipse): i) a species niche is entirely represented by sample space (species 1) (ii) the niche is 'truncated' because samples do not exist for part of one or more environmental gradients (species 2), and (iii) the edge of the niche abuts the edge of the sampled space, and no samples exist beyond it (species 3). The hatched square represents the 'implied' sample space that is implicitly assumed to be known when focussing on the sampled, univariate ranges of all environmental predictors individually instead of explicitly focussing on the multivariate combinations of environmental predictors represented in the sample.

For instance, partial dependence functions (i.e., plots of the fitted functions that show the effect of a variable on the response after accounting for the average effects of all other variables in the model) are plotted along the full gradient of each variable represented in the data, regardless of the coverage along that gradient of other environmental dimensions. MaxEnt's multivariate environmental similarity surface (MESS, Elith et al. 2010) takes a related box-like or envelope viewpoint by analysing environmental coverage one variable at a time, and reporting as novel those conditions outside the environmental hyper-dimensional rectangle. However, not all multivariate combinations of the environmental conditions may be represented in the data. We define those parts of the environmental space that are within that box but nevertheless outside the sample space as ‘implied sample space’ (hatched areas of Fig. 5.1). Here we show that existing methods can fail to clarify why predictions differ, and we provide new and complementary visualisation techniques that will be relevant for many species modelling problems.

5.3 Demonstrating prediction problems: simulated species

Fig. 5.1 illustrates three situations that can arise when sampling in geographic space (Williams and Jackson 2007, Albert et al. 2010). For species 2 and 3, no samples exist for parts of the environmental niche or for the niche edges. These may not be problematic if the intention is simply to model the distribution of that species in the sampled space, but as soon as models to these data are used for prediction to new times and places which might contain environments outside of the training sample, difficulties arise.

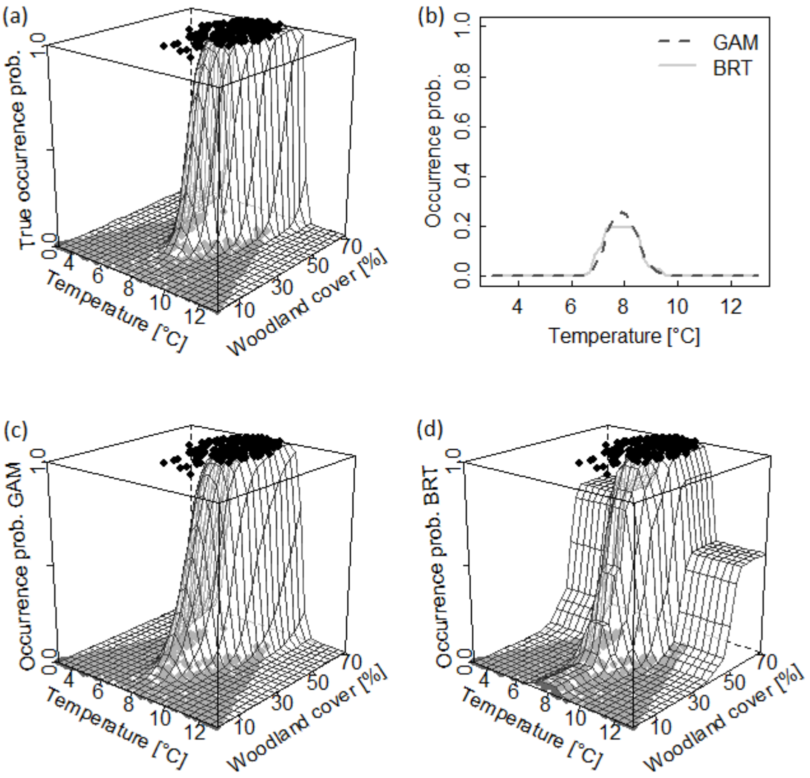


Figure 5.2. Simulated data example for species 2 with truncated niche. (a) True response surface. (b) Partial dependence plots for GAM and BRT. (c) and (d) show fitted response surfaces for GAM and BRT. Grey dots at p=0 in panels (a), (c) and (d) represent sampled absences, black dots at p=1 represent sampled presences.

To simulate data representing the situations of Fig. 5.1, a virtual species (Zurell et al. 2010, chapter 2) was created (using logistic regression) that exhibited a unimodal response to temperature and a positive linear response to percent woodland cover (Fig. 5.2a; for details see Appendix D.2 in Supporting Information). The entire simulation study was built in R (R Development Core Team 2010), and we provide code in Appendix D.1. For each situation, 1000 samples were drawn and converted to binary observations by using the simulated response (varying from 0 to 1) as the success rate for one sample of the binomial distribution. For species 1, samples cover the entire environmental space while for species 2 (truncated niche), the samples cover the full univariate range of each environmental variable individually, but combinations of the two are missing (Fig. 5.2a). SDMs were fitted to these samples using generalised additive models (GAMs) with cubic smoothing splines, four degrees of freedom and no interactions, and boosted regression trees (BRTs) with tree complexity of 1 (tree stumps; note that in our examples higher tree complexity results in similar extrapolation behaviour). We chose these methods as examples of the range of current methods, spanning standard regression techniques to advanced machine learning methods (for overviews see Elith et al. 2006, Heikkinen et al. 2006). The models were then used to predict across the full environmental space spanned by the environmental gradients of the individual predictors, meaning that for species 2, predictions were made to new combinations of variables.

For species 1 (entire niche sampled), both methods were successful in fitting the true response (Fig. D.1). Because the environmental niche of the species was truncated in the training data for species 2, predictions for the unsampled combinations required extrapolation. As a result of the way our cubic splines and regression trees extrapolate, GAM continued the fitted trend to ‘unknown’ sites while BRT predicted a constant value from the last ‘known’ site leading to inaccurate model predictions in those parts of the unsampled environment space with high woodland cover, and particularly those that also have lower or higher than optimal temperatures (Fig. 5.2d, Fig. D.2). The latter is not obvious from the usual partial dependence plots (Fig. 5.2b) because these are derived at average values of other predictors, for which this model performs reasonably well. Similar extrapolation errors also occur if niche edges coincide with the limits of the recorded environmental space (species 3; Fig. D.3).

5.4 New tools for visualisation

The simulation study was simple, and use of three-dimensional plots (e.g. Fig. 5.2d) was sufficient to demonstrate the model fit and its implications for predictions to unsampled combinations of predictors (cf. Fig. D.2). In most situations, though, models have more than two covariates and predictions are also mapped. Hence we suggest two new tools that will highlight predictions to new combinations of variables.

First, we propose to 'inflate' conventional response curves (partial dependence plots) by visualising the effects of all variables in the model over their full range, and at the same time plotting the available data in that space. Basically, inflated response curves are an abstracted 2D version of multidimensional response surfaces. These show the effect of a variable on the response while accounting not only for the average effects of the other variables but also for minimum and maximum (and median and quartile) values. Thus, the response plot for any one variable consists of many response curves representing all possible combinations of all other variables in the model (for code see Appendix D.1; for detailed description see Appendix D.3). Because the number of combinations grows exponentially with the number of variables and restricts computational feasibility, we use Latin hypercube sampling to reduce dimensionality for large numbers of variables. This is simply a means to efficiently sample a representative subset from all possible combinations of environmental predictors (Carnell 2009).

Second, we propose to extend the idea of MESS maps by not only focussing on the environmental range of predictors individually but also on combinations of environmental predictors. By that we are able to identify those parts of the environmental space that are within the sampled, univariate range of the individual predictors but nevertheless represent new multivariate combinations of these ('implied sample space' of Fig. 5.1). This 'environmental overlap' (or 'environmental gap' if one wants to emphasise that certain parts of the prediction space may not be represented in the sample space) can be determined by splitting the training or reference data into a specified number of bins where each bin holds a unique combination of environmental predictor values. Any bins in test or prediction data that do not overlap with these reference bins are defined as novel environments. An environmental overlap mask can be used to highlight predictions where the model must extrapolate to novel environments (cf. 'null prediction' in Fitzpatrick and Hargrove 2009), e.g. within inflated response curves and in prediction maps (for code see Appendix D.1; for detailed method description see Appendix D.3). Note that a bin number of one equates to the border that distinguishes novel space (negative values) in MESS maps.

We illustrate the usefulness of these two methods for black grouse (*Tetrao tetrix*) in Switzerland (Zurell et al. 2011, chapter 4, for more details see Appendix D.4). Conceptually the problem is slightly different to that of the simulated species. Clearly, we do not know the true niche of the species. But we know the environmental space covered by the sample, and could suppose that for predictions to other times or places, there may be combinations of environments not present in the training data. Hence, we are interested in how the model predicts to such new combinations outside the training data space (as we were for the simulated species).

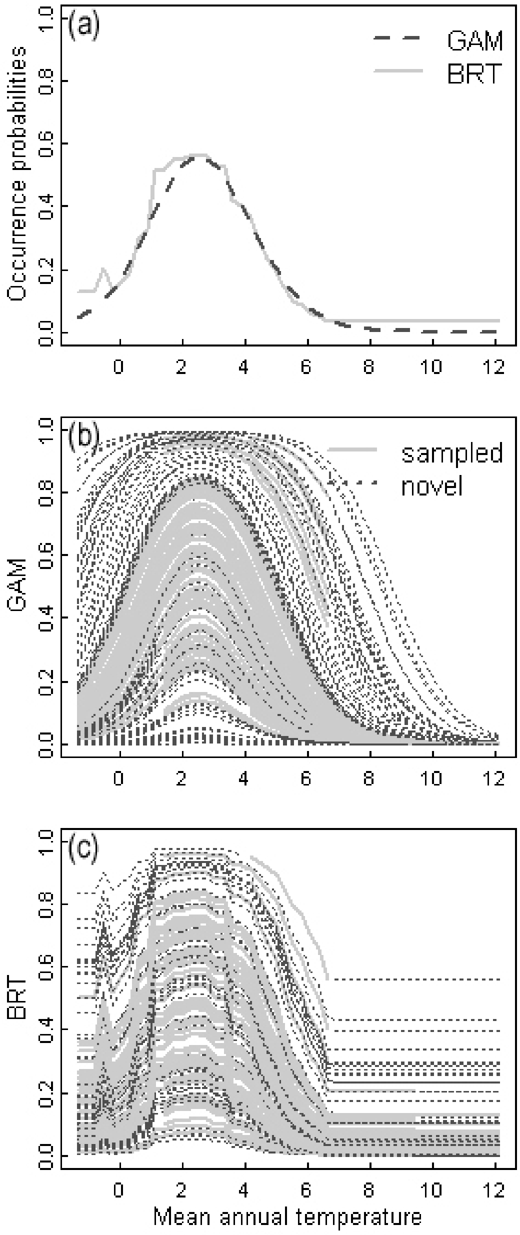


Figure 5.3. Swiss black grouse example. (a) shows the partial dependence of back grouse occurrence to mean annual temperature for GAM and BRT. (b)-(c) show the respective inflated response curves. Light grey lines and dotted dark grey lines depict the temperature effects over the full range of the other predictors (minimum, maximum, median, mean and quartiles). Light grey lines indicate combinations of environmental predictors that were observed in the sample space while dotted dark grey lines indicate extrapolations to novel, unsampled combinations. The plots represent *n*=150 Latin hypercube samples from all possible combinations of environmental predictors.

Again, we used a GAM with cubic smoothing splines, four degrees of freedom and no interactions and BRT with tree complexity of 1 to estimate the species environment relationship. We included six environmental predictors that covered large gradients yet only portions of all possible combinations were present (Fig. D.4). In consequence, GAM and BRT exhibited distinctly different extrapolation behaviour in the unsampled parts of the multivariate environmental space, particularly in those parts with high temperatures. These differences were not evident in conventional response plots plotted on the scale of the response, but were nicely represented by inflated response curves (Fig. 5.3; Figs. D.5, D.6).

We see the advantages of the inflated curves as: (1) they are explicit about the shape of the response at different values of other variables. Whilst in additive models this might be deduced, especially if partial plots are fitted on the scale of the link function, it requires some careful thought and is much more apparent with our methods, especially in the case of truncated responses; (2) they make clear the responses if interactions are included in the models. The increasing popularity of methods that can optionally fit interactions if detected in the data (e.g. tree-based methods), of ensembles that might include such models, and of all subsets regression where interactions are potentially allowed mean that model structure might not be superficially apparent. We believe that this increasing complexity of model structure requires tools that allow exploration and understanding. Here, we believe that black grouse response fitted by GAM is more plausible than that fitted by BRT. From an ecological perspective, it seems more intuitive to assume that species response to a bioclimatic variable such as mean annual temperature gradually decreases towards physiological limits (Thuiller et al. 2004).

However, different extrapolation behaviour will only constitute a problem to model transferability if models are used to extrapolate to places with non-analogue environments in which currently unobserved portions of the environmental niche become available for prediction (Williams and Jackson 2007, Fitzpatrick and Hargrove 2009, Dobrowski et al. 2011). We demonstrate in Fig. D.7 that plotting fitted values along each variable and comparing those obtained for training and prediction data can provide useful insights. Mapping these predictions and using environmental overlap masks to explicitly show predictions in sampled and non-analogue environmental spaces emphasises where differences in predictions are due to extrapolation behaviour of the models. Fig. 5.4 shows the mapped predictions of Swiss black grouse occurrence probability from GAM and BRT models. While predictions for the current environment are similar for GAM and BRT (year 2001; Fig. 5.4a, e), the mapped predictions for the year 2100 under climate change differ substantially (Fig. 5.4b,f). Using environmental overlap masks (with default number of 5 bins per environmental variable), we can distinguish between predictions in geographic space that are within the sampled environmental space (Fig. 5.4c,g) where the model is, in fact, interpolating, and predictions to novel environmental space (i.e., to environmental conditions beyond the sampled ranges of the variables as in MESS maps, and to novel combinations of environmental variables; Fig. 5.4d,h) where the model is, in fact, extrapolating. For our Swiss black grouse example we see that main differences between GAM and BRT predictions for the scenario of climate change indeed occur in those parts of the geographic space that exhibit novel environmental conditions compared to the sample space.

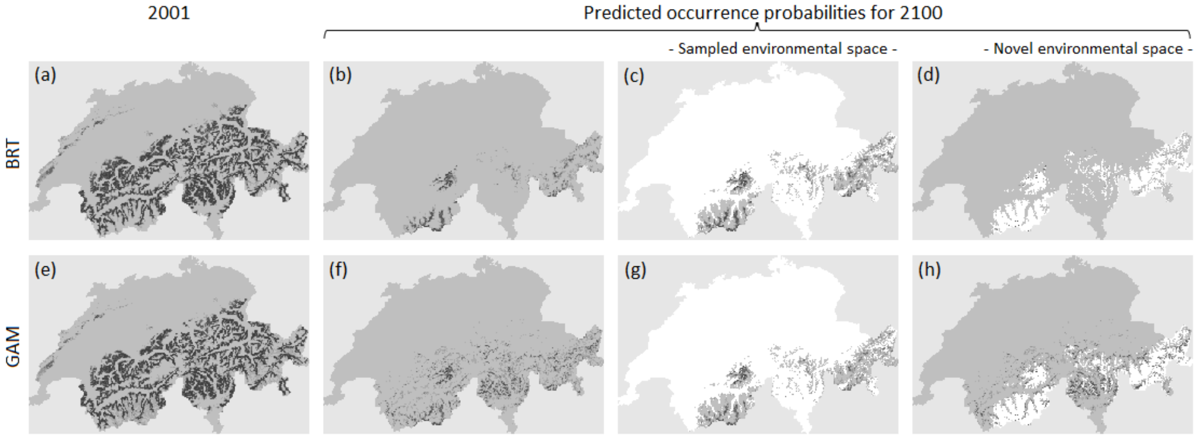


Figure 5.4. Predicted distributions of black grouse in Switzerland made by GAM (a-d) and BRT (e-h). (a) and (e) show current predictions while (b) and (f) show predictions to climate change scenario for the year 2100 (A1F1 scenario from HadCM3 with average temperature increase of 7.7 °C and average precipitation increase of 48 mm for Switzerland). Predicted distributions are logistic outputs from low (grey) to high values (black). Environmental overlap masks (with default number of 5 bins per environmental variable) are used for highlighting predictions to sampled (c)+(g) and to novel environmental space (d)+(h).

We do not intend these results as general advice about SDM algorithms. GAMs will not always extrapolate well (e.g. Elith et al. 2010) and BRTs might fit responses that extrapolate in ecologically realistic ways. The important issue is that using SDMs to predict to unsampled parts of the environmental space is inherently risky, and uncertainty in models as well as in predictions and maps need to be carefully assessed (Rocchini et al. 2011). The plots and maps presented here were useful for visualising the environmental space in more than one dimension and for understanding the predicted responses in this space. Plausibility of SDM fits needs to be judged individually for any species modelled and should comply with ecological theory and prior knowledge on the species (Guisan and Thuiller 2005, Austin 2007). As environmental variables generally correlate, linearly and non-linearly, we will rarely find all possible combinations in any one region (or the world). Also, species may be precluded from portions of their fundamental niche because of dispersal limitations, disturbance or biotic interactions (Colwell and Rangel 2009). In invasive species research, it has also been demonstrated that the realised niche in the native and invaded range may differ (Broennimann and Guisan 2008). Extrapolation behaviour may be improved by model smoothing (Elith et al. 2010) or by forcing the predicted probabilities to gradually approach zero outside observed environment (Thuiller et al. 2004). More research on the effect of including interactions in models used for extrapolation is needed; it may complicate extrapolation, and alternate means of representing the ecological response (e.g. by careful construction of predictors) might be preferable.

5.5 Summary

SDMs would yield reliable predictions under environmental change, if the entire niche was encompassed by data meaning that samples exist for all environmental conditions the species can occur in. However, truncated or edge niches are probably common, as not all possible environmental combinations are currently present. This may lead to erroneous predictions when extrapolating to novel environments, depending on how the model extrapolates. Thus, whenever prediction is the aim, we need to rule out unrealistic extrapolation behaviour of our models or at the very least indicate where extrapolation has occurred. The tools we provide here help to explore cases that were previously difficult to visualise.

6 Synthesis

6.1 Summary of achievements

This thesis focused on the ways dynamic and statistical modelling components can be integrated to improve current predictions of climate-induced range dynamics. I assembled different pieces of evidence which both provide momentum for predictive modelling of range dynamics but also call for more care and further research in applied as well as theoretical modelling issues.

Broadly, one can break down the key results of this thesis into three lessons. The first lesson deals with the benefits of simulation studies and, in particular, with the virtual ecologist (VE) approach as a rigorous evaluation tool for our analysis and modelling methods and the unique opportunities this approach holds in global change context. Lessons two and three concern uncertainty in predictions of range dynamics and deal with more practical problems we are facing in predictive modelling of species distributions for scenarios of environmental change. Throughout this thesis, I approached this complex issue from very different angles. First of all, I employed a VE approach to better understand how prediction accuracy of correlative species distribution models (SDMs) is affected by transient dynamics as well as ecological properties and processes (Zurell et al. 2009, chapter 3). Then, in order to improve predictions by explicitly depicting persistence and extinction rates as well as colonisation success in space and time I aimed to supplement projections of potential future habitat for black grouse in Switzerland with an individual-based model (IBM) that described demographic processes and dispersal (Zurell et al. 2011, chapter 4). Finally, I set out to identify reasons for fundamental differences in predictions across SDM algorithms (chapter 5). For ease of understanding, in lessons two and three I will summarise and discuss results separately for range predictions made by purely correlative models and by dynamic models.

6.1.1 Virtual ecologists

The VE approach played a prominent role throughout this thesis (chapters 2, 3 and 5) and, in fact, deserves more attention in theoretical as well as applied ecology. In chapter 2 (Zurell et al. 2010), I reviewed many published examples of the VE approach which underlined its wide practicality and the overall benefits. VE is a powerful evaluation tool that can foster the integration of theoretical and empirical work, it can help to design field studies and interpret data, and it can provide a means to explore new scientific questions and theories. Especially in the field of climate impact research VE holds great potential as chapters 3 and 5 nicely demonstrated. Predictive modelling of environmentally forced range dynamics is not yet fully explored although most methods employed have been around for decades. Much criticism and many questions remain regarding, for example, the applicability of different ecological modelling types in non-equilibrium situations, the ability of different models to appropriately capture the underlying species environment relationships or the interactive effect of sampling bias among others (Austin 2002, Guisan and Thuiller 2005, Elith and Leathwick 2009). These questions are difficult to approach because hardly any species is understood in every detail, long-term data of range dynamics may not be available or these data may be biased itself. Here, VE provides the means to conduct systematic experiments, test hypotheses and assess model behaviour under controlled conditions. Thus, VE allows approaching questions that are outside experimental manipulation in the real world. The study presented in chapter 3 (Zurell et al. 2009) is the first I am aware of to rigorously assess the potential impact of dispersal, demographic processes and biotic interactions on the prediction accuracies of SDMs when applied under different climate change scenarios. It therefore makes an important contribution to better understanding range dynamics and predictive modelling tools in conservation biogeography. Similarly, the simplified VE approach in chapter 5 allowed to theoretically exploring one possible cause of differing environmental change predictions across SDM algorithms which have been reported repeatedly but so far are not well understood (cf. Elith and Graham 2009).

For the future, I envision more model competitions like that presented in chapter 3 to describe the applicability of different modelling frameworks. For example, the same setting could be used to evaluate different approaches to consensus forecasting (Araujo and New 2007, Marmion et al. 2009, Thuiller et al. 2009), or to evaluate in how far models and subsequent predictions may be biased if the models are fitted in non-equilibrium situations (Zurell 2007). Also, a similar setting could be used to run competitions between correlative and mechanistic models. Such an approach has recently been employed by Pagel and Schurr (2011) who used a Hierachical Bayesian framework to fit a demography-based, spatially explicit dynamic population model to species occurrence and abundance data while accounting for the confounding effects of species environment relationship, population dynamics and observer effort. The authors used a VE approach to demonstrate the feasibility of the framework and compared predictions made by the process-based model and those obtained from simple SDMs (using generalised linear models, GLMs). However, their approach was not (and was not meant to be) a fair competition between SDMs and process-based models as the virtual data were sampled from the same dynamic population model that they aimed to fit within the Bayesian framework. In their case, VE simply served as a means to test the fitting procedure itself and to demonstrate its capability to model transient dynamics. To theoretically assess the applicability of correlative models opposed to mechanistic models in a fair competition, we would need to build a sufficiently complex, dynamic simulation model and, ideally, only pass virtually sampled data along with basic ecological knowledge about the virtual species on to independent modellers who will then build the models that are to compete. Such competitions may help to derive rules of thumb for optimal model choice for different situations and species groups. With the case studies and literature examples provided here, I hope that this thesis will call attention to the usefulness of VE in a wide array of ecological disciplines and, in particular, that it will inspire many researchers to more rigorously evaluate their prediction tools and explore theoretical questions related to environmentally forced range dynamics.

6.1.2 Range predictions by correlative models

In this thesis, I primarily employed theoretical approaches to assess prediction accuracy of SDMs. Thereby results were both reassuring and unsettling. First of all, in chapter 3 (Zurell et al. 2009), I used a VE approach to explicitly investigate model performance for transient range dynamics and the complicating effects of ecological properties and processes. As expected, it became evident that under environmental change we may not be able to make reliable predictions in time if dispersal and persistence ability are ignored in our models. These effects are confounded by species' ecological traits and other ecological processes as well as the direction and magnitude of environmental change. For example, SDM predictions will be better the faster the species is able to track climate change. Also, transient range dynamics may merely cause a time lag between potential range and occupied range. If environmental conditions remain static long enough for the species to fill its entire (new) range, then predictions made by SDMs can be quite accurate. If, on the other hand, environmental conditions shift continuously we can expect discrepancies between occupied and potential range to increase. Nevertheless, the models yielded useful predictions in most of the tested situations indicating that SDMs can in fact predict fairly well under climate change. However, these results were obtained under ideal conditions of a virtual world without taking into account other complicating ecological processes like (behavioural or phenotypic and genotypic) adaptation or changing community structures which are likely to influence species response under climate. For example, the results in chapter 3 also show that all becomes more complicated for strong biotic interactions because in such cases SDM prediction accuracy not only depends on ecological traits of the focal species but also on ecological traits of the species it is interacting with. If we can include information on biotic interactions in our models and are able to predict these satisfactorily, then predictions may render reasonably accurate. However, to date general guidelines and also practical modelling frameworks to account for biotic interactions in range dynamics are still rare and further research is needed in this field.

Many authors have highlighted that different SDM algorithms can lead to contrasting predictions under environmental change (Thuiller 2004, Pearson et al. 2006, Dormann et al. 2008, Buisson et al. 2010). Throughout this thesis, I repeatedly compared different SDM algorithms and got very different results in the various situations. Thereby, I employed widely used SDM algorithms representing different levels of flexibility ranging from standard regression techniques to advanced machine learning methods (Elith et al. 2006, Heikkinen et al. 2006), namely: generalised linear models (GLMs, cf. chapters 3 to 5), generalised additive models (GAMs, cf. chapter 4) and boosted regression trees (BRTs, cf. chapters 3 to 5). In the VE approach in chapter 3 (Zurell et al. 2009), I found that prediction accuracies achieved by BRTs increased for range contractions of the (virtual) butterflies because the absences were predicted with high precision while GLMs overpredicted the contracting ranges. However, these results are not generalisable but rather situational and should be regarded with great care. First of all, we have to note that the sample data from the virtual world were complete in coverage and that the SDM techniques hence merely reproduced the patterns in the data (according to model specification and algorithmic specific assumptions). Then, I suspect that it was the nature of the species environment relationship of the butterfly that played into the hands of BRTs. Because the butterfly depended on temperature both directly and indirectly (through its host plant), the apparent species-temperature relationship was rather crooked. Now, due to their flexibility BRTs are able to depict even such crooked, highly non-linear relationships accurately while GLMs aim to fit parametric, monotone relationships that are not able to depict such crookedness. In chapter 4 (Zurell et al. 2011), predictions of habitat suitability for Swiss black grouse were highly consistent across SDM algorithms. Only small differences between predictions became apparent and this only for the more extreme climate change scenarios. In chapter 5, I used simulated data to show the effect of having data that do not capture all aspects of the multidimensional niche. If the data do not represent all possible combinations of environmental conditions the species can occur in, then prediction to these combinations not represented in the data requires extrapolation. This may be a cause for controversial range predictions reported in the literature. My results are important in several ways. First, they call for more care in sampling, in model building and in appropriate model choice within an ensemble framework which also underscores the necessity of scrutinising model behaviour for any single species for which predictions are to be derived. To this end, it is crucial to not only assess model fit under current conditions but also to judge realism of model extrapolation behaviour and of predictions using for example inflated response curves as suggested in chapter 5. Inspecting the fitted response for scenarios of environmental change can also be informative. Unfortunately, in many instances we will not be able to do anything about the restrictedness of the data simply because not all possible environmental combinations currently exist on Earth, because the species is dispersal limited or because disturbance precludes it. In the first case, we may find ways and confidence to incorporate expert knowledge in our models, for example by defining expert-derived physiological limits for the species. In the other cases, a mechanistic determination of the niche (Pulliam 2000) may be more appropriate, for example by means of dynamic range models as introduced by Pagel and Schurr (2011).

6.1.3 Range predictions by dynamic models

Results from the VE study in chapter 3 (Zurell et al. 2009) indicated that in order to depict transient population dynamics more accurately we need to account for dispersal and persistence ability in our range predictions. This has been suggested by several authors before (Guisan and Thuiller 2005, Araújo and Guisan 2006, Heikkinen et al. 2006, Thuiller et al. 2008) and has spurred some attempts to integrate SDMs and spatially explicit population models (SEPMs, Dunning et al. 1995) to predict range dynamics for scenarios of environmental change (habitat-based SEPMs *sensu* Akçakaya 2000; for climate change applications see Keith et al. 2008, Anderson et al. 2009, Cheung et al. 2009). The rationale is ‘to provide more realistic forecasts of population change, habitat fragmentation and extinction risk under climate change’ (Brook et al. 2009). The study in chapter 4 (Zurell et al. 2011) showed that population trajectory of black grouse under climate change will be approximately proportional to expected changes in suitable habitat if the current population is stable. From this one might conclude that relative population change may well be inferred from available habitat alone if demographic rates are sufficient to sustain a stable population, thus giving support to SDMs as useful tools for vulnerability assessments under climate change. However, due to high site turnover mean density of black grouse across entire Switzerland was predicted to be below one individual per km^2 although local densities of up to 10 individuals per km^2 were possible. Thus, expected mean abundance and habitat suitability are not directly related but demographic functions determine how much of available habitat is maximally occupied at the time. Thereby, it seems also important how available habitat is distributed in space and how connected or fragmented it is. This corroborates previous views and findings that extinction risk may not directly relate to range size but that each species (and population) will show a distinct relationship between these (Jablonski 1986, Buckley and Roughgarden 2004). Also, sensitivity analysis showed that variability in predictions introduced through uncertainty in demographic parameters is much greater than variability across different climate scenarios or SDM algorithms. If initial population status was only slightly declining, then inferring extinction probabilities simply from quantity of suitable habitat strongly underestimated extinction risk. In this light, my results support a general movement away from purely correlative approaches to more dynamic simulation models in order to predict species vulnerability to environmental change more realistically. Nevertheless, the results also call for great care when designing and applying SEPMs in this context. If we aim at more directly assessing relative population change from dynamic population models then we have to start by obtaining reliable estimates of current population status and expected range of demographic rates under environmental change. Sensitivity or robustness analysis within ‘reasonable’ error margins can then help to target the most likely areas of species colonisation and persistence for a given range of demographic rates. Further research is needed to determine such ‘reasonable’ error margins and to define rules of thumb for predictions of range dynamics. Such rules of thumb may refer to model building and analysis steps as well as to appropriate model choice for specific situations and contingent on species’ traits.

The study in chapter 4 (Zurell et al. 2011) further underscores the more direct benefit of spatially explicit simulation models to test or improve current mechanistic understanding of a specific system and to test the response to different scenarios of environmental change (Jeltsch and Moloney 2002). Black grouse in Switzerland have been studied for a long time and are fairly well understood (e.g. Zbinden and Salvioni 2003, 2004). Yet, some questions remain regarding for example the precision of population size estimates and population status (Schmid et al. 1998). My modelling results show that given existing knowledge on demographic functions and rates the Swiss black grouse population may well be declining instead of being stable as was estimated by Schmid et al. (1998). The strong fluctuations in population size and the high site turnover rates predicted by the model suggest that longer observation periods are needed to accurately assess black grouse population status. Furthermore, my results show that even slightly decreased demographic rates, especially a lower survival rate, may result in considerable population declines over the 21st century. Survival and reproduction rates both constitute rewarding parameters to focus management on. Both may be improved through habitat restoration or, by any means, negative impact through further habitat destruction should be avoided. In the future, the relative impact of different land use scenarios on black grouse population and interactions with climate change should be tested.

6.2 Challenges in dynamic range predictions

There are many pressing questions in the prediction of environmentally forced range dynamics, several of which I have successfully addressed in this thesis. Nevertheless, although providing important conclusions and notions for conservation biogeography the work presented here merely scratches the surface of the complex issue of predicting environmental change-induced range dynamics. My thesis probably raised as many questions as it answered. Several of these open questions were brought up in the preceding chapters. Here, I want to provide some additional considerations about underlying assumptions and consequent application domains of the models presented in this thesis as well as current shortcomings in data availability.

6.2.1 Niche conservatism

My thesis provides further evidence that our models need to become more dynamic in order to predict transient range and population dynamics more realistically and provide more direct assessments of species vulnerability (cf. Guisan and Thuiller 2005, Thuiller et al. 2008, Brook et al. 2009). Nevertheless, we need to be aware that some assumptions of SDMs are also common to demography-based SEPMs and the hybrids between them which may hamper their overall applicability under environmental change, in particular for unprecedented environmental conditions (including non-analogue climate and land use as well as changing community structures among others). One fundamental assumption is that of niche conservatism as I have discussed in chapter 4 (Zurell et al. 2011). According to this the demographic model parameters are only valid for the environmental conditions under which they were measured or estimated. For non-analogue environments, demographic rates of species may change as they emerge from the complex interplay of environment and physiological as well as behavioural traits (Kearney 2006, Grimm et al. 2007). Moreover, Oliver et al. (2009) showed British butterfly species to exhibit varying habitat specificity throughout their range with constrained habitat associations at range boundaries. Their results also imply that population dynamics at leading range boundaries may differ from those towards the range core because of a more limited range of climatically suitable habitat types which should hence be taken into account when predicting range dynamics. Also, Burton et al. (2010) showed in a theoretical study that during range expansion different selection pressures between range core and expanding range edge can lead to varying demographic rates throughout the range.

6.2.2 Circularity

Some authors raised concerns about potential circularity problems in habitat-based SEPMs: as we aim to describe dispersal or biotic interactions using the dynamic population model but the underlying SDM may implicitly account for these factors as well, we may in fact account for these factors twice (Gallien et al. 2010, Thuiller and Münkemüller 2010). For example, if current species distribution is strongly affected by source-sink dynamics or dispersal barriers then ignoring these processes may bias the fitted SDM and, consequently, the dynamic population model as well (Thuiller et al. 2008, Thuiller and Münkemüller 2010). One suggested solution to this problem is to simultaneously fit the dynamic population model and underlying SDM within the same statistical framework. Pagel and Schurr (2011) only recently presented dynamic range models (DRMs) that are fitted within a hierarchical Bayesian framework and jointly estimate species niches and spatiotemporal population dynamics from occurrence records and local abundance time series. I believe that circularity may pose a problem in some but not in all species. Hence, the approaches of DRMs and habitat-based SEPMs as presented in chapter 4 (Zurell et al. 2011) could be complementary and useful for specific situations depending on species' traits, specific population dynamics, site history and quality of data among others. In the future, it would be desirable to assess and specify application domains for these frameworks. For example, in Switzerland black grouse are not dispersal limited and broad-scale distribution patterns do not seem to be biased by population dynamics in contrast to local abundances which may fluctuate widely due to high site turnover. The grouse system thus seems a good candidate for such a habitat-based SEPM as presented here where environmental correlations are used to describe large-scale distribution while independently observed demographic rates are used to describe population dynamics. For species that exhibit, for example, post-glacial dispersal limitations (cf. Svenning and Skov 2004) a framework like that presented by Pagel and Schurr (2011) may be more appropriate.

6.2.3 Model specification

One recurrent problem of all models correlative and mechanistic alike is uncertainty in model structure. Any model is a simplification of reality and, thus, any model makes artificial assumptions (Levins 1966). To account for model misspecification we can build several alternative models each with different simplifications and compare model results (Araújo and New 2007). Then, 'our truth is the intersection of independent lies' (Levins 1966). Thereby, I believe that care must be taken which ‘lies’ we assemble to get to the truth. As mentioned earlier in this thesis, the interesting question in model comparisons is why predictions differ (Elith and Graham 2009). SDM algorithms differ, for example, in their degree of flexibility or in whether interactions are modelled implicitly or need to be specified explicitly. Therefore, different algorithms may deal with problems differently and our task will be to disentangle problems and problem-makers (cf. chapter 5). One problem I see for model specification is the problem of multicollinearity in environmental predictors, in particular high correlation between two causal predictors (Dormann et al., unpublished manuscript). Envision a butterfly that depends on temperature directly and also indirectly through its host plant. In this case, SDMs are not able to estimate the butterfly’s relationship to temperature independently of the host plant-temperature relationship. If the temperature niches of butterfly and host plant drifted apart due to climate change (Williams and Jackson 2007), then SDM predictions might be fallacious (but see Schweiger et al. 2008 who suggested disentangling climate effects of butterfly and host plant by restricting the butterfly SDM to areas where the host plant is currently present). Results of chapter 5 also call for more care in model specification and integration of ecological theory. Sometimes, seemingly strong patterns in the data, for example strong interactions between environmental variables, may be delusive and rather the result of data limitations.

Of course, when making dynamic predictions of range changes then we should also consider uncertainty in the structure of the dynamic model. The dynamic model presented in chapter 4 (Zurell et al. 2011) is fairly simple and many processes are subsumed in demographic or environmental stochasticity. When adding processes (submodels) to make the model more realistic, then the structure and processes should be validated for example by means of pattern-oriented modelling (Grimm et al. 2005a).

6.2.4 Model complexity

At this stage, I need to spend some more words on the issue of model complexity. Generally, model building should follow the principle of parsimony which is also known as Occam’s razor: ‘Pluralitas non est ponenda sine necessitas’ (‘Plurality should not be assumed without necessity’, William of Ockham 14th century). Thereby, we have to trade off bias against variance. Too simple models may be inaccurate because they are too rigid to capture the true relationship and, thus, show large bias (Grimm and Railsback 2005). Too complex models may be inaccurate because they represent peculiarities of the data too closely and, thus, show large variance. Surely, model complexity is also a matter of scale which has been discussed elsewhere (e.g. Scott et al. 2002) and which I do not explicitly cover throughout this thesis. In environmental change context, SDMs have often been the tool of choice because they are easy-to-use, widely available, have comparably low data requirements and can, hence, easily be applied to a wide array of species (cf. chapter 1). The rationale behind habitat-based SEPMs is in part to keep this simplicity while being able to capture transient dynamics (Gallien et al. 2010). Hence, the dynamic population models are deliberately kept simple (cf. Zurell et al. 2011, chapter 4 of this thesis). However, we thereby have to keep in mind that this simplicity may hamper the reliability of such SEPMs in environmental change context. It is generally known from population viability analyses that in very simple population models even comparably small changes in parameter values can strongly affect population growth rate and predicted extinction risk (Beissinger and Westphal 1998, Grimm and Storch 2000) as was also apparent in the black grouse case study of chapter 4 (Zurell et al. 2011). However, systematic investigation of the likely causes is lacking. It may well be that high parameter sensitivity occurs because important mechanisms shaping population response are missing in the model structure or are inadequately taken into account. For example, the exact form of density dependence and carrying capacity can strongly affect predicted extinction risks (Beissinger and Westphal 1998). Moreover, Grimm et al. (2005b) raised concerns that simple population models might overestimate extinction risks because they do not include buffer mechanisms that reduce environmental stochasticity and because high environmental noise causes higher extinction risks (Wissel et al. 1994, Wichmann et al. 2003). In the future, more research should focus on investigating the effects of density dependence, carrying capacity and environmental stochasticity in more detail and efforts should be targeted at providing the necessary data base for model verification.

6.2.5 Response vs. effect traits

If we think of species not only responding to their environment but also actively shaping and exploiting it (cf. response and effect traits, Lavorel and Garnier 2002), a more direct limitation to the use of habitat-based SEPMs becomes apparent. So far, only one-way interactions between species and environment are incorporated in SDMs and associated habitat-based SEPMs (Gallien et al. 2010, Thuiller and Münkemüller 2010). Yet, two-way interactions in the models are necessary to account for species' effect traits on the environment, for example the depletion of a resource or interspecific effects. If a species expands or shifts its range due to climate change then it will at the same time invade new places with potentially large effects on available resources or on native species (for a nice anecdote about invasive wasps simply removing native ants from food resource see Grangier and Lester 2011). To account for species' effects on their abiotic as well as biotic environment we will need a numerical framework in which both the state of the species and the state of the environment are updated at each model time step. Explicit modelling of both response and effect traits (two-way interactions between species and environment) will, thus, require predictions of environmental change- induced development of resources as well (for SDM application, see for example Schweiger et al. 2008, 2011). Future research is required in this field to establish frameworks and guidelines how to model resource depletion and especially biotic interactions. For example, what will the appropriate scale be to model the interactions between a predator (e.g. Eagle) and its prey (e.g. hares), the scale of the Eagle's home range or that of the hares?

6.2.6 Data availability

We need to keep in mind that often in SDMs the environmental predictors are only proxies for the resources themselves. For example in the black grouse case study in chapter 4 (Zurell et al. 2011), I aimed to include only those climate and land use predictors that are relevant to the species biology. Unfortunately, the choice of potential predictors is also determined by availability and resolution of the data. Clearly, the land cover variable scattered forest is not the direct resource for black grouse but a proxy for shelter and for the availability of resources like Ericaceae and Vaccinium in particular. When predicting range dynamics for scenarios of environmental change then the choice of variables in our models is not only restricted by availability of current climate or vegetation data, but also by variables available in environmental change scenarios. Thus, refining environmental data and scenarios will be a crucial step in modelling of future species range changes. However, it is important to acknowledge that we may buy more realism in our species' models at the cost of larger uncertainties in environmental change scenarios which will also propagate through to predictions of range dynamics. While global circulation models are fairly consistent in their projections of future climate, downscaling of these global scenarios proves more difficult and finer scale projections carry larger uncertainties than broad scale projections (Schröter et al. 2005). Derivation of land use scenarios is even more problematic as these have to consider political, economic, demographic and technological developments as well as interactions with climate change (Holman et al. 2005a,b, Dormann 2007).

A crucial step for wide applications of dynamic models predicting range changes is the availability of demographic data to parameterise the models. In the future, more efforts should be targeted at assembling existing data (or at least metadata) in extensive trait databases (for an example see LEDA Traitbase, Kleyer et al. 2008). To achieve this we will also need to improve mutual understanding between empiricists and theoreticians. Often, theoreticians are not aware of the enormous data treasures already acquired by empiricists, partly because information (metadata) is missing. At the same time, empiricists may not be aware of the value their data may have for modellers. Also, a good portion of scepticism remains on the empiricist side that their data may not be handled correctly or that they may lose control over their data. Improving the exchange between empiricists and theoreticians may also have additional value for both parties. Empiricist could then acquire (additional) data that may be more meaningful for modelling purposes. At the same time models and predictions can serve as eye catchers for the general public and could make the hard empirical work more visible.

Unfortunately, for most species we currently lack truly independent data to validate our model predictions on. As outlined in chapter 1, today we often rely on resampling methods for model validation (Araújo et al. 2005, Thuiller et al. 2009, for application see Zurell et al. 2011, chapter 4). However, resampled data do not actually resemble truly independent test data. Rather, in such cases training and test data still share the same (or at least similar) statistical properties. That way, model validation may provide a performance measure of how good the model depicts current distribution but it does by no means provide a measure of model robustness against the full range of environmental conditions that we may expect under environmental change. The VE approach constitutes a powerful evaluation framework as shown in chapters 2, 3 (Zurell et al. 2009, 2010) and 5. Thereby, it may help in answering theoretical questions of models' application domains but does not lend itself as a general tool for robustness analysis. Yet, as anthropogenic environmental change has been going on for decades, we are now entering a stage at which we can validate our models on contemporary changes (Hill et al. 1999, Willis et al. 2009). For example, my black grouse case study was parameterised for the turn of the millenium and predictions could be validated on observed changes in the beginning of the 21st century as soon as the new breeding bird survey will be completed for Switzerland in a couple of years. New insights about species response and resilience could then also be used to update existing models, for example in a Bayesian framework the species environment relationships estimated on current data can be used as priors in second-generation models (Clark and Gelfand 2006).

6.3 Quo vadis?

Where to go from here? Predicting environmental change-induced range dynamics is a story with many facets. Among the different ecological model types discussed here, there are no clear winners or losers. Each family of models has its benefits and limitations which make the models more or less suitable for specific applications. Therefore, the biggest task I see for the near future is not primarily to further improve existing model systems. Rather, we need to develop conceptual guidelines and rules of thumb regarding general modelling strategies, model verification, necessary process detail and model application domains (cf. Gallien et al. 2010, Franklin 2010). Thereby, we do not have to reinvent the wheel. Many guidelines and general strategies already exist for species distribution modelling (e.g. Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith and Leathwick 2009) and also for population modelling (e.g. Beissinger and Westphal 1998, Lindenmayer et al. 2003, Grimm et al. 2005a, Grimm and Railsback 2005). However, in global change context we may have to rethink these guidelines and translate them for ecological systems that are changing rapidly and possibly in unprecedented manner.

For predicting environmental change-induced species' range dynamics we can follow a simple-to-complex strategy:

1. Use phenomenological models for screening purposes of potential impacts on available habitat. Instead of relying on 'one-step' projections as commonly done in SDM studies, I recommend a 'multi-step' approach with discrete time steps (cf. Midgley et al. 2006, Zurell et al. 2009, chapter 3). Step lengths should be as small as possible and/or determined by temporal patterns and rates of expected environmental change. Overlaying predicted habitat suitability maps by SDMs may provide a first indication of potential core areas of species' range and, thus, for nature conservation (cf. Osborne and Suarez-Seoane 2007).
2. For expected range shifts and range expansions, simple estimates of migration rates can provide valuable insights about potentially colonisable areas (cf. Midgley et al. 2006, Franklin 2010).
3. If adequate demographic data are available for the population(s) under study, demography-based, spatially explicit population models can be developed to explicitly model colonisation success and local persistence of populations (cf. Zurell et al. 2011, chapter 4).
4. In the rare cases where enough data and expert knowledge are available, mechanistic models (based on first principles, behaviour-based population models, cf. chapter 1) can be developed that account for ecophysiological and behavioural mechanisms and are, thus, able to predict to novel environments. To reduce computational burdens, such fully mechanistic models can be combined with demography-based SEPMs (Grimm et al. 2007). Thereby, the mechanistic models can be used to predict population-level demographic functions for a wide range of environmental conditions.

The resulting ranges of population-level demographic rates can then be used to set the boundary conditions for robustness analysis of demography-based population models to explore long-term and large-scale population response and associated extinction risks.

All modelling attempts should be accompanied by explicit sensitivity and robustness analysis to quantify prediction uncertainty. In SDM context, this can be achieved by comparing outputs from different SDM algorithms (ensemble framework, Araújo and New 2007, Thuiller et al. 2009; Zurell et al. 2011, chapter 4). Thereby, great differences between SDM predictions should alarm us to scrutinise model behaviour more thoroughly (Elith and Graham 2009) in order to exclude, for example, ecologically implausible extrapolation behaviour (chapter 5). I recommend scanning future environmental change scenarios for novel environmental conditions without contemporary analogue (e.g. by means of multivariate environmental similarity surface, MESS, Elith et al. 2010). We could then provide reliability maps for habitat suitability that delineate SDM predictions for analogue environment against predictions for non-analogue environment which require extrapolation to environmental conditions outside the calibrated parameter range (chapter 5). Assessing similarity between current and future environment may also help in determining error margins of demographic rates that could be expected under environmental change.

The above strategy on model choice for predicting environmental change-induced range dynamics is rather general and primarily guided by data quality and data availability as well as effort required for model development. In the future, more research is needed for better integration of ecological theory and on developing conceptual guidelines regarding application domains of specific modelling frameworks. Thereby, I see three different key challenges that we need to address in order to make best use of existing models, and to make models and predictions more reliable and also more worthwhile.

I. We need to address questions regarding applicability and feasibility of specific model frameworks. Thereby, a rather general question concerns the optimum in prediction improvement that could possibly be achieved considering general restrictions in data availability and quality as well as the trade-off between parameterisation effort and process detail (Jeltsch et al. 2008)? More specific questions may ask, for example, under which circumstances and for what kind of data will circularity in habitat-based SEPMs pose a problem. As first approximations, VE studies may help to theoretically answer such questions. Extensive VE model competitions may provide valuable insights how performance of different model frameworks is affected by species' traits and prevailing ecological and environmental processes (cf. chapters 2 and 3).

II. More empirical effort to improve available data bases is needed as well as better integration and digital processing of existing data and knowledge. Extensive, high quality process-level data are required concerning species' traits such as dispersal and persistence capacity, reproduction, behavioural adaptability, phenotypic and genotypic plasticity, genetic adaptability as well as historic and/or current population dynamics among others. On the one hand, such data are needed for efficient parameterisation of more realistic, mechanistic models of species' range dynamics. On the other hand, better understanding of species' traits and ecological as well as evolutionary processes will help us to determine the process detail required for modelling species-specific response to environmental change. Also, this may facilitate derivation of functional types (Gitay and Noble 1997) or response and effect groups (Lavorel and Garnier 2002), and provide generalised answers of how species respond to environmental change (Jeltsch et al. 2008).

III. For deriving long-term conservation and management options, models and predictions need to become more accessible to politicians and practitioners. This can be achieved by improving model description and documentation including information about theoretical foundations and underlying assumptions, boundary conditions and subsequent application domain (e.g. ODD protocol for describing individual-/agent-based models, Grimm et al. 2006, 2010). On the other hand, free software applications can be developed with quite general models and submodels that can easily be adjusted for different species or functional groups (e.g. BioMove platform for dynamic simulation of plant species' response to environmental change, Midgley et al. 2010). Thereby, results from (I) and (II) can guide optimal model and submodel choices for given species and, thus, facilitate better informed and, ultimately, more reliable predictions.

I believe that these steps will aid to overall feasibility and applicability of dynamic range predictions and that by making model conceptualisation and descriptions more transparent also model reliability will increase. At the end, I want to cite some smart words by Levins (1966) that I could not better phrase: 'All models are both true and false. Almost any plausible proposed relation among aspects of nature is likely to be true in the sense that it occurs (although rarely and slightly). Yet all models leave out a lot and are in that sense false, incomplete, inadequate. The validation of a model is not that it is 'true' but that it generates good testable hypotheses relevant to important problems.' Of course, making more reliable predictions of environmental change-induced range dynamics is a primary goal in conservation biogeography. But above that, models also facilitate conceptual understanding of ecological systems and of species’ response to environmental change. In that sense, making models more realistic by adding processes should go hand in hand with applying theoretical models to further investigate basic principles and derive general hypotheses regarding species’ distributions and range dynamics.

A The virtual ecologist approach: simulating data and observers – Supplementary material

Table A.1. Applications of the virtual ecologist approach. (ANN: Artificial neural networks; ENFA: Environmental niche factor analysis; GAM: Generalised additive model; GARP: Genetic algorithm of rule-set prediction; GLM: Generalised linear model; IBM: Individual-based model; IFM: Incidence function model; MARS: Multivariate adaptive regression splines; PVA: Population viability analysis; SDM: Species distribution model; SPOM: Stochastic patch occupancy model)

System modelled	Issues addressed	Virtual ecological model	Virtual sampling model	Main conclusions	Reference
(i) Testing and improving sampling schemes and methods					
Spatial configuration of sampling units and sampling frequency					
Plants	Designing dispersal experiments for plant point sources (for correct identification of underlying dispersal kernel).	Lattice model	Subsampling, seed trap sampling designs	Transect and sector placement of traps performed best for estimating dispersal kernels. In cases of anisotropic dispersal with isotropy unknown to observer, anulli and grid arrays performed better.	Skarpaas et al. 2005
Wildlife	Evaluation of sampling designs and sizes for species distribution modelling.	Descriptive model / SDM	Subsampling	Regular and equal-stratified sampling strategies were most accurate and robust. Greater sample sizes were advantageous. Guide to improve sample designs.	Hirzel and Guisan 2002
Seabirds (Marbled Murrelets)	Evaluation of transect-layouts and sampling frequencies to detect population declines.	Lattice model	Subsampling, transect designs	Stratified and unstratified zigzags, and ten 8km transects placed at random had high power to detect population trend, produced unbiased population estimates, and were logistically feasible.	Rachowicz et al. 2006
Coleoptera (Darkling beetles)	Effect of habitat-specific movements of individuals on capture rates and population size estimates in relation to trap geometry.	IBM	Subsampling, Pitfall traps	Rectangular trap arrangements have the highest capture probability when animals relatively sedentary and occupy territories or home ranges. Different geometries useful when individuals are transient to trap area and populations have open spatial structure.	Crist and Wiens 1995
Ground-dwelling	Evaluation of cross-shaped	IBM	Subsampling,	Method is promising, especially for more	Perner and

arthropods (Carabid beetles)	trap arrangements for estimating population density.		Pitfall traps	mobile species, and is worth testing in the field.	Schueler 2004
Micro.algal grazers (Gastropods)	Evaluation of sampling designs for species of different foraging strategies.	IBM	Subsampling, confinement experiments	Mixing of data derived from field-enclosure experiments and from quadrat-based methods seems to be ill-advised as biases arise especially for intelligent, decision-making organisms.	Mac Nally 2001
Trees	Comparison of structurally different models to analyse tree growth-mortality relationships.	IBM	Subsampling, tree-ring data, repeated forest inventories	Flexible statistical approaches were superior to less flexible models only for large sample sizes. Study provides theoretical basis for sound estimation of growth-mortality models, and guidelines for efficient sampling schemes in real forests.	Wunder et al. 2008
Animals (Grasshoppers)	Optimal observational interval for estimation of mobility of species and suitability of different mobility measures.	IBM	Probabilistic + Feedback, Mark-recapture	Differences between observation and real movements of animals increase with less frequent surveys and with animal mobility. Daily surveys should only be done if species are not disturbed easily.	Berger et al. 1999
Sampling bias					
Alien Plant (Giant Hogweed)	Probability of sampling negative growth in dependence of time since invasion.	IBM	Subsampling, permanent plots	Probability of sampling negative growth increases with time since first invasion. Populations stagnate in size when maximum of local invasive potential reached.	Nehrbass et al. 2006
Wildlife	Quantifying SDM parameter bias conditional on detection errors.	Descriptive model / SDM + stochasticity	Probabilistic	Estimating and correcting for non-detection error requires multiple sampling occasions. Estimating relationships between probability of detection and habitat covariates to identify patches with need for higher sampling effort.	Gu and Swihart 2004

Seabirds (Ascension Frigatebird)	Quantifying bias in the raw census totals owing to difficulties in counting and misinterpretation of data.	IBM	Subsampling	Ignoring bias in raw nest counts is likely to produce inaccurate population estimates for asynchronously nesting species such as frigatebirds. VE allows for simultaneous correction of all potential biases.	Ratcliffe et al. 2008
Threatened wetland birds	Estimate sampling error.	IBM	Probabilistic + Feedback, transect design	The applied sighting method cannot be used as a measure for population size or development.	Nott 1998
Animals (Eurasian Otter)	Introduce new visitation rate estimator taking into account age of indirect signs.	IBM	Subsampling, Repeated sampling	If possible, any effort should be made to distinguish between aged and new tracks/signs and to use this information with the combined maximum likelihood estimator.	Gruber et al. 2008
Mircotine rodents (Field voles)	Explain synchronized activity pattern.	IBM	Probabilistic, passage counters	Differences in activity patterns for different social groups might be blurred by sampling design.	Halle and Halle 1999
(ii) Evaluating and comparing models					
Species distribution models – SDMs					
Wildlife	Introducing a favourability function obtained from SDMs whose results are not affected by uneven proportions of presences and absences.	Descriptive model / SDM	Subsampling	Favourability model yielded more realistic potential distribution maps than conventional SDMs. Allows for direct comparisons between models for species with different presence/absence ratios in the study area.	Real et al. 2006
Wildlife	Improving favourability function proposed by Real et al. 2006 with a formula relying on ratio between sampling and true prevalence of a species.	Descriptive model / SDM	Subsampling	Improved formula efficient in reducing sampling-induced error, and more realistic than the one proposed by Real et al. (2006) although it will be difficult to apply to real species for which true prevalences are poorly known.	Albert and Thuiller 2008
Wildlife	Impact of false-negative	Descriptive	Probabilistic	Propose zero-inflated binomial models to	Tyre et al. 2003

	errors on SDM estimation.	model / SDM		overcome the problem. In general, with error rates <50% greater efficiency is gained by adding more sites, with error rates >50% it is better to increase the number of repeated visits.	
Wildlife	Effect of spatial autocorrelation on classical tests of significance of correlation or regression coefficients.	Descriptive model / SDM	Subsampling	Spatial autocorrelation in response and environmental variables disturbs classical tests of significance while spatial autocorrelation in a single variable has no effect.	Legendre et al. 2002
Virtual species (Snouter)	Comparison of methods to account for residual spatial autocorrelation in species distribution modelling.	Descriptive model / SDM + spatial autocorrelation	Full census	Recommends several approaches which show good performance in accounting for spatial autocorrelation.	Dormann et al. 2007
Wildlife	Effects of sampling design, spatial contiguity, and species detection probability on performance of autologistic regression.	Descriptive model / SDM	Probabilistic	Better model performance for random and stratified survey designs. Larger detection probabilities, larger sample sizes, contiguous distributions, and fewer environmental data errors generally improved model performance.	Reese et al. 2005
Wildlife	Comparison of threshold criteria for a wide range of sample sizes and prevalences.	Descriptive model / SDM	Subsampling	Sensitivity–specificity difference minimizer and sensitivity–specificity sum maximizer criteria produced the most accurate predictions. However, in all cases, the threshold value chosen and the research goals that determined its choice must be stated.	Jiménez-Valverde and Lobo 2007
Wildlife	Comparison of regularisation methods for SDMs.	Descriptive model / SDM	Subsampling	No regularization method performed best under all circumstances. Variable selection should be used with caution. *Ridge* and *lasso* are risk-averse model	Reineking and Schröder 2006

				strategies, preferably esp. for small sample sizes.	
Forests	Comparison modelling techniques for the broad-scale mapping of forest characteristics.	Descriptive model / SDM	Subsampling	MARS and ANN performed best within VE, but much smaller differences were seen with real data because of noise or possible lack of nonlinear relationships between response and predictor variables.	Moisen and Frescino 2002
Grasslands	Comparison of modelling techniques for predicting ecosystem attributes.	Descriptive model / SDM	Subsampling	For the six traits analysed, ANNs were able to make better predictions than regression models.	Paruelo and Tomasel 1997
Wildlife	Compare performance of SDM algorithms regarding underlying response shapes, direct and indirect predictors.	Descriptive model / SDM	Subsampling	Ecological knowledge and statistical skills of the analysts were more important than the method used.	Austin et al. 2006
Wildlife	Compare performance of SDM algorithms conditional on prevalence, sample size, selection procedure.	Descriptive model / SDM + stochasticity	Subsampling	Recommend the use of GAM or GLM over classification trees or GARP. SDMs for species with low prevalence can be improved through targeted sampling.	Meynard and Quinn 2007
Wildlife	Compare performance of SDM algorithms conditional on colonisation history.	Descriptive model / SDM + stochasticity	Subsampling	GLM was badly affected in the case of the spreading species but produced slightly better results than ENFA when the species was overabundant; at equilibrium, both methods produced equivalent results.	Hirzel et al. 2001
Arboreal marsupials (Greater Glider)	Suitability of SDMs for identifying source habitats.	IBM	Subsampling	SDMs based on logistic regressions measure the ability of species to reach/ colonize habitat, not their death/ birth rates.	Tyre et al. 2001
Cerrado vegetation (Savanna)	Performance of SDMs coupled with Spatial Eigenvector Mapping under	Cellular automata	Subsampling	Mechanisms that generate range cohesion and determine species’ distribution under climate changes can be captured by	de Marco et al. 2008

	range expansion.			spatial modelling.	
Fish (Stream trout)	Usefulness of SDMs for assessing the fitness potential provided by habitat and for predicting population responses to habitat alteration.	IBM	Subsampling	Little can be inferred about the fitness value of habitat from observed habitat selection. Recommend that SDMs be supplemented with mechanistic approaches.	Railsback et al. 2003
Wildlife (Arthropods)	Effects of transient dynamics and ecological properties and processes on the prediction accuracy of SDMs under climate change.	Lattice model	Subsampling	Different range dynamics lead to different prediction accuracies of SDMs under climate change. Study pinpoints relevant processes which should be incorporated into SDMs.	Zurell et al. 2009, chapter 3
Descriptive community assembly models					
Barro Colorado Island Forest	Evaluate phylogenetic community metrics and their statistical power to detect phylogenetic patterns formed by ecological (competition, habitat filtering, or neutral processes) and trait evolution processes (conserved and convergent traits).	IBM	Full census	Very few tests gave consistent type I error rates over a range of different conditions. Most tests reject the null hypothesis (that only neutral processes structured spatially the local community) too often when the randomization algorithm broke down a structure in the original data set. Tests often showed better conformance when applied to a single study site rather than to multi-study sites.	Hardy 2008
Natural communities		Descriptive model/	Full census	Patterns due to competition are better detected by nearest-relative tests; patterns due to habitat filtering are better detected with total community relatedness tests. Statistical power strongly depends on the size of the local community relative to the regional pool with larger pool sizes increasing power for habitat filtering patterns but decreasing power for	Kraft et al. 2007

				competition patterns.	
Natural communities	Compare performance of metrics measuring nestedness and co-occurrence in occurrence by side matrices.	Descriptive model	Full census	A null model that preserves matrix row and column totals has lower type I and type II error probabilities than a null model that relaxes row and column totals (which is used in the popular nestedness temperature calculator).	Ulrich and Gotelli 2007a, b; Fischer and Lindenmayer 2002; Higgins et al. 2006; Grewe and Chown 2006
Dynamic (meta-)population models					
Animals (Butterflies)	Introduce model of individual capture histories that allows to measure rates of migration and survival in metapopulations.	Patch network	Probabilistic, Mark-recapture	The model can be applied in studies of 10 or more populations with differing patch areas and isolation, and for several hundred counted individuals.	Hanski et al. 2000
Animals (Butterflies)	Evaluation of an improved method for parameter estimation of IFMs for a range of varying data scenarios.	Patch network	Subsampling	New method produced parameter estimates for IFM that were more accurate than those obtained by original method for all scenarios.	Moilanen 1999
Wildlife	Studying the effect of different types of error in data used to parameterise IFMs.	Patch network	Probabilistic	False zeros have the greatest impact and should be avoided. Given limited resources, it may be preferable to survey only part of a large patch network thoroughly rather than to hasty survey the complete set of patches.	Moilanen 2002
Wildlife	Comparing the susceptibility of different SPOMs to predicting spurious trends in metapopulation size.	Patch network	Subsampling	Logistic regression models (estimated from turnover data) are more sensitive to the implicit estimation of a trend than the IFM, esp. when only 2 snapshots of occupancy data are used. The latter also allows incorporating a quasi-equilibrium assumption.	Moilanen 2000
Animals	Investigate data	IBM	Subsampling,	Results suggest putting emphasis on	Hilker et al. 2006

(Grasshoppers)	requirements of IFM, and compare two different SPOMs.		repeated sampling	determining the migration parameters from additional, independent data rather than collecting more snapshot years.	
Wildlife	Examine how robust five PVA models are to neglected effects of species interactions.	stochastic, stage-structured predator-prey model	Subsampling	Simplifying the complexity of species interactions by population models, including PVA, can be misleading, but only when the single-species model is itself overly complex.	Sabo and Gerber 2007
Wildlife	Assessment of the reliability of predictions for extinction risks from PVA conditional on available data.	Ricker model	Subsampling	Despite considerable uncertainty in the predicted risk of decline, useful predictions for the ranking of species in terms of relative threat and for evaluation of different management options are possible using only 10 years of data.	McCarthy et al. 2003
Plants (Proteaceae)	Introduce likelihood framework for estimating demographic models for range dynamics of woody plants.	Lattice model	Probabilistic	Process-based models can quantitatively describe how large-scale abundance distributions arise from the local dynamics and dispersal between populations. The presented framework provides link between SDMs, empirical demography and theoretical ecology.	Cabral and Schurr 2010

B Static species distribution models in dynamically changing systems: how good can predictions really be? – Supplementary material

B.1 Submodels of dynamic population model

In the following, the processes occurring in each time step of the dynamic population model are described. Respective parameter values are given in Table 3.1.

B.1.1 Process 1: Climate states

At the beginning of each time step, the climate state, characterised by temperature and moisture, was updated. Each cell's temperature was calculated by climatological downscaling of mean summer temperature considering altitudinal differences, the adiabatic gradient T_{lapse} and radiation (Bellasio et al. 2005; Moore et al. 1993; Wilson and Gallant 2000):

$$T_{ij} = T - T_{lapse}\left(\frac{z_{ij}}{1000}\right) + \left(S_{ij} - \frac{1}{S_{ij}}\right) \qquad \text{(B.1)}$$

with z_{ij} being the elevation of the grid cell, S_{ij} the ratio between the insolation of the cell and the horizontal surface. The insolation was truncated to the cosine of the solar illumination angle i:

$$\cos(i) = \cos(\theta_0) + \sin(\theta_0)\sin(slope)\cos(\phi - A) \qquad \text{(B.2)}$$

with the solar zenith angle $\theta_0 = 78.25°$ and the solar azimuth $\varphi_0 = 180°$, A was the aspect and *slope* the surface slope (Dubayah and Loechel 1997). Potential soil moisture was approximated by the topographic wetness index (Beven and Kirkby 1979; O'Neill et al. 1997), standardised for a precipitation rate of 500 m/a:

$$W_{ij} = \ln\left(\frac{area_{ij}}{\tan(slope_{ij})}\right)\frac{1}{500} \qquad \text{(B.3)}$$

where $area_{ij}$ was the drainage area above the cell. Flow directions were assigned using the D8 method, i.e. flow occurred in steepest down-slope direction to one of the cell's eight neighbours, either adjacent or diagonal (Wilson and Gallant 2000). Thus, W_{ij} could be interpreted as the proportion of rainwater each cell was able to retain. Actual soil moisture was then calculated by multiplying the proportion of retained water with actual rainfall.

B.1.2 Process 2: Habitat state

The butterfly depended on the presence and abundance of the plant which induced a carrying capacity K in each lattice cell. K was proportional to the plant foliage projective cover F, with the maximum carrying capacity K_{max}. F was determined by temperature and moisture conditions of a cell, each representing a one-dimensional resource spectrum. The physiological response of the plant was described by a Gaussian utilisation function with the mean being the preferred position in the spectrum and a characteristic variance (May and Mac Arthur 1972). Following Liebig's law of the Minimum which says that growth is controlled by the scarcest resource, the limiting factor, *F* was calculated by multiplying the degree of utilisation of each resource. Resource competition at plant level was introduced by adding a second plant species, the competitor, whose fundamental niche overlapped with that of the host plant, and which did not serve as a host plant for the butterfly. The competitor always outcompeted the host plant resulting in a narrower, realised niche of the latter (Fig. 3.1). To simulate environmental stochasticity, the actual physiological response was drawn from a Normal distribution with mean *F* and a variance σ^2_F.

Global dispersal was assumed for host plant and competitor plant. Too abrupt changes in the plant distribution were avoided by incorporating a simple memory effect such that the actual capacity of the new time step was the arithmetic mean between the calculated capacity of time step $t+1$ and the old capacity of time t. This simple memory effect resulted in a time lag of several years.

B.1.3 Process 3: Dispersal

Early in each year, on emergence, a proportion of adult butterflies and parasitoids left their natal patch to colonise other cells in the lattice. Local dispersal was assumed, i.e. the dispersers were concentrated around the area in which they developed as juveniles. The probability p_{ij} that an individual dispersed from cell i to j over the integer distance d_{ij} was described by a two-parameter Weibull distribution allowing different dispersal strategies (Söndgerath and Schröder 2002):

$$p_{ij} = \frac{\exp(-\alpha d_{ij}^{\ \beta})}{\sum_j \exp(-\alpha d_{ij}^{\ \beta})} \qquad \text{(B.4)}$$

with the shape parameter β, and the scale parameter α determining the dispersal distance. A high value of α indicated short-range dispersal, a low one large-range dispersal. At α=0 the dispersers would be evenly distributed throughout the lattice (global dispersal). The integer distance d_{ij} between cells depended on the applied neighbourhood rule, in this case an 8-cell (Moore) neighbourhood (Hogeweg 1988). Individuals dispersing to unsuitable habitats, i.e. cells without butterfly and plants respectively, died.

B.1.4 Process 4: Reproduction and parasitism

The generalised form of the difference-equation framework for the reproduction and parasitism phase was as follows:

$$\begin{aligned} N_{t+1} &= \lambda N_t g(N_t) f(P_t) \\ P_{t+1} &= cN_t \left[1 - f(P_t)\right] \end{aligned} \qquad \text{(B.5)}$$

where N and P were the population abundances of the susceptible butterfly stage and the searching adult female parasitoid, respectively, in generations t and $t+1$, λ the net finite rate of increase of the butterfly population, $g(N_t)$ the density-dependent survival of the butterflies progeny, $f(P_t)$ the proportion of butterflies escaping parasitism, c included the average number of adult female parasitoids emerging from each butterfly parasitised. The parasitoids' functional response was linear (type I functional response) and the attacks were randomly distributed amongst the butterfly population (Nicholson 1933; Nicholson and Bailey 1935). The fraction of butterflies escaping parasitism was given by the zero term of a Poisson distribution (Eq. B.6) with mean aP_t where a was the area of discovery:

$$f(P_t) = \exp(-aP_t) \qquad \text{(B.6)}$$

Density dependence of butterfly reproduction entered the model system via $g(N_t)$ (Eq. B.7), a discrete version of the logistic equation (Hassell 2000; Ricker 1954):

$$g(N_t) = \exp\left(\frac{-\ln(\lambda)}{K} N_t\right) \qquad \text{(B.7)}$$

The intrinsic butterfly population growth rate λ was modelled temperature-dependent to reflect its metabolic dependence. To simulate the generally humped-shaped and left-skewed relationship between physiological rates and temperature, a Gumbel distribution was used with T_{opt} as location parameter, a scale parameter σ, and a maximum growth rate λ_{max}. Butterfly population growth rate was additionally restrained by introducing a simple but strong Allee effect (Allee 1931). Below a critical population size N_{crit}, the extinction threshold, no reproduction occurred and the local butterfly population went extinct.

C Uncertainty in predictions of range dynamics: black grouse climbing the Swiss Alps – Supplementary Material

C.1 Submodels of individual-based model

C.1.1 Carrying capacity

Carrying capacity is a function of habitat area and suitability (Keith et al. 2008), and is updated at the beginning of each time step. Habitat suitability is defined as black grouse occurrence probability determined by the statistical species distribution models. Suitable habitat is defined by a threshold minimum value of habitat suitability. This threshold is given by the present-day prevalence of black grouse (Liu et al. 2005). We assumed that habitat suitability was a direct surrogate of carrying capacity whenever the modelled habitat suitability exceeded this threshold (for examples see Anderson et al. 2009, Araújo et al. 2002, Keith et al. 2008). Maximum carrying capacity was defined as the maximum density of black grouse per km^2 that can be expected in Switzerland given the home range requirements of the species.

Individuals may persist for some time under suboptimal conditions. This is realised by a simple memory effect incorporated in the habitat suitability index. If the SDM prediction for a cell is lower than the cell's habitat suitability of the preceding time step, then habitat suitability of the actual time step is the mean of the preceding habitat suitability and the current SDM prediction. This simple memory effect prevents too abrupt shifts in habitat suitability.

C.1.2 Reproduction

The probability of a hen to reproduce successfully and lead young is *pleadYoung*. Some may fail to reproduce because eggs do not hatch or nests are predated or deserted. We calculated these probabilities from empirical data (Zbinden and Salvioni 2003, Zbinden unpublished data).

C.1.3 Fledging

Upon successful reproduction the probability of a hen to lead a certain number of young birds is *p(x)Fledglings*. Probabilities were calculated from empirically observed distribution of brood sizes (Zbinden and Salvioni 2003, Zbinden unpublished data). The probability for a fledgling to be female is *pYoungFemale*, otherwise it is a male and is subsequently ignored.

C.1.4 Natal dispersal

In autumn, first-year hens disperse from their natal patch with a probability *pDispersal* (Caizergues and Ellison 2002). Dispersal is assumed to be equally likely in eight directions, and subsequently each dispersing individual is assigned a random direction (N, NE, E, SE, S, SW, W, and NW). The expected mean natal dispersal distance of female black grouse *meanDist* and the range of dispersal distances *rangeDist* were compiled from Caizergues and Ellison (2002). These two values were used to draw the individual dispersal distances from an empirical model for natal dispersal distances in birds which was proposed by Sutherland et al. (2000, Equ. 2) and is based on the negative exponential distribution. In our model, individual birds perceive the environment as heterogeneous and avoid to settle in or to traverse wide stretches of unsuitable habitat (Zbinden, unpublished data). Hence, they will not settle in cells without any resources available. This is the case when habitat suitability is so low that carrying capacity $K < 1$, or when the cell is crowded and $N \geq K$. Dispersers will then search the (eight) nearest neighbour cells for better suited habitat or, if this search is of no avail, will make a second dispersal attempt. Individuals will not cross widely unsuitable areas, i.e. more than ten cells (i.e. max. 10 km) with carrying capacity $K < 1$. If they encounter such a stretch of unsuitable habitat, they will sidestep it and resume their original direction as soon as possible (cf. Graf et al. 2007).

C.1.5 Mortality and density dependence

All sources of mortality are subsumed under an annual survival probability (*pSurv*), the probability of an individual hen to survive until early spring (Zbinden and Salvioni 2003).

Mortality and emigration may increase with density due to increased predation risk or simply due to shortage of resources. As no information is available for density dependence in Alpine black grouse populations, we assumed carrying capacity K to have a ceiling effect on the local population. If the number of adults in a cell exceeds K, random individuals are removed from this cell according to two rules: (1) Individuals will be randomly assigned to the (eight) nearest neighbour cells, if these are not crowded ($N < K$). Thereby, we accounted for some adaptability of home ranges. Then, (2) if local population size N still exceeds K, random individuals will be removed from the cell until the local population size is equal to K (Grimm and Storch 2000).

C.2 Supplementary Tables and Figures

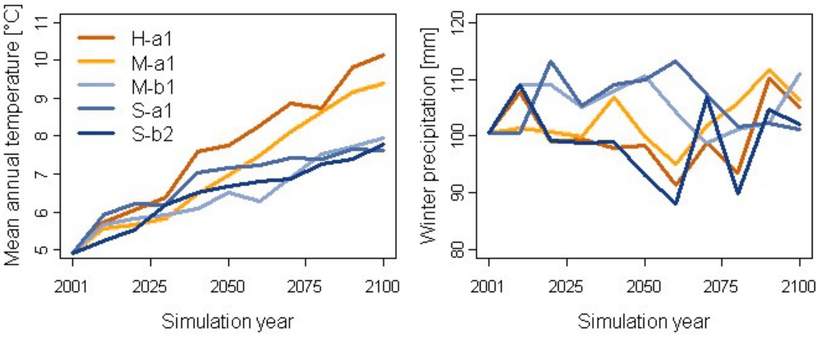


Figure C.1. Predicted mean temperature and precipitation changes for scenarios of climate change. For abbreviations see Table 4.1.

Table C.1. SDM evaluation statistics (mean ± SD of 100 split-sample runs).

Performance criterion	BRT	GAM	GLM
AUC	0.950 ± 0.01	0.949 ± 0.01	0.946 ± 0.01
Explained deviance R^2	0.590 ± 0.02	0.583 ± 0.03	0.572 ± 0.03
TSS	0.785 ± 0.02	0.784 ± 0.02	0.782 ± 0.02
Sensitivity (True presences)	0.926 ± 0.01	0.939 ± 0.01	0.947 ± 0.01
Specificity (True absences)	0.859 ± 0.01	0.845 ± 0.01	0.836 ± 0.01
Calibration slope (Spread)	1.005 ± 0.07	0.975 ± 0.10	0.955 ± 0.13
Calibration intercept (Bias)	0.003 ± 0.14	0.006 ± 0.14	0.013 ± 0.14

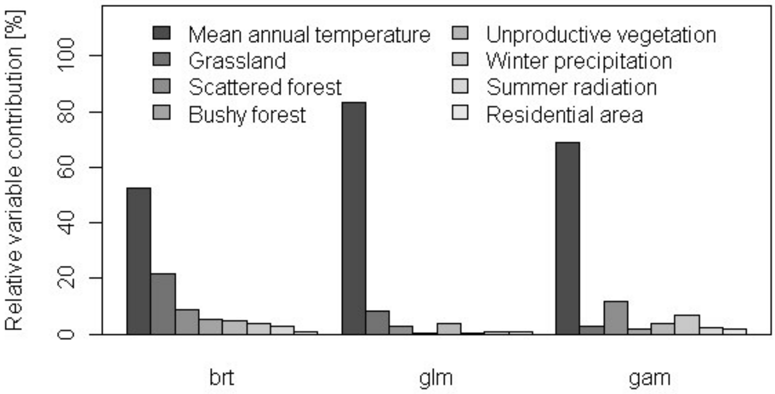


Figure C.2. Relative variable contribution in SDMs.

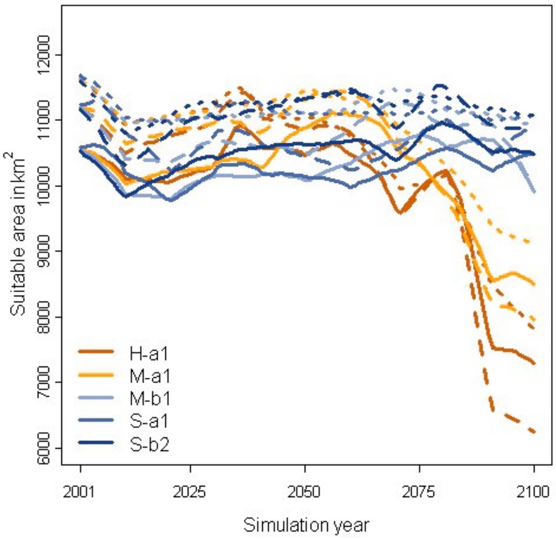


Figure C.3. Predicted suitable area size for scenarios of climate change and different SDM algorithms. Solid lines indicate predictions made by BRT, dashed lines GAM and dotted lines GLM. Suitable area is defined as the sum of all 1 km^2 cells with habitat suitability exceeding the prevalence threshold. For abbreviations see Table 4.1.

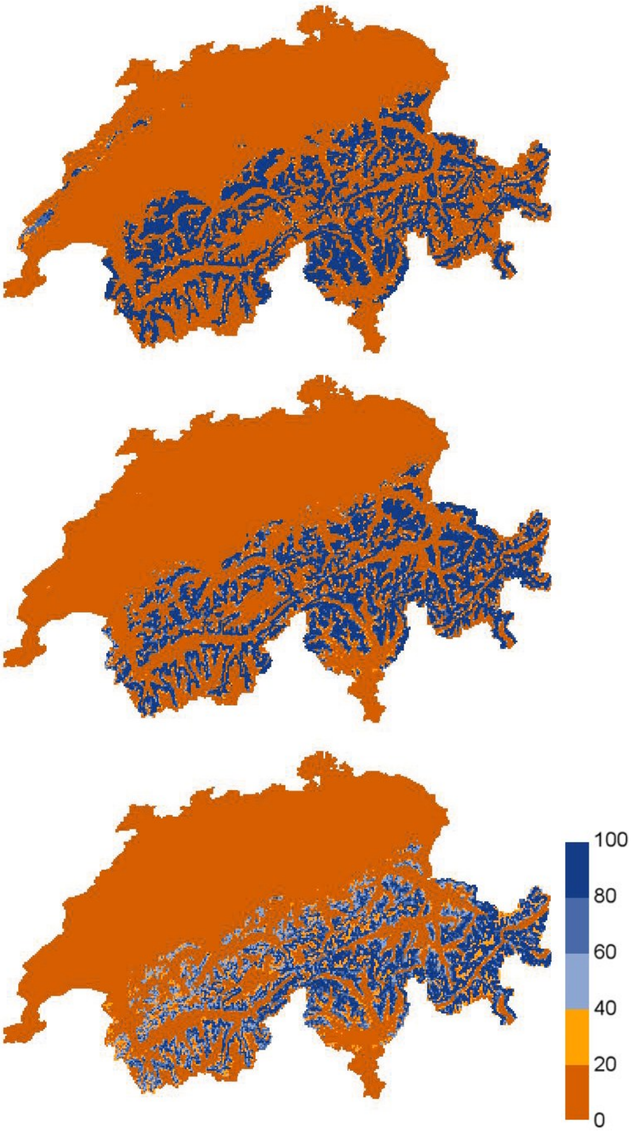


Figure C.4. Consensus on black grouse presence across different SDMs and climate scenarios for years 2001, 2050 and 2100 (from top to bottom), calculated as fraction of simulations (n = 15) predicting black grouse to be present. IBM was run with default parameterisation. (Note that zero percent consensus on presence equal 100 % consensus on black grouse absence).

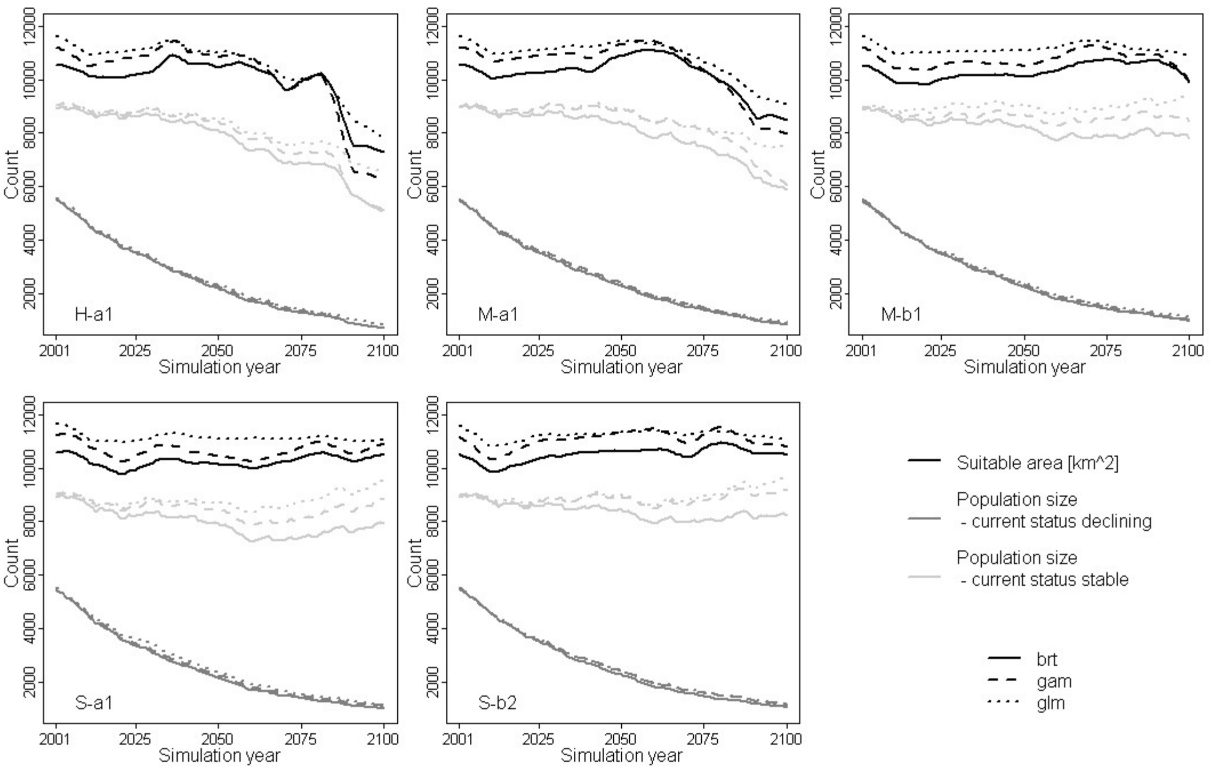


Figure C.5. Predicted suitable area size and population size for scenarios of climate change, different SDM algorithms and different IBM parameterisations. Suitable area is defined as the sum of all 1 km^2 cells with habitat suitability exceeding the prevalence threshold. Population size with current status 'declining' is predicted by running the IBM with default parameterisation. Population size is with current status 'stable' is predicted by increasing survival probability in IBM (*pSurv*=0.51). For abbreviations of climate scenarios see Table 4.1.

D Predicting to new environments: tools for visualising model behaviour and impacts on mapped distributions – Supplementary Material

D.1 Code for simulated data and inflated response curves

The subsequent code is written for R (R Development Core Team 2010) under Windows XP Professional.

```
# example with simulated data:
# species' occurrence described by species' tolerance to temperature, woodland;
# three cases with different data coverage of two-dimensional environmental niche:
# (1) species niche entirely encompassed by data;
# (2) species niche truncated, i.e. portions of the niche are not represented in data;
# (3) species niche abuts environmental data, i.e. niche edge coincides with data limits;
# For all cases, different SDMs are estimated on training data, and fitted values are compared.
# Then, predictions are made for changing climate (=warmer temperature while land cover remains constant)
# and again fitted values for future climate are compared.

#*********************************************
# set working directory
setwd("...")

# load libraries
library(Design)
library(boot)
library(gam)
library(gbm)
source("brt.functions.R") #this is extract code provided in Elith et al. (2008) JAnimEcol 77:802-813
# note that the inflated.response() function will additionally require the package 'lhs' to be installed

#*******************************************************
# some functions for creating species data, for evaluation and plotting
# define species (lrm)
species=function(temp,wood,sdev=3){
  return(inv.logit(-170+40*temp-2.5*temp^2+
  .35*wood+
  rnorm(max(length(temp),length(wood)),0,sdev)))}

#-----------------------------------------------------------
# plot fitted values for all three predictors + true response curve
myplot<- function(x,y,main,thresh=F,ylab="Occurrence probability"){
  plot(x$temp,y,xlab="Temperature",ylab=ylab,main=main,ylim=c(0,1),xlim=c(3,16))
  i=seq(3,16,length=100)
  lines(i,species(i,70,sdev=0),lty="solid",col="grey80",lwd=2)
  plot(x$woodlandCover,y,xlab="Woodland cover",ylab="",main=main,ylim=c(0,1))
  i=seq(min(x$woodlandCover),max(x$woodlandCover),length=100)
  lines(i,species(8,i,sdev=0),lty="solid",col="grey80",lwd=2)
  }

#--------------------------------------------------------------------------
# plot 'inflated' response curves - 'inflated' partial dependence plots
inflated.response=function(object,predictors,select.columns=NULL,label=NULL,len=50,lhsample=100,lwd=1,
    ylab="Occurrence probabilities",method="stat3",disp="all",overlay.mean=T,
    col.curves='grey',col.novel='grey',col.mean='black',lwd.known=2,lwd.mean=2,...){

  # plot inflated response curves;
  # plot effect of one variable over range of other predictors;
  # method determines at which values the other predictors are held constant:
  # method='mean' corresponds to conventional partial dependence plots,
  # method='stat3' (Default) considers minimum, mean and maximum values of predictors,
  # method='stat6' considers min,mean,median,max and quartiles.
  # for 'stat3' and 'stat6' effects of one variables is plotted for all possible
  # combinations of remaining predictors - as the number of combinations increases exponentially,
  # the maximum number of combinations can be set with lhsample. Whenever lhsample is exceeded,
```

```
  # candidate combinations are drawn by latin hypercube sampling.
  # len determines the number of intervals along the environmental gradient plotted,
  # i.e. smoothness of response curves.
  # disp can take options 'all' or 'eo.mask' - in the latter case, eo.mask() is used
  # to distinguish between areas of the estimated environmental niche / plotting areas
  # that are supported by data and those that require extrapolation.
  # if overlay.mean is true, then the mean response curve is overlaid on the inflated plot.

  if (is.null(select.columns)) select.columns=1:ncol(predictors)

  require(lhs,quietly=T)
  for (i in select.columns)
  {
  summaries=data.frame(matrix(0,6,ncol(predictors)))
  for (iz in 1:ncol(predictors)) summaries[,iz]=summary(predictors[,iz])
  if (method=="stat3") {summaries.j=as.matrix(summaries[c(1,4,6),-i],ncol=(ncol(predictors)-
1));comb=min(lhsample,3^(ncol(predictors)-1));nc=3} else
  if (method=="stat6") {summaries.j=as.matrix(summaries[,-i],ncol=(ncol(predictors)-
1));comb=min(lhsample,6^(ncol(predictors)-1));nc=6} else
  if (method=="mean") {summaries.j=as.matrix(summaries[4,-i],ncol=(ncol(predictors)-
1));comb=1;nc=1;overlay.mean=F}
  dummy.j=as.matrix(predictors[1:len,-i],ncol=(ncol(predictors)-1))
  if (comb<lhsample) {
    mat=vector("list",ncol(dummy.j))
    for (m in 1:ncol(dummy.j)) mat[[m]]=1:nc
    mat=expand.grid(mat)
    } else
  mat=round(qunif(randomLHS(lhsample,ncol(dummy.j)),1,nrow(summaries.j)),0)
  if (is.null(label)) label=names(predictors)

  for (r in 1:nrow(mat))
    {
      for (j in 1:ncol(dummy.j))
      {
      dummy.j[,j]=as.vector(rep(summaries.j[mat[r,j],j],len))
      }

    dummy=data.frame(seq(min(predictors[,i]),max(predictors[,i]),length=len),dummy.j)
    names(dummy)[-1]=names(predictors)[-i]
    names(dummy)[1]=names(predictors)[i]

    if (is(object,"gbm")) curves<-predict.gbm(object, dummy,n.trees=object$gbm.call$best.trees,
type="response") # when using brt code from Elith et al. (2008) JAnimEcol
    else if (is(object,"glm")) curves<-predict(object, dummy, type="response")
    else if (is(object,"randomForest")) curves<-predict(object,dummy)
    else if (is(object,"tree")) curves<-predict(object,dummy)
    else if (is(object,"list")) curves<-mars.predict(object, dummy)$prediction[[1]]   #when using mars code from
Elith and Leathwick (2007) Div Distr
    else if (is(object,"fda")) curves<-predict(object,dummy,type="post")[,2]
    else if (is(object,"nnet")) curves<-predict(object,dummy,type="raw")
    else {print("SDM class unknown");break}

    # display all lines in same type
    if (disp=='all')
    {
    if (r==1)
    {
    if (i==1) plot(dummy[,names(predictors)[i]],
      curves,type="l",ylim=c(0,1),xlab=label[i],ylab=ylab,
      lwd=lwd,col=col.curves,...)
    else plot(dummy[,names(predictors)[i]],
      curves,type="l",ylim=c(0,1),xlab=label[i],ylab="",lwd=lwd,col=col.curves,...)
```

```
  }
  else lines(dummy[,names(predictors)[i]],
   curves,lwd=lwd,col=col.curves,...)
  }

  # highlight extrapolation to novel environmental conditions
  if (disp=='eo.mask')
  {
  novel=eo.mask(predictors,dummy)
  curves.known=curves
  curves.known[novel==1]=NA
  curves.novel=curves
  curves.novel[novel==0]=NA

  if (r==1)
  {
  if (i==1) {plot(dummy[,names(predictors)[i]],
   curves.known,type="l",ylim=c(0,1),xlab=label[i],ylab=ylab,
   lwd=lwd.known,col=col.curves,...)
   lines(dummy[,names(predictors)[i]],
   curves.novel,lwd=lwd,col=col.novel,lty='dotted',...)}
  else {plot(dummy[,names(predictors)[i]],
   curves.known,type="l",ylim=c(0,1),xlab=label[i],ylab="",lwd=lwd.known,col=col.curves,...)
   lines(dummy[,names(predictors)[i]],
   curves.novel,lwd=lwd,col=col.novel,lty='dotted',...)}
  }
  else {lines(dummy[,names(predictors)[i]],
   curves.known,lwd=lwd.known,col=col.curves,...)
   lines(dummy[,names(predictors)[i]],
   curves.novel,lwd=lwd,col=col.novel,lty='dotted',...)}
  }
  }

  #-------------------------------------------------
  # now, this is for overlaying mean response curve
  if (overlay.mean==T)
  {
  dummy=predictors[1:len,]
  dummy[,i]=seq(min(predictors[,i]),max(predictors[,i]),length=len)
  for (j in 1:ncol(predictors))
   {
   if (j!=i)
    {
    dummy[,j]=rep(mean(predictors[,j]),len)
    }
   }

  if (is(object,"gbm")) curves<-predict.gbm(object, dummy,n.trees=object$gbm.call$best.trees,
type="response")
  else if (is(object,"glm")) curves<-predict(object, dummy, type="response")
  else if (is(object,"randomForest")) curves<-predict(object,dummy)
  else if (is(object,"tree")) curves<-predict(object,dummy)
  else if (is(object,"list")) curves<-mars.predict(object, dummy)$prediction[[1]]
  else if (is(object,"fda")) curves<-predict(object,dummy,type="post")[,2]
  else if (is(object,"nnet")) curves<-predict(object,dummy,type="raw")
  else {print("SDM class unknown");break}

  lines(dummy[,names(predictors)[i]],
   curves,lwd=lwd.mean,col=col.mean,...)
  }
 }}
```

```
#------------------------------------------------------------------------------
# calculate environmental overlap mask
# extension of MESS that was proposed by Elith et al. 2010 MethodsEcolEvol 1:330-342.

eo.mask=function(traindata,newdata,nbin=5,type="EO")
  {
  # a bin size of one corresponds to MESS
  # type 'EO' returns a vector of zeros and ones for analog(0) and novel(1) environments
  # type 'ID' returns a character vector defining the combination of bins each data entry
  # belongs to - this may help finding the problem maker parts of the prediction space

  train.minima=apply(traindata,2,min)
  train.maxima=apply(traindata,2,max)

  train.ids=apply(apply(ceiling(apply(round(
    sweep(sweep(traindata, 2, train.minima, "-"), 2, train.maxima - train.minima, "/")*nbin,4),
    c(1,2),FUN=function(x){if(x==0)x=1 else x=x})),
    c(1,2),FUN=function(x){if(x<1)x=0 else if(x>nbin)x=nbin+1 else x=x}),1,paste,collapse=".")

  new.ids=apply(apply(ceiling(apply(round(
    sweep(sweep(newdata[,names(train.minima)], 2, train.minima, "-"), 2, train.maxima - train.minima,
"/")*nbin,4),
    c(1,2),FUN=function(x){if(x==0)x=1 else x=x})),
    c(1,2),FUN=function(x){if(x<1)x=0 else if(x>nbin)x=nbin+1 else x=x}),1,paste,collapse=".")

  if (type=="ID") return(new.ids)
  else if (type=="EO") return(sapply(new.ids%in%train.ids,FUN=function(x){if(x==T) x=0 else if(x==F)x=1}))
  }

#**************************************************************************
#**************************************************************************
#**************************************************************************

# global variables:
minTemp=3
maxTemp=13
minWood=0
maxWood=70

#**************************************************************************
#assumed response surface (lrm)
temperature<-seq(minTemp,maxTemp,length=25)
woodland<-seq(minWood,maxWood,length=25)

dat=data.frame(expand.grid(woodlandCover=woodland,temp=temperature))
response=inv.logit(-170+40*dat$temp-2.5*dat$temp^2+.35*dat$woodlandCover)
windows()
wireframe(response~dat$woodlandCover*dat$temp,,
        scales=list(arrows=F,tck=.6,distance=.7,z=list(at=c(0,.5,1),labels=c("0.0","","1.0"),cex=2),
        x=list(at=c(10,30,50,70),cex=2),y=list(cex=2),col="black"),
        zlim=c(0,1),zlab=list('True response',rot=94,cex=2),
        xlab=list("Woodland cover [%]",rot=33,cex=2),ylab=list("Temperature [°C]",rot=-26,cex=2),
        par.settings = list(axis.line = list(col = "transparent")), screen=list(z=50,x=-70,y=0),
        alpha.regions=.7)

rm(list=c("woodland","temperature","dat","response"))

#************************************************************************
#************************************************************************
#************************************************************************
# case 1: species niche entirely encompassed by data;
```

```
# training data + future
CurrentTemperature=runif(1000,min=minTemp,max=maxTemp)
woodlandCover=runif(1000,min=minWood,max=maxWood)
occurrence=species(CurrentTemperature,woodlandCover)
occurrence<-sapply(occurrence,function(x){rbinom(1,1,x)})
train1=data.frame(occurrence,temp=CurrentTemperature,woodlandCover)
plot(train1)
cor(train1)

FutureTemperature=CurrentTemperature+3
occurrence=species(FutureTemperature,woodlandCover)
occurrence<-sapply(occurrence,function(x){rbinom(1,1,x)})
future1=data.frame(occurrence,temp=FutureTemperature,woodlandCover)

# independent test data for current conditions
CurrentTemperature=runif(1000,min=minTemp,max=maxTemp)
woodlandCover=runif(1000,min=minWood,max=maxWood)
occurrence=species(CurrentTemperature,woodlandCover)
occurrence<-sapply(occurrence,function(x){rbinom(1,1,x)})
test1=data.frame(occurrence,temp=CurrentTemperature,woodlandCover)

#************************************
# fit models

# generalised additive model
gam1=gam(occurrence~s(temp)+s(woodlandCover),binomial,data=train1)
# boosted regression tree
brt1 <- gbm.step(data=train1,gbm.x = c(2:3),gbm.y = 1,family = "bernoulli",
   tree.complexity = 1,learning.rate = 0.02,bag.fraction = 0.75)

#**************************************************
# predictions under current conditions
pred.gam=predict(gam1,newdata=test1,type="response")
pred.brt=predict.gbm(brt1,newdata=test1,n.trees=brt1$gbm.call$best.trees, type="response")

# plot fitted values
windows()
par(mfrow=c(2,2))
myplot(test1,pred.gam,main="GAM - current")
myplot(test1,pred.brt,main="BRT - current")

# plot response curves
windows()
par(mfrow=c(2,2))
inflated.response(gam1,train1[,2:3],main="GAM",method="stat6")
inflated.response(brt1,train1[,2:3],main="BRT",method="stat6")

#*********************************
# projections into future
pred.gam=predict(gam1,newdata=future1,type="response")
pred.brt=predict.gbm(brt1,newdata=future1,n.trees=brt1$gbm.call$best.trees, type="response")

# plot fitted values
windows()
par(mfrow=c(2,2))
myplot(future1,pred.gam,main="GAM - future")
myplot(future1,pred.brt,main="BRT - future")
```

```
#*****************************************************************************
#*****************************************************************************
#*****************************************************************************
# case 2: species niche truncated

# training data + future
CurrentTemperature=runif(1000,min=minTemp,max=maxTemp)
woodlandCover=numeric(1000)
# woodland occurs above 3°C and below 13°C with maximum woodland cover between 7 and 9°C
woodlandCover[CurrentTemperature>3&CurrentTemperature<=7]=
  sapply((CurrentTemperature[CurrentTemperature>3&CurrentTemperature<=7]-3)*maxWood/4,
  function(x){runif(1,min=minWood,max=x)})
woodlandCover[CurrentTemperature>7&CurrentTemperature<9]=

runif(length(woodlandCover[CurrentTemperature>7&CurrentTemperature<9]),min=minWood,max=maxWood)
woodlandCover[CurrentTemperature>9&CurrentTemperature<13]=
  sapply((13-CurrentTemperature[CurrentTemperature>9&CurrentTemperature<13])*maxWood/4,
  function(x){runif(1,min=minWood,max=x)})
occurrence=species(CurrentTemperature,woodlandCover)
occurrence<-sapply(occurrence,function(x){rbinom(1,1,x)})
train2=data.frame(occurrence,temp=CurrentTemperature,woodlandCover)
plot(train2)
cor(train2)

FutureTemperature=CurrentTemperature+3
occurrence=species(FutureTemperature,woodlandCover)
occurrence<-sapply(occurrence,function(x){rbinom(1,1,x)})
future2=data.frame(occurrence,temp=FutureTemperature,woodlandCover)
plot(future2)
cor(future2)

# test data current conditions
CurrentTemperature=runif(1000,min=minTemp,max=maxTemp)
woodlandCover=numeric(1000)
woodlandCover[CurrentTemperature>3&CurrentTemperature<=7]=
  sapply((CurrentTemperature[CurrentTemperature>3&CurrentTemperature<=7]-3)*maxWood/4,
  function(x){runif(1,min=minWood,max=x)})
woodlandCover[CurrentTemperature>7&CurrentTemperature<9]=

runif(length(woodlandCover[CurrentTemperature>7&CurrentTemperature<9]),min=minWood,max=maxWood)
woodlandCover[CurrentTemperature>9&CurrentTemperature<13]=
  sapply((13-CurrentTemperature[CurrentTemperature>9&CurrentTemperature<13])*maxWood/4,
  function(x){runif(1,min=minWood,max=x)})
occurrence=species(CurrentTemperature,woodlandCover)
occurrence<-sapply(occurrence,function(x){rbinom(1,1,x)})
test2=data.frame(occurrence,temp=CurrentTemperature,woodlandCover)


#******************************************
# fit models

# generalised additive model
gam2=gam(occurrence~s(temp)+s(woodlandCover),binomial,data=train2)
# boosted regression tree
brt2 <- gbm.step(data=train2,gbm.x = c(2:3),gbm.y = 1,family = "bernoulli",
    tree.complexity = 1,learning.rate = 0.01,bag.fraction = 0.75)


#************************************************
# predictions under current conditions
pred.gam=predict(gam2,newdata=test2,type="response")
```

```
pred.brt=predict.gbm(brt2,newdata=test2,n.trees=brt2$gbm.call$best.trees, type="response")

# plot fitted values
windows()
par(mfrow=c(2,2))
myplot(test2,pred.gam,main="GAM - current")
myplot(test2,pred.brt,main="BRT - current")

# plot response curves
windows()
par(mfrow=c(2,2))
inflated.response(gam2,train2[,2:3],main="GAM",method="stat6",disp='eo.mask')
inflated.response(brt2,train2[,2:3],main="BRT",method="stat6",disp='eo.mask')

#*************************************************
# projections into future
pred.gam=predict(gam2,newdata=future2,type="response")
pred.brt=predict.gbm(brt2,newdata=future2,n.trees=brt2$gbm.call$best.trees, type="response")

# plot fitted values
windows()
par(mfrow=c(2,2))
myplot(future2,pred.gam,main="GAM - future")
myplot(future2,pred.brt,main="BRT - future")




#*****************************************************************************
#*****************************************************************************
#*****************************************************************************
# case 3: edge niche

# training data + future
CurrentTemperature=runif(1000,min=minTemp,max=maxTemp)
woodlandCover=numeric(1000)
woodlandCover[CurrentTemperature<10.5]=
  runif(length(woodlandCover[CurrentTemperature<10.5]),min=minWood,max=maxWood)
occurrence=species(CurrentTemperature,woodlandCover)
occurrence<-sapply(occurrence,function(x){rbinom(1,1,x)})
train3=data.frame(occurrence,temp=CurrentTemperature,woodlandCover)
plot(train3)
cor(train3)

FutureTemperature=CurrentTemperature+3
occurrence=species(FutureTemperature,woodlandCover)
occurrence<-sapply(occurrence,function(x){rbinom(1,1,x)})
future3=data.frame(occurrence,temp=FutureTemperature,woodlandCover)
plot(future3)
cor(future3)

# test data current conditions
CurrentTemperature=runif(1000,min=minTemp,max=maxTemp)
woodlandCover=numeric(1000)
woodlandCover[CurrentTemperature<10.5]=
  runif(length(woodlandCover[CurrentTemperature<10.5]),min=minWood,max=maxWood)
occurrence=species(CurrentTemperature,woodlandCover)
occurrence<-sapply(occurrence,function(x){rbinom(1,1,x)})
test3=data.frame(occurrence,temp=CurrentTemperature,woodlandCover)


#******************************************
```

```
# fit models

# generalised additive model
gam3=gam(occurrence~s(temp)+s(woodlandCover),binomial,data=train3)
# boosted regression tree
brt3 <- gbm.step(data=train3, gbm.x = c(2:3), gbm.y = 1, family = "bernoulli",
   tree.complexity = 1, learning.rate = 0.02, bag.fraction = 0.75)

#********************************************
# predictions under current conditions
pred.gam=predict(gam3,newdata=test3,type="response")
pred.brt=predict.gbm(brt3,newdata=test3,n.trees=brt3$gbm.call$best.trees, type="response")

# plot fitted values
windows()
par(mfrow=c(2,2))
myplot(test3,pred.gam,main="GAM - current")
myplot(test3,pred.brt,main="BRT - current")

# plot response curves
windows()
par(mfrow=c(2,2))
inflated.response(gam3,train3[,2:3],main="GAM",method="stat6",disp='eo.mask')
inflated.response(brt3,train3[,2:3],main="BRT",method="stat6",disp='eo.mask')

#************************************************
# projections into future
pred.gam=predict(gam3,newdata=future3,type="response")
pred.brt=predict.gbm(brt3,newdata=future3,n.trees=brt3$gbm.call$best.trees, type="response")

# plot fitted values
windows()
par(mfrow=c(2,2))
myplot(future3,pred.gam,main="GLM - future")
myplot(future3,pred.brt,main="BRT - future")
```

D.2 Details for simulated data example

We simulated a virtual species (Zurell et al. 2010, chapter 2) from a logistic regression model with two environmental variables, temperature and woodland cover. The virtual species showed a unimodal response to temperature and a linear positive response to percent woodland cover, in an additive model (cf. Fig. 5.2a):

$$Y_i = Bernoulli(p_i)$$

$$\ln\left(\frac{p_i}{1-p_i}\right) = a + b_1 \times temperature_i + b_2 \times (temperature_i)^2 + b_3 \times woodland_i + \varepsilon$$

$$\begin{array}{llll}
a = -170 & & \min(temperature) = 3 & \\
b_1 = 40 & i = 1 \cdots 1000 & \max(temperature) = 13 & \varepsilon \sim \mathrm{N}(\mu = 0, \sigma = 3) \\
b_2 = -2.5 & & \min(woodland) = 0 & \\
b_3 = 0.35 & & \max(woodland) = 70 &
\end{array}$$

Three species were created whose niches were differently covered by data representing the situations of Fig. 5.1. (1) The niche of species 1 was entirely represented by data. Temperature and percent woodland cover at site *i* were drawn from uniform distributions between their minimum and maximum values (Fig. D.1). (2) The niche of species 2 was truncated meaning that no samples existed for parts of the environmental niche of the species. Here, we assumed that high percent woodland cover would only occur within a specific temperature range (7-9 °C) and would linearly decline towards extreme temperatures (Fig. 5.2). (3) The niche of species 3 coincided with the edge of the sampled environmental space. In this case, we assumed zero percent woodland cover for all sites *i* with temperatures >10.5 °C (Fig. D.3). Significant correlations between environmental variables were only found for species 3 ($\rho = -0.46$). For all three cases, climate warming was simulated by increasing the temperature values of sites *i* in the training data by +3 °C. The entire code necessary to repeat the simulated data example is contained in Appendix D.1.

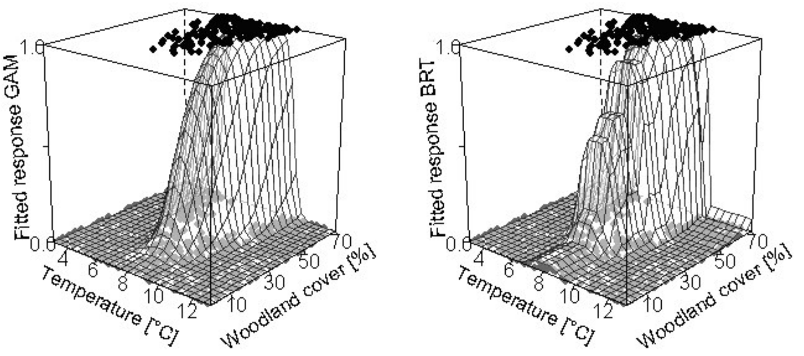


Figure D.1. Response surfaces for simulated species 1 whose niche is entirely encompassed within sample space. Both methods, GAM (left) and BRT (right), show congruent model behaviour.

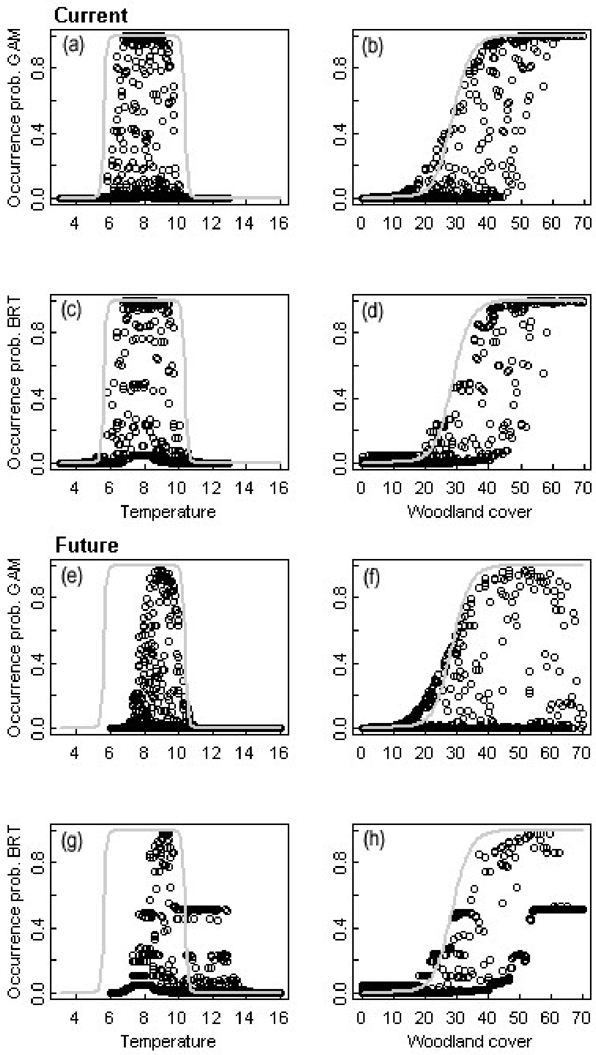


Figure D.2. Fitted values for simulated species 2 with truncated niche. Panels show the fitted values of GAM (a-b, e-f) and BRT (c-d, g-h) plotted along temperature gradient (left) and woodland cover gradient (right) for predictions to current environment (a-d) and for predictions under climate warming (+3 °C; e-h). Grey lines depict true response of species 2.

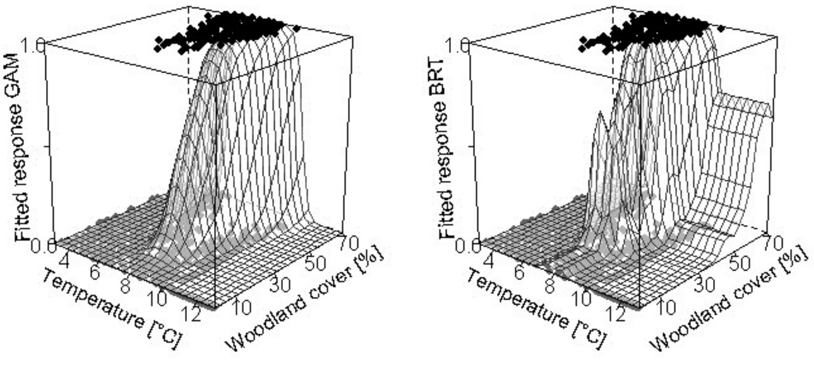


Figure D.3. Response surfaces for simulated species 3 whose niche edge coincides with edge of sample space. BRT (right) shows erroneous extrapolation behaviour in those parts of the environment space where no samples exist beyond the species niche edge.

D.3 Method descriptions for visualisation tools

Here, we describe the environmental overlap masks and inflated response curves in more details. Respective R codes are contained in Appendix D.1.

Environmental overlap mask

Function call: eo.mask( )

Description: The environmental overlap mask is an extension of MaxEnt's multivariate environmental similarity surface (MESS) maps (Elith *et al.*, 2010). The latter are BIOCLIM-style estimates that take the full gradients of the environmental variables that are covered by data, extend these into a hyper-dimensional rectangle and define all environmental conditions outside that rectangle or box as novel conditions. We could think of these boxes as 'implied sample space' because they pretend that all possible combinations of environmental variables within the box are represented in the sample data which may not be the case (Fig. 5.1). Now, the environmental overlap mask splits these hyper-dimensional rectangles or boxes into smaller bins. Then, it compares the bins in the test or prediction data set to the bins in the training data and defines all non-overlapping bins as novel environmental conditions. Thus, depending on the number of bins the box is split into, the environmental overlap mask will also allow identifying those parts of the box that are within the sampled ranges of each predictor variable treated individually but are nevertheless outside the sample space. Note that a bin number of one equates to the border that distinguishes novel space (negative values) in MESS maps.

Arguments: eo.mask( ) takes four arguments, two of which are obligatory.

- traindata must be a data.frame (obligatory)
- newdata must be a data.frame (obligatory)
- nbin determines the number of bins the environmental gradients are split into (default nbin=5). Thereby, nbin refers to the number of bins each univariate predictor is split into. The actual number of bins is then $nbin^n$ where n is the number of predictors.
- type defines the output. This could either be a vector of length nrow(newdata) containing for each entry in newdata zeros for analogue environments and ones for novel environments (type='EO', the default) or a character vector returning for each entry in newdata a unique identifier for the bin the data point belongs to (type='ID'). The latter may help distinguishing data entries from sample space, 'implied sample space' or novel space beyond that.

Required R packages: base.

Inflated response curves

Function call: inflated.response( )

Description: Inflated response curves are an abstracted 2D version of multidimensional response surfaces that help to visualise the combined effects of all variables in the model over their full range. They show the effect of a variable on the response while accounting not only for the average effects of the other variables but also for minimum and maximum (and median and quartile) values. Thus, the response plot for any one variable consists of many response curves representing all possible combinations of all other variables in the model. Because the number of combinations grows exponentially with the number of variables and restricts computational feasibility, we use Latin hypercube sampling to reduce dimensionality for large numbers of variables. This is simply a means to efficiently sample a representative subset from all possible combinations of environmental predictors (Carnell, 2009). Note that due to stochasticity different replicates of inflated response plots may differ depending on the number of variables and the Latin hypercube sample size.

Arguments: inflated.response( ) takes 17 arguments, two of which are obligatory.

- object denotes the model object for which response plots are desired, e.g. a GAM model (obligatory)
- predictors is as data.frame containing the predictor variables of object (usually the training data) (obligatory)
- select.columns allows to determine a subset of predictors for which inflated response plots are to be drawn (defaults to NULL meaning that one plot is made for each column of predictors)
- label can be a character vector of names used to label the x axes of the plots (defaults to NULL meaning that column names of predictors are used for labelling)
- ylab takes a character string for labelling the y axis (defaults to ‘Occurrence probabilities’).
- len determines the number of data points used to draw the response curves (defaults to 50)
- lhsample determines the number of Latin hypercube samples (defaults to 100 meaning that 100 LH samples are drawn if more than 100 combinations of environmental predictor values exist)

- method determines the summary statistics that are used to characterise the predictors. ‘mean’ corresponds to conventional partial dependence plots. ‘stat3’ (the default) considers mean, minimum and maximum values of predictors. ‘stat6’ considers min, mean, median, max and quartiles. Thus, 3^{n-1} combinations of environmental predictor values exist for ‘stat3’ and 6^{n-1} for ‘stat6’ where n is the number of predictors in object.
- disp can take options ‘all’ (the default) or ‘eo.mask’. In the latter case, eo.mask( ) is used to mask all combinations outside the sample space as novel conditions. These parts of the response curves can then be displayed differently.
- overlay.mean takes a Boolean value determining whether the mean response should be overlayed over the inflated response curves (defaults to ‘True’)
- col.curves (defaults to ‘grey’), col.novel (defaults to ‘grey’), col.mean (defaults to ‘black’) are graphic parameters determining the color of the response curves, those parts of the curves that are identified as novel by eo.mask( ), and the overlayed mean response curve.
- lwd (defaults to 1), lwd.mean (defaults to 2), lwd.known (defaults to 2) are graphic parameters. If disp=’all’ then lwd determines the line width of all curves. If disp=’eo.mask’ then lwd determines the line width of the novel parts and lwd.known the line width for those predictor combinations present in the sample space. lwd.mean determines the line width of the overlayed mean response curve.
- ylim sets the y axis limits (defaults to c(0,1))

Required R packages: base, lhs (Latin Hypercube Sample package), any packages relating to specific SDM methods one wants to include (e.g. gam or gbm library), additional code for eo.mask( ).

D.4 Swiss black grouse example

A case study for Swiss black grouse was developed in Zurell et al. (2011; chapter 4) and we here give only a very brief description of the species and data. In the Swiss Alps, black grouse (*Tetrao tetrix*) mainly occur in treeline habitats at altitudes of up to 2500 m above sea level. Species distribution data at 1 km resolution were obtained from the Swiss Breeding Bird Atlas (Schmid et al. 1998). Environmental predictors included climatic variables as well as land use and vegetation data at 1 km resolution. These were pre-selected so that bivariate Spearman correlations were below $|r|=0.7$. Climate data were derived from the BIOCLIM database (Swiss Federal Research Institute WSL). We here used only the most important climatic predictors, namely mean annual temperature, potential solar radiation in summer months (June-August) and winter precipitation (sums December-February). Land use and vegetation data were compiled from the land use and land cover database GEOSTAT (Swiss Federal Statistical Office). From these, we chose the three most important predictors namely percentage cover of scattered forest, bushy forest and grassland (Fig. D.4). For illustrative purposes, we chose a rather extreme climate change scenario from the HadCM3 global circulation model which corresponded to the socio-economic scenario A1F1 for the year 2100 downscaled to a 1 km resolution (Swiss Federal Research Institute WSL). For this scenario, mean annual temperature increased by +7.7 °C and winter precipitation increased by +48 mm on average.

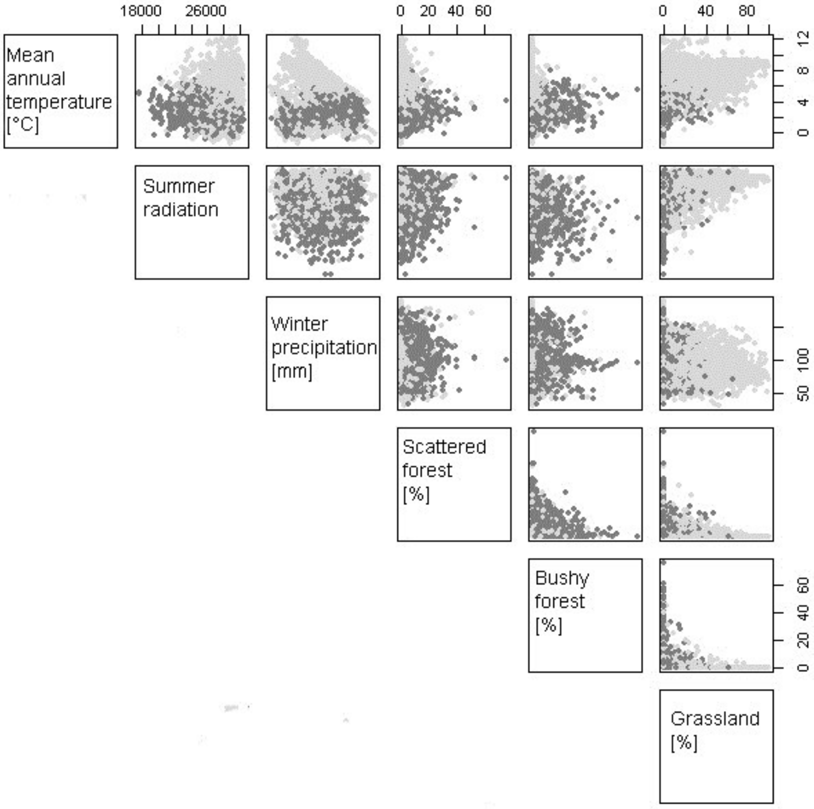


Figure D.4. Scatterplots of black grouse presences (dark grey) and absences (light grey) along environmental gradients. Although the single environmental predictors cover large gradients, only portions of all possible combinations were present in the sample.

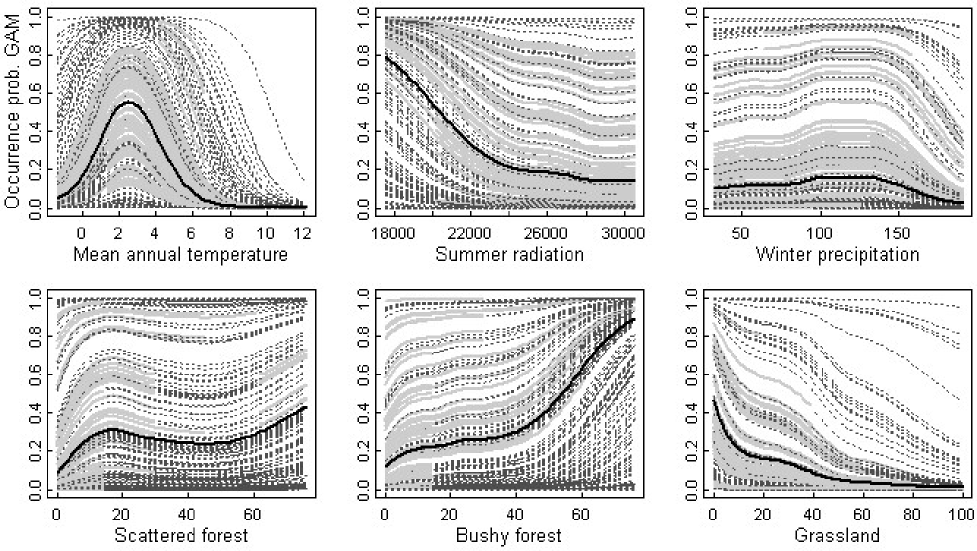


Figure D.5. Inflated response curves for GAM along the sampled environmental gradients. Bold black lines show the mean effects as provided by conventional partial dependence plots. Light grey lines and dotted dark grey lines depict predictor effects over the full range of the other predictors (minimum, maximum, median, mean and quartiles). Light grey lines indicate combinations of environmental predictors that were observed in the sample space while dotted dark grey lines indicate extrapolations to novel, unsampled combinations. The plots represent *n*=150 Latin hypercube samples from all possible combinations of environmental predictors.

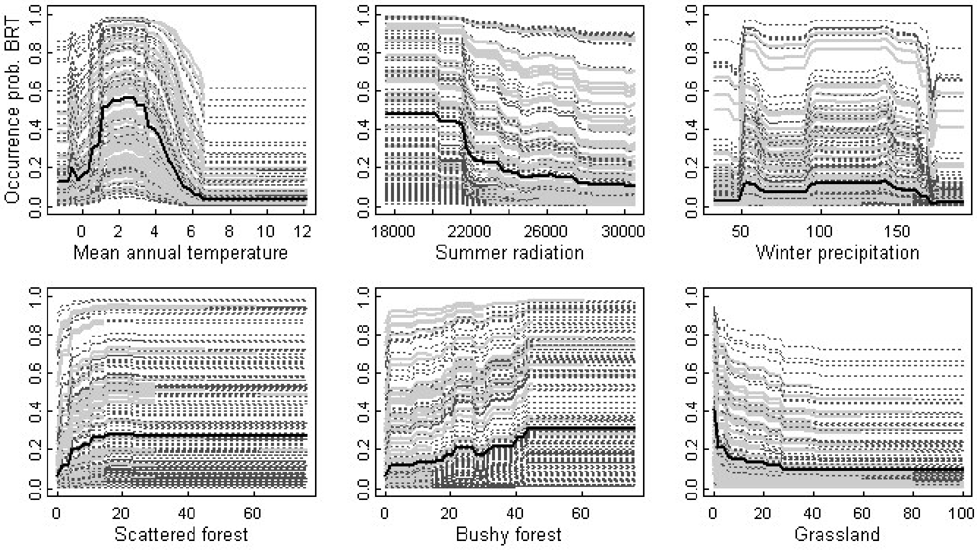
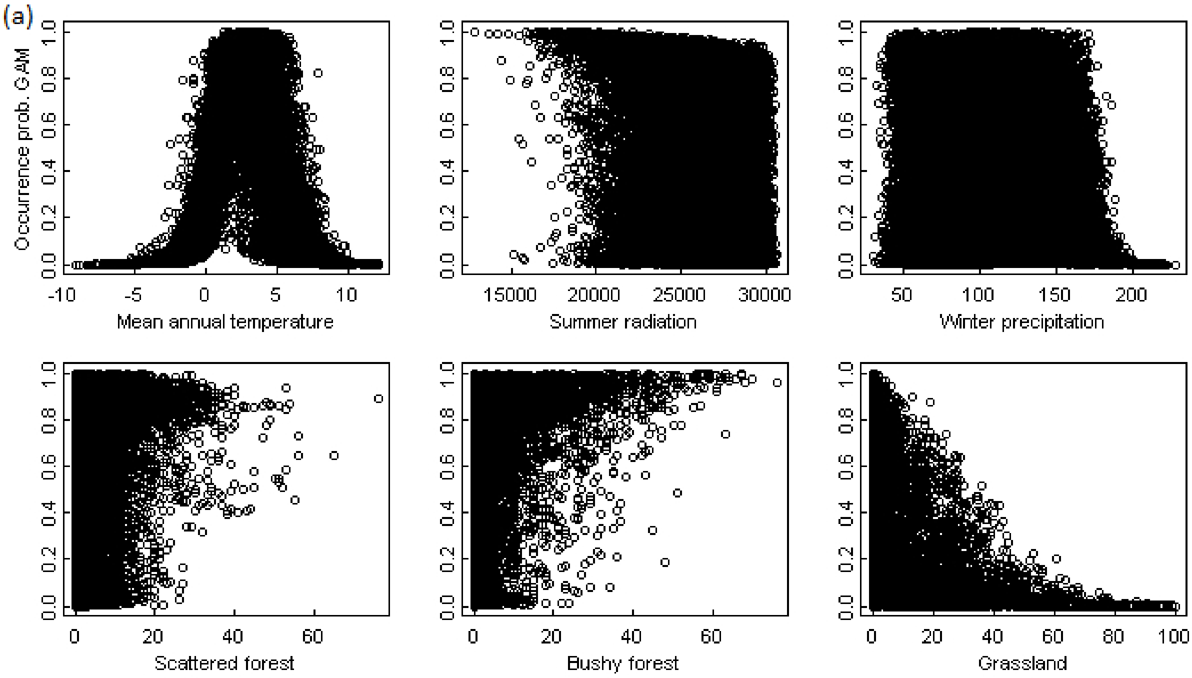
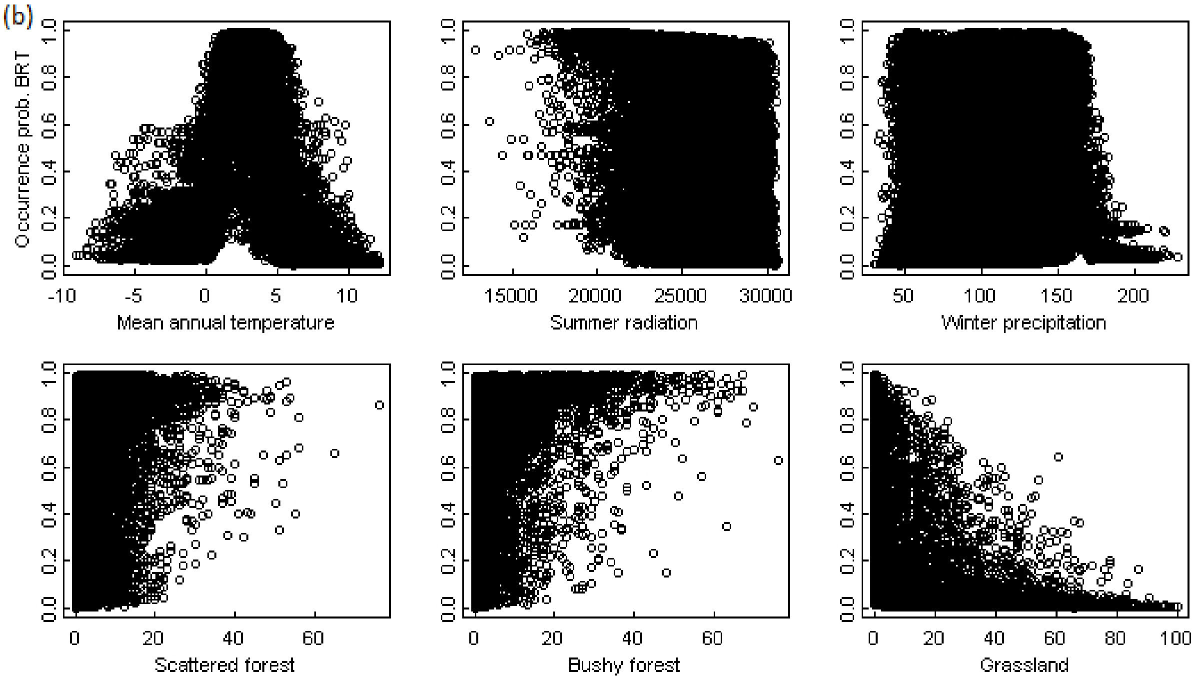


Figure D.6. Inflated response curves for BRT along the sampled environmental gradients. Bold black lines show the mean effects as provided by conventional partial dependence plots. Light grey lines and dotted dark grey lines depict predictor effects over the full range of the other predictors (minimum, maximum, median, mean and quartiles). Light grey lines indicate combinations of environmental predictors that were observed in the sample space while dotted dark grey lines indicate extrapolations to novel, unsampled combinations. The plots represent *n*=150 Latin hypercube samples from all possible combinations of environmental predictors.


(a)
Occurrence prob. GAM
0.0
0.2
0.4
0.6
0.8
1.0
-10
-5
0
5
10
Mean annual temperature
15000
20000
25000
30000
Summer radiation
50
100
150
200
Winter precipitation
0
20
40
60
Scattered forest
0
20
40
60
Bushy forest
0
20
40
60
80
100
Grassland


(b)
Occurrence prob. BRT
0.0
0.2
0.4
0.6
0.8
1.0
-10
-5
0
5
10
Mean annual temperature
15000
20000
25000
30000
Summer radiation
50
100
150
200
Winter precipitation
0
20
40
60
Scattered forest
0
20
40
60
Bushy forest
0
20
40
60
80
100
Grassland

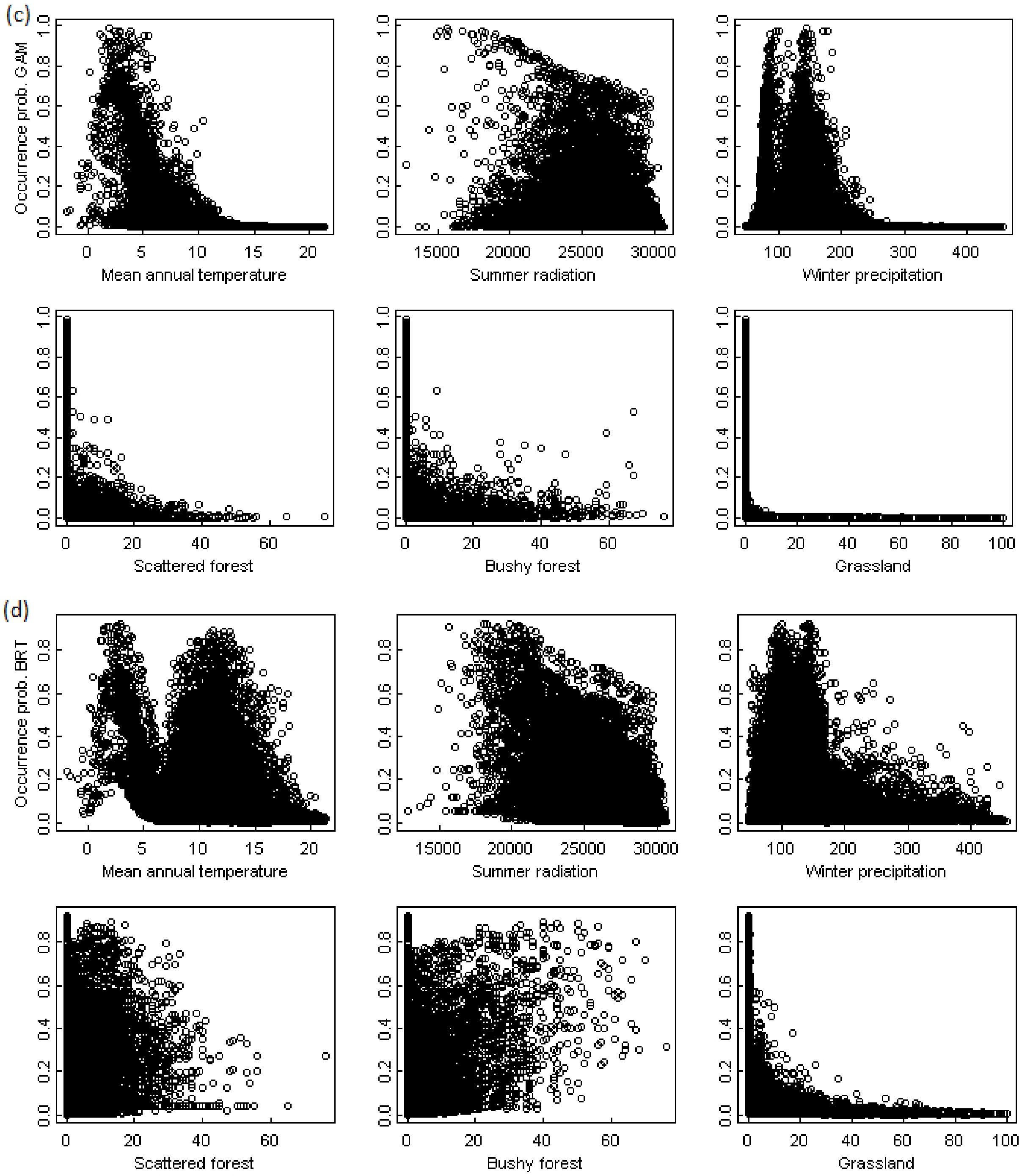


Figure D.7. Predictions for Swiss black grouse. Panels show the fitted values of GAM (a, c) and BRT (b, d) plotted along the environmental gradients for predictions to current environment (a-b) and for predictions to climate change scenario for the year 2100 (A1F1 scenario from HadCM3 with average temperature increase of 7.7 °C and average precipitation increase of 48 mm for Switzerland). While fitted values are largely congruent for current predictions (a-b), we see marked differences in fitted values for the climate change scenario (c-d) most noticeably in the temperature and forest predictors. While GAM predicts low occurrence probabilities for high temperatures (c) as is also suggested by current fits (a) and which could imply a physiological limit to temperature, BRT predicts high occurrence probabilities even for high temperatures (d).

Bibliography

Akaike, H. 1974. A new look at the statistical model identification. - IEEE Transactions on Automatic Control 19: 716-723.

Akçakaya, H. R. 2000. Viability analyses with habitat-based metapopulation models. - Population Ecology 42: 45-53.

Akçakaya, H. R. et al. 2006. Use and misuse of the IUCN Red List Criteria in projecting climate change impacts on biodiversity. - Global Change Biology 12: 2037-2043.

Albert, C. H. and Thuiller, W. 2008. Favourability functions versus probability of presence: advantages and misuses. - Ecography 31: 417-422.

Albert, C. H. et al. 2008. Land-use change and subalpine tree dynamics: colonization of *Larix decidua* in French subalpine grasslands. - Journal of Applied Ecology 45: 659-669.

Albert, C. H. et al. 2010. Sampling in ecology and evolution – bridging the gap between theory and practice. – Ecography 33: 1028-1037.

Allee, W. C. 1931. Animal aggregations. A study in general sociology. - University of Chicago Press.

Allouche, O. et al. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). - Journal of Applied Ecology 43: 1223-1232.

Anderson, B. J. et al. 2009. Dynamics of range margins for metapopulations under climate change. - Proceedings of the Royal Society B 276: 1415-1420.

Araújo, M. B. and Guisan, A. 2006. Five (or so) challenges for species distribution modelling. - Journal of Biogeography 33: 1677-1688.

Araújo, M. B. and Luoto, M. 2007. The importance of biotic interactions for modelling species distributions under climate change. - Global Ecology and Biogeography 16: 743-753.

Araújo, M. B. and New, M. 2007. Ensemble forecasting of species distributions. - Trends in Ecology and Evolution 22: 42-47.

Araújo, M. B. et al. 2008. Quaternery climate changes explain diversity among reptiles and amphibians. - Ecography 31: 8-15.

Araújo, M. B. et al. 2005. Validation of species-climate impact models under climate change. - Global Change Biology 11: 1504-1513.

Araújo, M. B. and Rahbek, C. 2006. How does climate change affect biodiversity? - Science 313: 1396-1397.

Araújo, M. B. et al. 2002. Dynamics of extinction and the selection of nature reserves. - Proceedings of the Royal Society B 269: 1971-1980.

Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. - Ecological Modelling 157: 101-118.

Austin, M. P. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. – Ecological Modelling 200: 1-19.

Austin, M. P. et al. 2006. Evaluation of statistical models used for predicting plant species distributions: Role of artificial data and theory. - Ecological Modelling 199: 197-216.

Austin, M. P. and Gaywood, M. J. 1994. Current problems of environmental gradients and species response curves in relation to continuum theory. - Journal of Vegetation Science 5: 473-482.

Bakkenes, M. et al. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. - Global Change Biology 8: 390-407.

Begon, M. et al. 2006. Ecology: From individuals to ecosystems. - Wiley-Blackwell.

Beissinger, S. R. and Westphal, M. I. 1998. On the use of demographic models of population viability in endangered species management. - Journal of Wildlife Management 62: 821-841.

Bellasio, R. et al. 2005. Algorithms to account for topographic shading effects and surface temperature dependence on terrain elevation in diagnostic meteorological models. - Boundary-Layer Meteorology 114: 595-614.

Berger, U. et al. 1999. Virtual biologists observe virtual grasshoppers: an assessment of different mobility parameters for the analysis of movement patterns. - Ecological Modelling 115: 119-127.

Beven, K. J. and Kirkby, M. J. 1979. A physically-based variable contributing area model of basin hydrology. - Hydrological Science Bulletin 24: 43--69.

Bolker, B. M. 2008. Ecological models and data in R. - Princeton University Press.

Bonsall, M. B. and Hassel, M. P. 2000. The effects of metapopulation structure on indirect interactions in host-parasitoid assemblages. - Proceedings of the Royal Society of London 267: 2207-2212.

Bosch, J. et al. 2007. Climate change and outbreaks of amphibian chytridiomycosis in a montane area of Central Spain; is there a link? - Proceedings of the Royal Society B 274: 253-260.

Bossel, H. 1992. Real-structure process description as the basis of understanding ecosystems and their development. - Ecological Modelling 63: 261-276.

Both, C. et al. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? - Journal of Animal Ecology 78: 73-83.

Broennimann, O. and Guisan, A. 2008. Predicting current and future biological invasions: both native and invaded ranges matter. - Biology Letters 4: 585-589.

Broennimann, O. et al. 2007. Evidence of climatic niche shift during biological invasion. - Ecology Letters 10: 701-709.

Brook, B. W. et al. 2000. Predictive accuracy of population viability analysis in conservation biology. - Nature 404: 385-387.

Brook, B. W. et al. 2009. Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. - Biology Letters 5: 723-725.

Buckley, L. B. and Roughgarden, J. 2004. Biodiversity conservation: Effects of changes in climate and land use. - Nature 430: 34.

Buisson, L. et al. 2010. Uncertainty in ensemble forecasting of species distribution. - Global Change Biology 16: 1145-1157.

Burgman, M. A. et al. 1993. Risk assessment in conservation biology. - Chapman and Hall.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multi-model inference: A practical information-theoretic approach. - Springer.

Burton, O. J. et al. 2010. Trade-offs and the evolution of life-histories during range expansion. - Ecology Letters 13: 1210-1220.

Cabral, J. S. 2009. Demographic processes determining the range dynamics of plant species, and their consequences for biodiversity maintenance in the face of environmental change. – University of Potsdam.

Cabral, J. S. and Schurr, F. M. 2010. Estimating demographic models for the range dynamics of plant species. - Global Ecology and Biogeography 19: 85-97.

Caizergues, A. and Ellison, L. N. 2002. Natal dispersal and its consequences in Black Grouse *Tetrao tetrix*. - Ibis 144: 478-487.

Carnell, R. 2009. lhs: Latin Hypercube Samples. - R package version 0.5.

Cheung, W. W. L. et al. 2009. Projecting global marine biodiversity impacts under climate change scenarios. - Fish and Fisheries 10: 235-251.

Clark, J. S. and Gelfand, A. E. 2006. A future for models and data in environmental science. - Trends in Ecology and Evolution 21: 375-380.

Colwell, R. K. and Rangel, T. F. 2009. Hutchinson's duality: The once and future niche. - Proceedings of the National Academy of Sciences 106: 19651-19658.

Comins, H. N. et al. 1992. The spatial dynamics of host-parasitoid systems. - Journal of Animal Ecology 61: 735-748.

Crist, T. O. and Wiens, J. A. 1995. Individual movements and estimation of population size in darkling beetles (Coleoptera: Tenebrionidae). - Journal of Animal Ecology 64: 733-746.

Davis, A. J. et al. 1998. Making mistakes when predicting shifts in species range in response to global warming. - Nature 391: 783-786.

De Marco, P., Jr. et al. 2008. Spatial analysis improves species distribution modelling during range expansion. - Biology Letters 4: 577-580.

DeAngelis, D. L. and Mooij, W. M. 2005. Individual-based modeling of ecological and evolutionary processes. - Annual Review of Ecology, Evolution, and Systematics 36: 147-168.

del Barrio, G. et al. 2006. Integrating multiple modelling approaches to predict the potential impacts of climate change on species' distributions in contrasting regions: comparison and implications for policy. - Environmental Science and Policy 9: 129-147.

Diez, J. M. and Pulliam, H. R. 2007. Hierarchical analysis of species distributions and abundance across environmental gradients. - Ecology 88: 3144-3152.

Dobrowski, S. Z. et al. 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. - Ecological Monographs 81: 241-257.

Dormann, C. F. 2007. Promising the future? Global change projections of species distributions. - Basic and Applied Ecology 8: 387-397.

Dormann, C. F. et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. - Ecography 30: 609-628.

Dormann, C. F. et al. 2008. Components of uncertainty in species distribution analysis: A case study of the Great Grey Shrike. - Ecology 89: 3371-3386.

Dubayah, R. and Loechel, S. 1997. Modeling topographic solar radiation using GOES data. - American Meteorological Society 36: 141-154.

Dunning, J. B., Jr. et al. 1995. Spatially explicit population models: current forms and future uses. - Ecological Applications 5: 3-11.

Elith, J. and Graham, C. H. 2009. Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. - Ecography 32: 66-77.

Elith, J. et al. 2006. Novel methods improve prediction of species' distribution from occurence data. - Ecography 29: 129-151.

Elith, J. et al. 2010. The art of modelling range-shifting species. - Methods in Ecology and Evolution 1: 330-342.

Elith, J. and Leathwick, J. R. 2009. Species distribution models: ecological explanation and prediction across space and time. - Annual Review of Ecology, Evolution, and Systematics 40: 677-697.

Elith, J. et al. 2008. A working guide to boosted regression trees. - Journal of Animal Ecology 77: 802-813.

Engler, R. et al. 2011. 21st century climate change threatens mountain flora unequally across Europe. - Global Change Biology 17: 2330-2341.

Fielding, A. H. 2002. What are the appropriate characteristics of an accuracy measure? - In: Scott, J. M. et al. (eds.), Predicting species occurrences: issues of accuracy and scale. Island Press, pp. 271-280.

Fielding, A. H. and Bell, J. F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. - Environmental Conservation 24: 38-49.

Fielding, A. H. and Haworth, P. F. 1995. Testing the generality of bird-habitat models. - Conservation Biology 9: 1466-1481.

Fischer, J. and Lindenmayer, D. B. 2002. Treating the nestedness temperature calculator as a black box can lead to false conclusions. - Oikos 99: 193-199.

Fitzpatrick, M. C. and Hargrove, W. W. 2009. The projection of species distribution models and the problem of non-analog climate. - Biodiversity Conservation 18: 2255-2261.

Fortin, M.-J. et al. 1989. Spatial autocorrelation and sampling design in plant ecology. - Vegetatio 83: 209-222.

Franklin, J. 2010. Moving beyond static species distribution models in support of conservation biogeography. - Diversity and Distributions 16: 321-330.

Gallien, L. et al. 2010. Predicting potential distributions of invasive species: where to go from here? - Diversity and Distributions 16: 331-342.

Garrison, B. A. and Lupo, T. 2002. Predicting species occurences - issues of accuracy and scale. - In: Scott, J. M. et al. (eds.). Island Press, pp. 367-375.

Gates, D. M. 2003. Biophysical ecology. - Courier Dover Publications.

Gelman, A. and Hill, J. 2007. Data analysis using regression and multilevel/hierarchical models. - Cambridge University Press.

Gitay, H. and Noble, I. R. 1997. What are functional types and how should we seek them? - In: Smith, T. M. et al. (eds.), Plant functional types: their relevance to ecosystem properties and global change. Cambride University Press, pp. 3-19.

Goss-Custard, J. D. et al. 2006. Test of a behavior-based individual-based model: response of shorebird mortality to habitat loss. - Ecological Applications 16: 2215-2222.

Gotelli, N. J. et al. 2009. Patterns and causes of species richness: a general simulation model for macroecology. - Ecology Letters 12: 873-886.

Graf, R. F. et al. 2005. The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. - Landscape Ecology 20: 703-717.

Graf, R. F. et al. 2007. What you see is where you go? Modeling dispersal in mountainous landscapes. - Landscape Ecology 22: 853-866.

Grangier, J. and Lester, P. J. 2011. A novel interference behaviour: invasive wasps remove ants from resources and drop them from a height. - Biology Letters.

Greve, M. and Chown, S. L. 2006. Endemicity biases nestedness metrics: a demonstration, explanation and solution. - Ecography 29: 347–356.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? - Ecological Modelling 115: 129-148.

Grimm, V. et al. 2006. A standard protocol for describing individual-based and agent-based models. - Ecological Modelling 198: 115-126.

Grimm, V. et al. 2010. The ODD protocol: a review and first update. - Ecological Modelling.

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

Grimm, V. et al. 2005a. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. - Science 310: 987-991.

Grimm, V. et al. 2005b. Importance of buffer mechanisms for population viabilty analysis. - Conservation Biology 19: 578-580.

Grimm, V. et al. 2007. Modeling adaptive behavior in event-driven environments: temporally explicit individual-based ecology. - In: Bissonette, J. and Storch, I. (eds.), Temporal dimensions of wildlife ecology: Wildlife responses to variable resources. Springer, pp. 59-73.

Grimm, V. and Storch, I. 2000. Minimum viable population size of capercaillie *Tetrao urogallus*: results from a stochastic model. - Wildlife Biology 6: 219-225.

Grimm, V. et al. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. - Ecological Modelling 115: 275-282.

Gruber, B. et al. 2008. A new method for estimating visitation rates of cryptic animals via repeated surveys of indirect signs. - Journal of Applied Ecology 45: 728-735.

Gu, W. and Swihart, R. K. 2004. Absent or undetected? Effects of non-detection of species occurence on wildlife-habitat models. - Biological Conservation 116: 195-203.

Guisan, A. and Theurillat, J. P. 2000. Equilibrium modeling of alpine plant distribution and climate change: how far can we go? - Phytocoenologia 30: 353-384.

Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. - Ecology Letters 8: 993-1009.

Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. - Ecological Modelling 135: 147-186.

Guisan, A. et al. 2007. What matters for predicting the occurrences of trees: Techniques, data, or species' characteristics? - Ecological Monographs 77: 615-630.

Halle, S. and Halle, B. 1999. Modelling activity synchronisation in free-ranging microtine rodents. - Ecological Modelling 115: 165-176.

Hampe, A. 2004. Bioclimate envelope models: what they detect and what they hide. - Global Ecology and Biogeography 13: 469-476.

Hänninen, H. 1995. Assessing ecological implications of climatic change: Can we rely on our simulation models? - Climate Change 31: 1-4.

Hanski, I. 1998. Metapopulation dynamics. - Nature 396: 41-49.

Hanski, I. 1999. Metapopulation Ecology. - Oxford University Press.

Hanski, I. et al. 2000. Estimating the parameters of survival and migration of individuals in metapopulations. - Ecology 81: 239-251.

Hanski, I. and Gaggiotti, O. E. (eds.) 2004. Ecology, genetics, and evolution of metapopulations. – Elsevier Academic Press.

Hanski, I. and Thomas, C. D. 1994. Metapopulation dynamics and conservation: A spatially explicit model applied to butterflies. - Biological Conservation 68: 167-180.

Hardy, O. J. 2008. Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. - Journal of Ecology 96: 914–926.

Harrell, J., Frank E. 2001. Regression modeling strategies. - Springer-Verlag New York, Inc.

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

Harvell, C. D. et al. 2002. Climate warming and disease risks for terrestrial and marine biota. - Science 296: 2158 - 2162.

Hassell, M. P. 2000. Host-parasitoid population dynamics. - Journal of Animal Ecology 69: 543-566.

Hassell, M. P. et al. 1991. Spatial structure and chaos in insect population dynamics. - Nature 353: 255-258.

Hawkins, B. A. and Porter, E. E. 2003. Does herbivore diversity depend on plant diversity? The case of California butterflies. - American Naturalist 161: 40-49.

Heikkinen, R. K. et al. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. - Progress in Physical Geography 30: 1-27.

Hernandez, P. A. et al. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. - Ecography 29: 773-785.

Higgins, C. L. et al. 2006. The role of stochastic processes in producing nested patterns of species distributions. - Oikos 114: 159–167.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. - International Journal of Climatology 25: 1965-1978.

Hilker, F. M. et al. 2006. Parameterizing, evaluating and comparing metapopulation models with data from individual-based simulations. - Ecological Modelling 199: 476-485.

Hill, J. K. et al. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. - Proceedings of the Royal Society of London - B 266: 1197-1206.

Hirzel, A. and Guisan, A. 2002. Which is the optimal sampling strategy for habitat suitability modelling. - Ecological Modelling 157: 331-341.

Hirzel, A. H. et al. 2001. Assessing habitat-suitability models with a virtual species. - Ecological Modelling 145: 111-121.

Hogeweg, P. 1988. Cellular automata as a paradigm for ecological modeling. - Applied Mathematics and Computation 27: 81-100.

Holman, I. P. et al. 2005a. A regional, multi-sectoral and integrated assessment of the impacts of climate and socio-economic change in the UK. Part II. Results. - Climatic Change 71: 43–73.

Holman, I. P. et al. 2005b. A regional, multi-sectoral and integrated assessment of the impacts of climate and socio-economic change in the UK. Part I. Methodology. - Climatic Change 71: 9–41.

Hosmer, D. W. and Lemeshow, S. 2000. Applied Logistic Regression. - John Wiley and Sons.

Houghton, J. T. et al. (eds.) 2001. Climate change 2001: the scientific basis. - Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Huntley, B. et al. 2004. The performance of models relating species geographical distributions to climate is independent of trophic level. - Ecology Letters 7: 417-426.

Huston, M. A. 2002. Introductory essay: critical issues for improving predictions. - In: Scott, J. M. et al. (eds.), Predicting species occurrences: issues of accuracy and scale. Island Press, pp. 7-21.

Hutchinson, G. E. 1957. Concluding remarks, Cold Spring Harbor Symposium. - Quantitative Biology 22: 415-427.

Jablonski, D. 1986. Background and mass extinctions: the alternation of macroevolutionary regimes. - Science 231: 129-133.

Jeltsch, F. and Moloney, K. 2002. Spatially-explicit vegetation models: what have we learned? – Progress in Botany 63: 326-343.

Jeltsch, F. et al. 2008. The state of plant population modelling in light of environmental change. - Perspectives in Plant Ecology, Evolution and Systematics 9: 171-189.

Jetz, W. et al. 2007. Projected impacts of climate and land-use change on the global diversity of birds. - PLoS Biology 5: e157.

Jiménez-Valverde, A. and Lobo, J. M. 2007. Threshold criteria for conversion of probability of species presence to either–or presence–absence. - Acta Oecologica 31: 361-369.

Kearney, M. 2006. Habitat, environment and niche: what are we modelling? - Oikos 115: 186-191.

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

Kearney, M. et al. 2010. Modelling the ecological niche from functional traits. - Philosophical Transactions of the Royal Society B 365: 3469-3483.

Keith, D. A. et al. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. - Biology Letters 4: 560-563.

King, A. A. and Hastings, A. 2003. Spatial mechanisms for coexistence of species sharing a common natural enemy. - Theoretical Population Biology 64: 431-438.

Kleyer, M. et al. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. - Journal of Ecology 96: 1266-1274.

Kraft, N. J. B. et al. 2007. Trait evolution, community assembly, and the phylogenetic structure of ecological communities. - American Naturalist 170: 271–283.

Lavorel, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. - Functional Ecology 16: 545-556.

Leathwick, J. R. 1998. Are New Zealand's Nothofagus species in equilibrium with their environment? - Journal of Vegetation Science 9: 719-732.

Leathwick, J. R. et al. 2006. Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. - Marine Ecology Progress Series 321: 267-281.

Legendre, P. et al. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. - Ecography 25: 601-615.

Levins, R. 1966. The strategy of model building in population ecology. - American Scientist 54: 421-431.

Lindenmayer, D. B. et al. 2003. How accurate are population models? Lessons from landscape-scale tests in a fragmented system. - Ecology Letters 6: 41-47.

Liu, C. et al. 2005. Selecting thresholds of occurrence in the prediction of species distributions. - Ecography 28: 385-393.

Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: The distinction between - and reconcilation of - 'predictive' and 'explanatory' models. - Biodiversity and Conservation 9: 655-671.

Mac Nally, R. 2001. Interaction strengths and spatial scale in community ecology: simulated quadrat-sampling and confinement experiments involving animals of different mobilities. - Ecological Modelling 144: 139-152.

Mackey, B. G. and Lindenmayer, D. B. 2001. Towards a hierarchical framework for modelling the spatial distribution of animals. - Journal of Biogeography 28: 1147-1166.

Malcolm, J. R. et al. 2006. Global Warming and Extinctions of Endemic Species from Biodiversity Hotspots. - Conservation Biology 20: 538-548.

Marmion, M. et al. 2009. Evaluation of consensus methods in predictive species distribution modelling. - Diversity and Distributions 15: 59-69.

Martinez, I. et al. 2011. Disentangling the formation of contrasting tree line physiognomies combining model selection and Bayesian parameterization for simulation models. - American Naturalist. 177 E136-152.

May, R. M. and Mac Arthur, R. H. 1972. Niche overlap as a function of environmental variability. - Proceedings of National Academy of Sciences 69: 1109-1113.

McCarthy, M. A. et al. 2003. Reliability of relative predictions in population viability analysis. - Conservation Biology 17: 982-989.

McCarthy, M. A. et al. 1995. Sensitivity analysis for models of population viability. - Biological Conservation 73: 93-100.

McMahon, S. M. and Diez, J. M. 2007. Scales of association: hierarchical linear models and the measurement of ecological systems. - Ecology Letters 10: 437-452.

McPherson, J. M. and Jetz, W. 2007. Effects of species' ecology on the accuracy of distribution models. - Ecography 30: 135-151.

MEA. 2005. Ecosystems and Human Well-Being: Biodiversity Synthesis. World Resources Institute.

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

Meier, E. S. et al. 2011. Climate, competition and connectivity affect future migration and ranges of European trees. - Global Ecology and Biogeography. doi: 10.1111/j.1466-8238.2011.00669.x.

Menard, S. 2000. Coefficients of determination for multiple logistic regression analysis. - The American Statistician 54: 17-24.

Menzel, A. and Fabian, P. 1999. Growing season extended in Europe. - Nature 397: 659.

Meynard, C. N. and Quinn, J. F. 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. - Journal of Biogeography 34: 1455-1469.

Midgley, G. F. et al. 2010. BioMove – an integrated platform simulating the dynamic response of species to environmental change. - Ecography 33: 612-616.

Midgley, G. F. et al. 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. - Global Ecology and Biogeography 11: 445-451.

Midgley, G. F. et al. 2006. Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. - Diversity and Distributions 12: 555-562.

Mills, N. J. and Getz, W. M. 1996. Modelling the biological control of insect pests: a review of host-parasitoid models. - Ecological Modelling 92: 121-143.

Moilanen, A. 1999. Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. - Ecology 80: 1031-1043.

Moilanen, A. 2000. The equilibrium assumption in estimating the parameters of metapopulation models. - Journal of Animal Ecology 69: 143-153.

Moilanen, A. 2002. Implications of empirical data quality for metapopulation model parameter estimation and application. - Oikos 96: 516-530.

Moisen, G. G. and Frescino, T. S. 2002. Comparing five modelling techniques for predicting forest characteristics. - Ecological Modelling 157: 209-225.

Moore, I. D. et al. 1993. Modeling environmental heterogeneity in forested landscapes. - Journal of Hydrology 150: 717-747.

Morin, X. and Thuiller, W. 2009. Shifts in species ranges under climate change - reducing prediction uncertainty through comparison of niche- and process-based modeling approaches. – Ecology 90: 1301-1313.

Nehrbass, N. et al. 2006. Empirical and virtual investigation of the population dynamics of an alien plant under the constraints of local carrying capacity: Heracleum mantegazzianum in the Czech Republic. - Perspectives in Plant Ecology, Evolution and Systematics 7: 253-262.

Nicholson, A. J. 1933. The balance of animal populations. - Journal of Animal Ecology 2: 131-178.

Nicholson, A. J. and Bailey, V. A. 1935. The balance of animal populations. - Proceedings of the Zoological Society of London 3: 551-598.

Nott, M. P. 1998. Effects of abiotic factors on population dynamics of the Cape Sable seaside sparrow and continental patterns of herpetological species richness: an appropriately scaled landscape approach. - University of Tennessee.

O'Neill, M. P. et al. 1997. Identifying sites for Riparian wetland restoration: application of a model to the upper Arkansas river basin. - Restoration Ecology 5: 85-102.

Oliver, T. et al. 2009. Changes in habitat specificity of species at their climatic range boundaries. - Ecology Letters 12: 1091 - 1102.

Osborne, P. E. and Suarez-Seoane, S. 2007. Identifying core areas in a species' range using temporal suitabilty analysis: an example using little bustards *Tetrax tetrax* L. in Spain. - Biodiversity and Conservation 16: 3505-3518.

Pagel, J. and Schurr, F. M. 2011. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. - Global Ecology and Biogeography. In press.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. - Nature 421: 37-42.

Parry, M. L. et al. (eds.) 2007. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. – Cambridge University Press.

Paruelo, J. M. and Tomasel, F. 1997. Prediction of functional characteristics of ecosystems: a comparison of artificial neural networks and regression models. - Ecological Modelling 98: 173-186.

Parysow, P. and Gertner, G. 1997. Virtual experimentation: conceptual models and hypothesis testing of ecological scenarios. - Ecological Modelling 98: 59-71.

Parysow, P. and Gertner, G. 1999. The role of interactions in hypothesis testing of ecological scenarios with process models. - Ecological Modelling 116: 107-124.

Pearce, J. and Ferrier, S. 2000. An evaluation of alternative algorithms for fitting species distribution models using logistic regression. - Ecological Modelling 128: 127-147.

Pearce, J. et al. 2001. An evaluation of the predictive performance of distributional models for flora and fauna in north-east New South Wales. - Journal of Environmental Management 62: 171-184.

Pearman, P. B. et al. 2008a. Prediction of plant species distributions across six millennia. - Ecology Letters 11: 357-369.

Pearman, P. B. et al. 2008b. Niche dynamics in space and time. - Trends Ecology and Evolution 23: 149 - 21 158.

Pearson, R. 2007. Species' distribution modeling for conservation educators and practitioners. - American Museum of Natural History; Available at http://ncep.amnh.org.

Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? - Global Ecology and Biogeography 12: 361-371.

Pearson, R. G. et al. 2002. SPECIES: A spatial evaluation of climate impact on the envelope of species. - Ecological Modelling 154: 289-300.

Pearson, R. G. et al. 2006. Model-based uncertainty in species range prediction. - Journal of Biogeography 33: 1704-1711.

Pereira, H. M. et al. 2010. Scenarios for global biodiversity in the 21st century. - Science 330: 1496-1501.

Perner, J. and Schueler, S. 2004. Estimating the density of ground-dwelling arthropods with pitfall traps using a nested cross-array. - Journal of Animal Ecology 73: 469-477.

Platts, P. J. et al. 2008. Predicting tree distributions in an East African biodiversity hotspot: model selection, data bias and envelope uncertainty. - Ecological Modelling 218: 121-134.

Pompe, S. et al. 2008. Climate and land use change impacts on plant distributions in Germany. - Biology Letters 4: 564-567.

Pounds, J. A. et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. - Nature 439: 161-167.

R Development Core Team. 2010. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.

Rachowicz, L. J. et al. 2006. Evaluating at-sea sampling designs for Marbled Murrelets using a spatially explicit model. - Ecological Modelling 196: 329-344.

Rahmstorf, S. et al. 2007. Recent climate observations compared to projections. - Science 316: 709.

Railsback, S. F. and Harvey, B. C. 2002. Analysis of habitat-selection rules using an individual-based model. - Ecology 83: 1817-1830.

Railsback, S. F. et al. 2003. What can habitat preferences models tell us? Tests using a virtual trout population. - Ecological Applications 13: 1580-1594.

Ratcliffe, N. et al. 2008. Resolving the population status of Ascension Frigatebird *Fregata aquila* using a 'virtual ecologist' model. - Ibis 150: 300-306.

Real, R. et al. 2006. Obtaining environmental favourability functions from logistic regression. - Environmental and Ecological Statistics 13: 237-245.

Reese, G. C. et al. 2005. Factors affecting species distribution predictions: A simulation modeling experiment. - Ecological Applications 15: 554-564.

Reineking, B. and Schröder, B. 2006. Constrain to perform: Regularization of habitat models. - Ecological Modelling 193: 675-690.

Ricker, W. E. 1954. Stock and recruitment. - Journal of the Fish Research Board of Canada 11: 559-623.

Ridgeway, G. 1999. The state of boosting. - Computing Science and Statistics 31: 172-181.

Rocchini, D. et al. 2011. Accounting for uncertainty when mapping species distributions: the need for maps of ignorance. - Progress in Physical Geography 35: 211-226.

Rossmanith, E. et al. 2007. Pattern-oriented modelling for estimating unkown pre-breeding survival rates: The case of the Lesser Spotted Woodpecker (*Picoides minor*). - Biological Conservation 135: 571-580.

Rossmanith, E. et al. 2006. Behavioural flexibility in the mating system buffers population extinction: lessons from the lesser spotted woodpecker *Picoides minor*. – Journal of Animal Ecology 76: 540-548.

Sabo, J. L. and Gerber, L. R. 2007. Predicting extinction risk in spite of predator-prey oscillations. - Ecological Applications 17: 1543-1554.

Sala, O. E. et al. 2000. Global biodiversity scenarios for the year 2100. - Science 287: 1770-1774.

Salant, S. W. et al. 1995. Deducing implications of fitness maximization when a trade-off exists among alternative currencies. - Behavioral Ecology 6: 424-434.

Schifferli, A. et al. 1980. Verbreitungsatlas der Brutvögel der Schweiz. - Swiss Ornithological Institute.

Schmid, H. et al. 1998. Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und im Fürstentum Liechtenstein 1993-1996. - Swiss Ornithological Institute.

Schröder, B. 2008a. Challenges of species distribution modelling belowground. - Journal of Plant Nutrition and Soil Science 171: 325-337.

Schröder, B. 2008b. Species in dynamic landscapes - Patterns, processes, and functions. - University of Potsdam.

Schröder, B. et al. 2008. A landscape model for quantifying the trade-off between conservation needs and economic constraints in the management of a semi-natural grassland community. - Biological Conservation 141: 719-732.

Schröder, B. and Seppelt, R. 2006. Analysis of pattern-process interactions based on landscape models - Overview, general concepts, and methodological issues. - Ecological Modelling 199: 505-516.

Schröter, D. et al. 2005. Ecosystem service supply and vulnerability to global change in Europe. - Science 310: 1333-1337.

Schweiger, O. et al. 2008. Climate change can cause spatial mismatch of trophically interacting species. - Ecology 89: 3472-3479.

Schweiger, O. et al. 2011. Increasing range mismatching of interacting species under global change is related to species traits. – Global Ecology and Biogeogrpahy. In press.

Scott, J. M. et al. (eds.) 2002. Predicting species occurrences: issues of accuracy and scale. - Island Press.

Segurado, P. and Araújo, M. B. 2004. An evaluation of methods for modelling species distributions. - Journal of Biogeography 31: 1555-1568.

Seoane, J. et al. 2005. Species-specific traits associated to prediction errors in bird habitat suitability modelling. - Ecological Modelling 185: 299-308.

Sharpe, P. J. H. 1990. Forest modeling approaches: Compromises between generality and precision. - In: Dixon, R. K. et al. (eds.), Forest Modeling Approaches: Compromises between Generality and Precision. Timber Press, pp. 180-190.

Skarpaas, O. et al. 2005. Optimizing dispersal study design by Monte Carlo simulation. - Journal of Applied Ecology 42: 731-739.

Söndgerath, D. and Schröder, B. 2002. Population dynamics and habitat connectivity affecting the spatial spread of populations - a simulation study. - Landscape Ecology 17: 57-70.

Stickel, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. - Journal of Mammalogy 35: 1-15.

Stillman, R. A. 2008. MORPH - An individual-based model to predict the effect of environmental change on foraging animal populations. - Ecological Modelling 216: 265-276.

Stillman, R. A. and Goss-Custard, J. D. 2010. Individual-based ecology of coastal birds. – Biological Reviews 85: 413-434.

Stockwell, D. R. B. and Peterson, A. T. 2002. Effects of sample size on accuracy of species distribution models. - Ecological Modelling 148: 1-13.

Sutherland, G. D. et al. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. - Conservation Ecology 4: 16.

Svenning, J.-C. and Skov, F. 2004. Limited filling of the potential range in European tree species. - Ecology Letters 7: 565-573.

Thomas, C. D. et al. 2001. Ecological and evolutionary processes at expanding range margins. - Nature 411: 577-581.

Thomas, C. D. et al. 2004. Extinction risk from climate change. - Nature 427: 145-148.

Thuiller, W. 2004. Patterns and uncertainties of species' range shifts under climate change. - Global Change Biology 10: 2020-2027.

Thuiller, W. et al. 2008. Predicting global change impacts on plant species' distributions: Future challenges. - Perspectives in Plant Ecology, Evolution and Systematics 9: 137-152.

Thuiller, W. et al. 2004. Effects of restricting environmental range of data to project current and future species distributions. - Ecography 27: 165-172.

Thuiller, W. et al. 2009. BIOMOD – a platform for ensemble forecasting of species distributions. - Ecography 32: 369-373.

Thuiller, W. et al. 2005. Climate change threats to plant diversity in Europe. – Proceedings of the National Academy of Sciences 102: 8245-8250.

Thuiller, W. et al. 2006. Predicting patterns of plant species richness in megadiverse South Africa. - Ecography 29: 733-744.

Thuiller, W. and Münkemüller, T. 2010. Habitat suitability modeling. - In: Moeller, A. P. et al. (eds.), Effects of climate change on birds. Oxford University Press, pp. 77-85.

Tyre, A. J. et al. 2001. Inferring process from pattern: can territory occupancy provide information about life history parameters? - Ecological Applications 11: 1722-1737.

Tyre, A. J. et al. 2003. Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. - Ecological Applications 13: 1790-1801.

Ulrich, W. and Gotelli, N. J. 2007a. Disentangling community patterns of nestedness and species co-occurrence. - Oikos 116: 2053-2061.

Ulrich, W. and Gotelli, N. J. 2007b. Null model analysis of species nestedness patterns. - Ecology 88: 1824–1831.

van Vuuren, D. P. et al. 2006. The future of vascular plant diversity under four global scenarios. – Ecology and Society 11: 25.

Vaughan, I. P. and Ormerod, S. J. 2005. The continuing challenges of testing species distribution models. - Journal of Applied Ecology 42: 720-730.

Visser, M. E. and Both, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. - Proceedings of the Royal Society B 272: 2561-2569.

Wallace, A. R. 1878. Tropical Nature. - Macmillan and Co.

Walther, G.-R. et al. 2002. Ecological responses to recent climate change. - Nature 416: 389-395.

Warren, D.L. et al. 2008.Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. - Evolution 62: 868-2883.

Wichmann, M. C. et al. 2003. Implication of climate change for the persistence of raptors in arid savanna. - Oikos 102: 186-202.

Wiegand, T. et al. 2003. Using pattern-oriented modelling for revealing hidden information: a key for reconceiling ecological theory and application. - Oikos 100: 209-222.

Williams, J. W. and Jackson, S. T. 2007. Novel climates, no-analog communities, and ecological surprises. - Frontiers in Ecology and the Environment 5: 475-482.

Williams, J.W. et al. 2007. Projected distributions of novel and disappearing climates by 2100 AD. - Proceedings of the National Academy of Sciences 104: 5738–5742.

Willis, S. G. et al. 2009. Dynamic distribution modelling: predicting the present from the past. - Ecography 32: 5-12.

Wilson, J. P. and Gallant, J. C. (eds.) 2000. Terrain analysis: principles and applications. – John Wiley and Sons.

Wissel, C. 1992. Aims and limits of ecological modelling exemplified by island theory. - Ecological Modelling 63: 1-12.

Wissel, C. et al. 1994. Modelling extinction and survival of small populations. - In: Remmert, H. (ed.) Minimum animal populations. Springer, pp. 67-103.

Wolfram, S. 1984a. Cellular automata as models of complexity. - Nature 311: 419-424.

Wolfram, S. 1984b. Computer Software in Science and Mathematics. - Scientific American 251: 188-203.

Wootton, J. T. 1995. Effects of birds on sea urchins and algae – a lower-intertidal trophic cascade. - Ecoscience 2: 321-328.

Wunder, J. et al. 2008. Predicting tree mortality from growth data: how virtual ecologists can help real ecologists. - Journal of Ecology 96: 174-187.

Zbinden, N. and Salvioni, M. 2003. Verbreitung, Siedlungsdichte und Fortpflanzungserfolg des Birkhuhns *Tetrao tetrix* im Tessin 1981-2002. - Der Ornithologische Beobachter 100: 211-226.

Zbinden, N. and Salvioni, M. 2004. Bedeutung der Temperatur in der frühen Aufzuchtzeit für den Fortpflanzungserfolg des Birkhuhns *Tetrao tetrix* auf verschiedenen Höhenstufen im Tessin, Südschweiz. - Der Ornithologische Beobachter 101: 307-318.

Zimmermann, N. E. and Kienast, F. 1999. Predictive mapping of alpine grasslands in Switzerland: Species versus community approach. - Journal of Vegetation Science 10: 469-482.

Zimmermann, N. E. et al. 2010. New trends in species distribution modelling. - Ecography 33: 985-989.

Zurell, D. 2007. Can static models depict dynamic populations? A virtual ecologist investigates. - University of Potsdam, p. 57.

Zurell, D. et al. 2010. The virtual ecologist approach: simulating data and observers. - Oikos 119: 622-635.

Zurell, D. et al. 2011. Uncertainty in predictions of range dynamics: black grouse climbing the Swiss Alps. Ecography. doi: 10.1111/j.1600-0587.2011.07200.x

Zurell, D. et al. 2009. Static species distribution models in dynamically changing systems: How good can predictions really be? - Ecography 32: 733-744.

Danksagung

In den letzten Jahren haben mich viele Menschen in ganz unterschiedlichen Weisen unterstützt. Dafür herzlichen Dank.

Besonderer Dank gilt meinen Betreuern Prof. Dr. Boris Schröder und PD Dr. Volker Grimm für die Bereitstellung und viel Freiheit bei der Ausarbeitung des Themas, immerwährende Diskussionsbereitschaft, konstruktive Kritik und viele Spaßmomente.

Allen Koautoren sei gedankt für die konstruktive und spannende Zusammenarbeit, für anregende Diskussionen sowie die Bereitstellung von Daten.
(Great thanks to all coauthors for constructive and enthralling teamwork, exciting discussions as well as provision of data.)

Catherine H. Graham und Janine Bolliger danke ich für die spontane Bereitschaft zur Begutachtung meiner Arbeit.
(I want to thank Catherine H. Graham and Janine Bolliger for their willingness to review my thesis.)

Für finanzielle Unterstützung danke ich der Universität Potsdam Graduierteninitiative UPGradE, der Potsdam Graduate School PoGS sowie dem Helmholtz-Zentrum für Umweltforschung UFZ.

Den vielen Kollegen am Institut für Erd- und Umweltwissenschaften (ehemals Institut für Geoökologie) herzlichen Dank für die schöne Zeit, vielen Lachern, Kuchen und Kaffee. Daniel Bazant sowie dem restlichen W3-Team danke ich für technische Unterstützung, Sabine Schrader für das organisatorische ‚Drumherum'.

Der größte Dank gebührt meiner Familie und Freunden, allen voran meinem Mann Andreas Zurell für Geduld, Unterstützung und aufbauende Worte. Vor allem aber ihm und Anna Danke fürs Dasein.

Models are intellectual instruments for thinking people,
not crutches for the thoughtless.

Christian Wissel (1992)