A gradient analytic perspective on distribution modelling

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Halvorsen, R. A gradient analytic perspective on distribution modelling. – Sommerfeltia 35: 1-165. Oslo. ISBN 82-7420-049-7. ISSN 2084-0098. DOI: 10.2478/v10208-011-0015-3.

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After massive proliferation over the last decade, distribution modelling (DM) – research with the purpose of modelling the distribution of observable objects of a specific type – has grown into an independent branch of ecological science. There is consensus that this new discipline needs a stronger theoretical foundation. I describe DM as an inductive scientific process with 12 steps, organised into three composite steps: ecological model, data model, and statistical model. Step 8, modelling of the overall ecological response, places DM unambiguously among gradient analysis techniques and motivates for a gradient analytic (GA) perspective on DM. DM terminology is reviewed and revised accordingly.

Three fundamental insights of the GA perspective are described: (1) that external 'factors' do not influence the species one by one, but act on the species in concert; (2) that a few major complex-gradients normally account for most of the variation in species composition that can be explained environmentally; and (3) that species occur within a restricted interval along each major complex-gradient. These insights are developed into a theoretical platform for DM. General patterns of species performance variation along environmental complex-gradients and the structuring processes responsible for these patterns are reviewed. Three categories of ecoclines, i.e., gradients of variation in species composition and the environment, are recognised: regional ecoclines, local ecoclines, and condition or impact ecoclines. Causes and implications of the unimodal shape of species' responses to environmental complex-gradients are reviewed. Structuring processes are divided into three categories: limited physiological tolerance, interspecific interactions, and demographic processes. Relationships between categories of ecoclines, the processes responsible for variation in species performance along them, and the spatial and temporal scale intervals in which variation is large, are reviewed.

The GA perspective forms the basis for discussions of important steps in the DM process. Initially, the controversial concepts of the habitat and the niche are reviewed and their role in the ecological model (Step 1) discussed. I conclude that neither of these concepts are necessary, nor useful, for DM. As an alternative to conceptual models based upon the niche concept, I propose a new conceptual modelling framework for DM, the HED framework, which is rooted in the gradient analytic perspective. I show how this new framework can be used, in initial phases of a DM study to formulate a meta-model for factors that influence distributions, and in the analytic phase to guide important choices of methods and options and to assist interpretation of modelling results. Important data model issues are: collection of data for the modelled target and preparation of raw response variables (Steps 2 and 6); collection of explanatory data (Step



3); conceptualisation of the study area (Step 4); collection of data for calibration and evaluation (Step 9); and transformation of explanatory variables to derived variables subjected to DM (Step 5,ii). Important statistical model issues are: statistical model formulation, i.e. choice of method (Step 7,i) and model specification (Step 7,ii); model selection and internal assessment of model performance (Steps 8,i and 8,ii); and model evaluation (Step 10). Two points are emphasised: (1) that modelling purpose should inform choice of methods and options; and (2) the importance of an independently collected presence/absence data set, which can be used to calibrate, evaluate and iteratively improve models.

Finally I list seven challenges of particular importance for progress in DM: (1) that more knowledge of patterns of natural variation is needed; (2) that a better mechanistic understanding of causes of patterns of natural variation is needed; (3) that the availability of relevant rasterised explanatory variables needs to be improved; (4) that more studies of patterns at local and micro spatial scales, in addition to multiple-scale studies using DM methods, are needed; (5) that evaluation by independent data should be established as a standard in DM; (6) that further insights into statistical modelling methods and their options, with particular reference to appropriateness for different types of data and DM purposes, are needed; and (7) that DM methods should be incorporated in studies with a broader scope. I conclude that there are considerable potentials for improvement of DM methods and practice. Increased return from DM in terms of contributions that improve our understanding of patterns of natural variation and their causes, should be expected.

Keywords: Conceptual model; Distribution modelling; Ecocline; Gradient analysis; Grain; Habitat; Niche; Spatial scale; Statistical model; Temporal scale; Terminology.

Abbreviations: ALS = airborne laser scanning (= LiDAR); AOR = abundance-occupancy relationship; AUC = area under the (ROC) curve; BAM diagram = a conceptual model for distribution modelling; BIOCLIM = bioclimatic envelope model; BRT = boosted regression trees; CCA = canonical correspondence analysis; CO = constrained ordination; CSR model = competitorstress tolerator-ruderal model; CURS = core-urban-rural-satellite (model); DCA = detrended correspondence analysis; DEM = digital elevation model; DM = distribution modelling; EFL = empirical forest limit; ENFA = ecological niche factor analysis; ENM = ecological niche modelling; ERM = ecological response modelling; EUNIS = the European habitat classification system; GA = gradient analysis; GAM = generalised additive models; GAP = the gradient analytic perspective; GARP = genetic algorithm for rule-set production; GBIF = Global Biodiversity Information Facility; GIS = geographic information system; GLM = generalised linear models; GLMM = generalised linear mixed models; HED = conceptual modelling framework for distribution modelling with three components: (1) heuristic factor diagrams (H-diagrams), (2) ecological response curves (E-curves), and (3) distribution maps (D.maps); HOF = Huisman-Olff-Fresco (models); LC = linear combination; LPT = lack of physiological tolerance; MaxEnt = maximum entropy (model); MAUP = modifiable area unit problem; MNM = mechanistic niche modelling; NiN = Norwegian nature types [*Naturtyper i Norge*]; P/A = presence/absence; PCA = principal component analysis; PO = presence-only; PPM = projective distribution modelling; PPP = predicted probability of presence; RDA = redundancy analysis; ROC = receiver operating characteristic (curve); RPPP = relative predicted probability of presence; RSD = remote sensing data; SAR = species richness-area relationship; SD = standard deviation; SDM = species distribution modelling; SEM = structural equation model; SPM = spatial prediction modelling; SS = sum of squares; UPCFL = upper potential climatic forest line; UTM = Universal Transverse Mercator (grid reference); VP = variation partitioning; WA = weighted average.

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INTRODUCTION

SETTING THE SCENE: A SIMPLE EXPLANATION OF WHAT DISTRIBUTION MODELLING IS

Distribution modelling (DM) can be explained, simply, as research with the purpose of modelling the distribution of observable objects of a specific type, the **modelled target**, as a response to supplied explanatory variables. Five important terms are used in this explanation, which themselves need to be explained: 'observable object', 'distribution', 'model', 'response variable', and 'explanatory variable'. In this essay review, the expression 'observable objects of a specified type' includes all natural phenomena, resulting from geological, biological, or ecological processes, which are more or less discrete, observable, and which, according to a set of explicit criteria, belong to a specific type category. Relevant object types include species or other biological taxa, communities of plants and animals, ecosystems, landscape types, landforms, minerals, and bedrock types. Also direct physical manifestations of ecological and geological processes, such as earthslides and extensive windthrows, may be targets for distribution modelling. The collective term 'distribution' adresses the physical arrangement of objects belonging to a specific type category – where and when they occurred, occur, or are expected to occur. The terms 'model', 'response variable', and 'explanatory variable' are closely linked to each other. In the most inclusive sense, a **model** is 'anything used in any way to represent anything else' (http:// en.wikipedia.org/wiki/Conceptual_model, accessed 30 June 2012). A model is a description - in words, by diagrams, or in mathematical or statistical terms - of how one phenomenon is related to one or more other phenomena. A model can describe general or context-dependent relationships between the phenomena in question. The term **response variable** is used in mathematical and statistical modelling contexts for a variable that is used to characterise the phenomenon that is modelled. The term targeted response variable addresses the response variable in a distribution model, i.e., the variable used to characterise the modelled target. The term explanatory variable is used for a variable that, alone or in combination with other variables, is used to characterise a phenomenon that represents, or describes, the modelled target. In a statistical modelling context, the term is used for any variable that potentially may account for some variation in the response variable. Explanatory variables may be causally related to the response variable, proxies for putatively causal factors, or any other variable used for modelling, regardless of their relationship to the modelled phenomenon. Thus, the term 'explanatory variable' should be understood in a strictly statistical meaning, without any assumptions of, or allutions to, causality (Økland et al. 2001). Most 'explanatory variables' used in DM contexts are environmental variables, but biotic variables, i.e., descriptors of potential influences from other organisms, are also used. With environment I here mean environmental variation in the widest sense, comprising all external factors that potentially may influence organisms.

This simple explanation for distribution modelling establishes DM as a multidisciplinary

field of research which, depending on which natural phenomenon is modelled, integrates skills in botany, zoology, ecology, geology, or physical geography, with methods for processing geographical information and statistical modelling methods.

HISTORICAL BACKGROUND

Describing and understanding distributions have been focal issues in natural sciences since the early 19th century (e.g., see Guisan & Zimmermann 2000), e.g., recognised under names such as biogeography, vegetation geography, and physical geography. Distribution modelling developed from these fields during the 25-year period from 1975 to 2000, when natural sciences developed from being mainly descriptive to addressing a wide range of questions by use of a multitude of approaches and methods.

DM partly originated in biogeographers' search for climatic factors that could explain distributions of species (e.g., Salisbury 1926) and biomes (e.g., Walter 1968), partly in community ecologists' search for general 'species response curves', i.e., for models of species' distributions with respect to important environmental variables (Whittaker 1967, Austin 1976, 1980, Økland 1990a). Starting out by means of simple graphs (e.g., Iversen 1944, Ellenberg 1953, Whittaker 1956, Grime & Lloyd 1973), all-round modelling methods like generalised linear modelling (GLM; e.g., Austin et al. 1984) and generalised additive modelling (GAM; e.g., Austin & Meyers 1997) gradually came into use during the 1980s and 1990s. In recent years, new modelling tools, such as HOF modelling (Huisman et al. 1993, Oksanen & Minchin 2002), have been developed for analysis of species' responses to single explanatory variables. Examples of studies in which these tools are used include Oksanen & Minchin (2002), Rydgren et al. (2003), Kalusova et al. (2009), and Peper et al. (2011).

DM developed into a scientific discipline on its own by inorporating geographic information systems (GIS; Burrough & McDonnell 1998, O'Sullivan & Unwin 2003) and statistical modelling methods (e.g., Hastie et al. 2009, Zuur et al. 2009) into a distinctive methodological framework for analysis of georeferenced biogeographic data. Furthermore, the development of DM has been strongly facilitated by advances in computer science, among others under the heading of biodiversity informatics (Peterson et al. 2010). Advances in this field have opened for digitisation of vast amounts of data, among others in natural history museum collections, access to these data via web services such as the Global Biodiversity Information Facility (GBIF; Telenius 2011), and processing of increasingly large sets of data by use of increasingly complex methods.

A large number of statistical modelling methods have been applied to analysis of georeferenced distributional data; from all-round modelling methods like GLM (e.g., Pearce & Ferrier 2000a; see Fig. 9) and GAM (Leathwick 1995, Lehmann et al. 2002), to methods specifically developed for DM, available in software applications specifically adapted for DM. Development of methods of the last-mentioned type started out with simpler methods such as bioclimatic envelope modelling (BIOCLIM; Busby 1991) and continued with more complex methods such as GARP (Stockwell & Peters 1999) and ENFA (Hirzel et al. 2002). Two of the currently most popular DM methods, which also perform the best in comparative tests [see Elith et al. (2006), Guisan et al. (2007), Elith & Graham (2009), Phillips et al. (2009), Mateo et al. (2010), Rupprecht et al. (2011)], are MaxEnt (Phillips et al. 2006, Phillips & Dudík 2008, Elith et al. 2011, Halvorsen in press), which is based upon the maximum entropy principle, and machine learning methods like boosted regression trees (BRT; De'ath 2007, Elith et al. 2008). A recent trend is towards use of ensemble modelling approaches such as BIOMOD (Thuiller et al. 2009), by which models obtained by different methods are combined into one ensemble model (e.g., Beaumont et al. 2009, Lomba et al. 2010, Nenzén & Araújo 2011). Comprehensive overviews of DM methods are provided by Franklin (2009); alse see Elith & Leathwich (2009) and Peterson et al. (2011).

The increasing rates by which new modelling methods for DM have come into regular use (e.g., Phillips & Dudík 2008, Thuiller et al. 2009), and the steadily growing rate by which papers with a DM approach are published (Lobo et al. 2010), indicate that the proliferation of DM will continue in the near future.

The category of nature phenomena by far most often targeted by DM methods is the species, as exemplified by studies of plants by Parolo et al. (2008), Jones et al. (2010), and Ed-vardsen et al. (2011); of animals by Luoto et al. (2006) and Lozier et al. (2009); and of fungi by Wollan et al. (2008). Other natural phenomena that have been subjected to DM include species assemblages ('communities' or 'vegetation types'; Cawsey et al. 2002, Weber 2011, Hemsing & Bryn 2012), species diversity variables like richness or evenness (Miller & Franklin 2002, Buhk et al. 2007, Baselga & Araújo 2009, Dubuis et al. 2011), and land-cover types (Dobrowski et al. 2008). Phenomena that are not yet physically observable, such as the upper potential climatic forest line, have also been subjected to distribution modelling (Bryn et al. 2012). While in recent textbooks (Franklin 2009, Peterson et al. 2011) attention is restricted to modelling distributions of other natural phenomena. This is reflected in the use in this essay review of the term 'modelled target' rather than 'species' for situations where no specific category of natural phenomena is addressed.

An important reason for the recent proliferation of DM is the proven value of DM results for applied purposes (Elith & Leathwick 2009, Franklin 2009). Important applied uses of DM include assistance to conservation biologists in their search for, and sampling of, rare species for monitoring purposes (Edwards et al. 2005, Guisan & Thuiller 2005, Guisan et al. 2006a, Marage et al. 2008, Parviainen et al. 2008, de Siqueira et al. 2009, Gogol-Prokurat 2011, Marino et al. 2011), judgement of conservation priority (Platts et al. 2010, Bombi et al. 2011), management of invasive species (Crawford & Hoagland 2009, Václavík & Meentemeyer 2009, Catford et al. 2011, Gormley et al. 2011) and prediction of range shifts in response to climate change (Heikkinen et al. 2006, Zurell et al. 2009, Engler et al. 2011). A result of the strong applied interest in DM is the recent recognition of conservation biogeography as an ecological discipline on its own (Whittaker et al. 2005, Franklin 2010, Richardson & Whittaker 2010).

WHY DISTRIBUTION MODELLING NEEDS A STRONGER THEORETICAL FOUNDATION

All branches of science, distribution modelling included, depend on the firm foothold offered by a strong theoretical foundation: in-depth understanding of the major processes and mechanisms that are responsible for observed patterns, built upon a conceptual basis that consists of precisely defined terms. In spite of the proliferation of DM methodology and applications, it is recurrently claimed that distribution modelling lacks such a foundation, and that more explicit links with ecological theory is needed (Araújo & Guisan 2006, Austin 2007, Hirzel & Le Lay 2008, Jiménez-Valverde et al. 2008, Elith & Leathwick 2009, Peterson et al. 2011). Even though several recent contributions have improved the theoretical basis for DM, notably by attempts to clarify relationships between DM and niche concepts (e.g., Pulliam 2000, Kearney 2006, Austin 2007, Soberón 2007, 2010, Godsoe 2010, Barve et al. 2011, Cassini 2011, Peterson et al. 2011), DM still faces a multitude of fundamental challenges. This is exemplified by the lack of consensus on important methodological questions, such as the relative performance of different modelling methods and their options (Elith et al. 2006, Hirzel et al. 2006, Elith & Graham 2009, Mateo et al. 2010, Rota et al. 2011); how to deal with the commonly occurring lack of true absence information (and the related question of how pseudo-absence 'observations' should be generated) and how choices in this respect influence DM results (Chefauoi & Lobo 2008, Lobo et al. 2010, Stokland et al. 2011); how to select explanatory variables to be used in DM studies and, notably, determine which types of variables generally improve (or fail to improve) distribution models (Randin et al. 2009a, 2009b, Ko et al. 2011, Marino et al. 2011); how the choice of explanatory variables interacts with the spatial scale addressed by the study (Pearson & Dawson 2003, Jones et al. 2010, Kriticos & Leriche 2010); and, finally, how to evaluate distribution models, i.e., how to tell good from poor models (Lobo et al. 2008, Jiménez-Valverde et al. 2009, Edvardsen et al. 2011, Merckx et al. 2011, Warren & Seifert 2011).

Development of 'schools' with different research paradigms is typical of research areas tenuously rooted in theory (Austin 2007). A typical example of 'school formation' in ecology is the fragmentation of phytosociology in the early 20th century (Whittaker 1962) into schools which differed fundamentally in their basic understanding of the nature of natural variation (Whittaker 1962, McIntosh 1985, Økland & Bendiksen 1985). Examples of topics that were vigourously debated are: if distinct community units exist (Clements 1916, Du Rietz 1921, Braun-Blanquet 1928), or communities are social constructions [in the sense of Hacking (1999)] as argued for by Nordhagen (1920) and Kylin (1926); if variation in single-species abundances is predominantly individualistic and variation in species composition, i.e., vegetation, predominantly continuous under natural conditions (Gleason 1926), or if distinct discontinuities in vegetation exist also when environmental conditions vary continuously (Cajander 1909; Du Rietz 1921); how to define the fundamental unit in the phytosociological hierarchy, the association (e.g., Du Rietz 1936); and how to describe and name plant communities (see, e.g., Whittaker 1962, van der Maarel 2005). Similar tendencies for fragmentation into 'schools' characterised by separate paradigms (Kuhn 1996) can now be observed within DM (Austin 2007, Peterson et al. 2011). This is reflected in different conceptual frameworks and the role of the niche concept in these; different agreed sets of facts - types of data and methods by which they are collected; different questions asked; different spatial scales addressed; and different standard methods used. Perhaps the most obvious example of school formation is offered by the diversity of opinions on, and lack of consensus with respect to, the applicability of niche concepts to DM: if the concept of the niche is important for DM or rather a nonconcept which 'has been defined in such various and disparate ways that it now conveys no information other than "something to do with [the relationships of species to their surroundings]", quoting Hurlbert's (1971) critique of the concept of 'species diversity'. While some authors argue that the niche concept is the essence of distribution modelling and, accordingly, use the term 'ecological niche modelling' (ENM; Peterson 2003, Peterson et al. 2007, Ebeling et al 2008, de Sigueira et al. 2009, Guinan et al. 2009, Lozier et al. 2009, Costa et al. 2010, Barve et al. 2011, Pearman et al. 2011, Peterson et al. 2011, Warren & Seifert 2011), 'environmental niche modelling' (Warren et al. 2008), 'niche modelling' (Parolo et al. 2008, Kearney & Porter 2009, Veloz 2009, Kriticos & Leriche 2010) or 'niche-based modelling' (Guisan et al. 2006a, Randin et al. 2006, Segurado et al. 2006, Bahn & McGill 2007, Bartel & Sexton 2009, Capinha & Anastacio 2011), others, such as Guisan & Zimmermann (2000), Guisan & Thuiller (2005), Araújo & Guisan (2006), and Franklin (2009) recognise the importance of niche concepts in general but admit that the relationship of DM modelling to the niche concept is a complex one. Many authors use the term 'habitat' instead of 'niche', as exemplified by terms like 'predictive habitat distribution modelling' (Guisan & Zimmermann 2000), 'predictive distribution modelling' (Lobo et al. 2008, Marmion et al. 2009b), 'habitat suitability modelling' (Hirzel et al. 2006, Murphy & Lovett-Doust 2007, Hirzel & Le Lay 2008, Cianfrani et al. 2010), 'habitat distribution modelling' (Dirnböck & Dullinger 2004) or,

simply, 'habitat modelling' (Pearce & Ferrier 2000b, Burger & Page 2007). A different standpoint is taken by Elith & Leathwick (2009) who explicitly advocate use of neutral terminology to describe distribution models. Many authors have followed this recommendation, using the simple, neutral term 'species distribution modelling' (Pearce & Ferrier 2000a, Rushton et al. 2004, Araújo & Guisan 2006, Edwards et al. 2006, Elith et al. 2006, Hernandez et al. 2006, Leathwick et al. 2006, Lütolf et al. 2006, Araújo & Luoto 2007, Raes & ter Steege 2007, Tsoar et al. 2007, Dobrowski et al. 2008, Jiménez-Valverde et al. 2008, 2009, Elith & Graham 2009, Elith & Leathwick 2009, Franklin 2009, Phillips et al. 2009, Pineda & Lobo 2009, Zurell et al. 2009, Santika & Hutchinson 2009, Lobo et al. 2010, Mateo et al. 2010, Stankowski & Parker 2010, Syphard & Franklin 2010, Aranda & Lobo 2011, Austin & van Niel 2011a, 2011b, Phillips & Elith 2011, Synes & Osborne 2011). On closer view, it is evident from the extensive literature cited above that opinions on fundamental DM issues such as the relevance of habitat and niche concepts are often coupled with the modellers' preferences for methods and their choice of terminology. This indicates existence of 'schools', as suggested by Austin (2007).

In order to mitigate further segregation into 'schools', consensus solutions to fundamental methodological challenges in DM should be actively searched for with the aim of establishing a unified theoretical platform for this new branch of ecological science (Austin 2007, Peterson et al. 2011). This is, however, difficult when no unified ecological theory exists (Austin 1986, 1990, 1999b, 2005). As pointed out by Austin (2005), 'there are many unanswered questions' as well as 'many unquestioned answers'. Nevertheless, the statement of Austin's (2005) that the views may be less different than they seem, because of apparent differences resulting from different focuses, from different scales of observation, and from differences between the ecosystems investigated, opens for the possibility that a common theoretical platform for DM may be established. Similar views are expressed by Peterson et al. (2011) in their recent synthesis of DM concepts. DM obviously needs a stronger theoretical foundation.

ABOUT THIS ESSAY REVIEW: THEORETICAL PLATFORM, AIMS STATEMENT, AND STRUC-TURE

Theoretical platform

Distribution modelling can be conceptualised in different ways, and the appropriateness of each conceptual framework will have to be judged by its contribution to progress in the field. In the recent book 'Ecological niches and geographic distributions', which by the authors is characterised as 'a first synthesis of concepts in this emerging field', Peterson et al. (2011) present a conceptual framework for DM based upon niche theory: '... a body of terminology and schemes by which to understand and discuss phenomena of distributional ecology ... [based upon] the complex relationships between ecological niches and geographic distributions of species ...' (Peterson et al. 2011: 3). The focal point of niche theory is the species, as demonstrated by the following statement of Peterson et al.'s (2011: 17): 'neither Grinnellian nor Eltonian niches can be operationalised without reference to a particular species ... no "empty" Grinnellian or Eltonian niches can exist.'

The conceptualisation of natural variation adopted in this essay review is diametrically opposite to that of Peterson et al. (2011): rather than starting with the species, I use an 'environment-centred' approach to DM. This choice of mine is certainly a product of my training as vegetation ecologist with strong interests in biostatistics, and experience gained by participation in studies of species–environment relationships. However, more fundamentally, my choice is motivated by reflections over the fact that all individuals of all extant species are direct descendants of individuals that managed to cope with the environmental factors experienced by them (Dawkins 2009). While I acknowledge that species influence the environment to the extent that several aspects of 'environmental' variation are modified by, or direct results of, the existence of living organisms, my opinion is that the environment is the fundament for understanding natural variation: it is the totality of environmental impacts that determines the fate of each individual of each species, which in turn sum up to species' distributions in space and time. Accordingly, variation in the environment is my obvious choice as reference frame for describing and understanding distributions.

The 'environment-centred' (as opposed to a 'species-centred') understanding of natural variation adopted in this essay review implies that distribution modelling is explained from knowledge about environmental gradients and species' responses to these gradients. The term **gradient** is used to denote the more or less gradual variation of a property of the environment, or of a specific type category of natural phenomena. This knowledge is referred to as the **gradient analytic perspective** (GAP).

Placing DM in a gradient analytic perspective is not a new idea. Guisan & Zimmermann (2000: 148) started their influential review of 'predictive habitat models' with the statement that 'the analysis of species–environment relationship has always been a central issue in ecology'. Furthermore, in two reviews, Austin calls for a stronger link between 'spatial prediction of species distributions' (Austin 2002) and 'species distribution modelling' (Austin 2007) on one hand and ecological theory on the other, with explicit reference to gradient analysis. However, these reviews are exceptions to the current tendency for distribution modellers to neglect the rooting of DM in basic gradient analysis.

Aims statement

My main ambition with this essay review is to contribute to the anchoring of distribution modelling in ecological sciences by development of terminology and a conceptual framework rooted in the gradient analytic perspective. Based upon this theoretical basis, my intention is to explore several aspects of current practices in distribution modelling. Finally, I also intend to explore potential contributions of distribution modelling to ecological theory. Although my theoretical basis differs from that of Peterson et al. (2011), my aim concurs with theirs: 'to move the discourse in this field to a new level' (Peterson et al. 2011: 4).

This essay review is *not* an exhaustive review of, or textbook in, distribution modelling. For an overview of DM methods the reader is referred to Franklin (2009); Franklin (2009) and Peterson et al. (2011) should be consulted for examples of practical applications of these methods.

Structure and overview

This essay review is divided into five chapters, of which each is one piece in the puzzle of explaining distribution modelling from a gradient analytic perspective (Fig. 1). The first chapter provides a brief outline of basic concepts and terminology of gradient analysis, starting with the three fundamental insights of the gradient analytic perspective. This fundament is used in the subsequent chapter to redefine distribution modelling in gradient analytic terms as a 12step process. The third of the five chapters contains a review of current knowledge of patterns of variation in species composition in relation to environmental conditions and the extent to



Fig. 1. Interactions between the gradient analytic perspective and distribution modelling and the structure of this essay review; the five chapters are shown as boxes on yellow background.

which these patterns can be generalised, as well as of the processes and mechanisms responsible for these patterns, drawing extensively upon examples from Fennoscandian vegetation which I have had the opportunity to study for more than 30 years. The extended gradient analytic perspective outlined in this chapter forms the basis for the discussion, in the fourth of the five chapters, of implications for critical steps in the distribution modelling process. This discussion is structured by the three main components needed for statistical modelling listed by Austin (2002): (1) 'ecological model', i.e., 'theory to be used or tested'; (2) 'data model', i.e., the 'collection and measurement of ... data'; and (3) 'statistical model', i.e., 'the statistical theory and methods used'. These 'components' will be referred to as the composite steps of the DM process elsewhere in this essay review. The discussion of ecological model starts with nicherelated concepts and conceptual models, and concludes with a proposal for a new conceptual framework for DM based upon the gradient analytic perspective. This framework is used in the discussions of data model and statistical model. I conclude this essay review with a brief discussion of potential contributions from DM to ecological theory and finally provide a list of challenges for DM.

BASIC CONCEPTS AND TERMINOLOGY OF GRADIENT ANALYSIS

THE GRADIENT ANALYTIC PERSPECTIVE

The gradient analytic perspective, i.e., explanations of natural variation based upon knowledge about environmental gradients and species' responses to these gradients, consists of insights obtained by gradient analysis of different species groups in different ecosystems in different parts of the world. Several important terms are used in this explanation, which themselves need to be explained. The first of these is **environmental gradient** (Whittaker 1967), which denotes the more or less gradual variation in any anvironmental 'factor'. In the DM context the term is mostly used for 'factors' that may potentially impact a species or another modelled target. Such 'factors' may or may not be 'environmental' in the strict meaning of the word. Examples of strictly 'environmental' factors are concentrations of nitrate or calcium in the upper soil layers, and volumetric soil moisture. However, in principle, 'factors' of all kinds may be of relevance for modelling distributions of natural phenomena, including, e.g., historical factors and other aspects of human influence (e.g., Hamre et al. 2010). Another example of an environmental gradient in this wide sense is disturbance severity, which can be approximated by the soil depth to which the impact of a tree uprooting incident can be traced (Schaetzl et al. 1989b). This broad concept of an environmental gradient also comprises 'factors' that are essentially biotic, e.g., tree-layer cover which indirectly impacts forest understorey vegetation by giving rise to variation in several strictly environmental 'factors', such as incident radiation, throughfall precipitation, and litterfall (Økland & Eilertsen 1993).

The term **gradient analysis** (GA) is defined according to ter Braak & Prentice (1988: 272), as 'the interpretation of community composition in tems of species' responses to environmental gradients in the broadest sense'. The term **community**, which appears in this definition of 'gradient analysis', is here defined as organisms which live together at the same time within a restricted area (cf. Ricklefs 1973), i.e. the biotic component of ecosystems. Whittaker (1967: 207) defines the term 'gradient analysis' simply as 'a research approach for study of spatial patterns'. The similarity between Whittaker's definition and the definition of distribution modelling provided at the very start of the introduction to this essay review should be noted.

Gradient analysis has been an important part of ecological research for almost a century, performed with increasingly sophisticated analytical methods. A multitude of methods for gradient analysis exists, ranging from simple graphical tools for visualisation (e.g., Whittaker 1952, 1956) to more sophisticated, univariate and multivariate, statistical methods (e.g., Økland 1990a, McCune & Grace 2002, ter Braak & Šmilauer 2002, Zuur et al. 2007). The concept of gradient analysis covers variation from the finest spatial scales (near the size of individuals) to the regional scale, and from time scales of seasonal and year-to-year variation to variation on geological time scales (Birks 1993b). The gradient analytic perspective therefore includes environmental variation on all spatial and temporal scales, and the relationships of species to all of this variation.

The most fundamental insights of the gradient analytic perspective can be summarised in three points as follows (Whittaker 1967, Austin & Smith 1989, Økland 1990a, Austin 2005):

- External 'factors' do not influence the species one by one, but act on the species in concert. Explanatory variables used to characterise environmental gradients of importance for species and other modelled targets tend to be more or less strongly correlated with other explanatory variables. Therefore, the concept of the **environmental complexgradient** (Whittaker 1956), or, simply, **complex-gradient**, i.e., a set of more or less strongly correlated environmental variables, is fundamental for describing and understanding variation in species' responses to the environment.
- 2. A few major complex-gradients normally account for most of the variation in species composition that can be explained environmentally. While innumerable complex-gradients may, in principle, explain variation in the 'degree of presence' of a taxonomically, functionally and/or geographically delimited set of species, such as vascular plants in Norway (Pedersen 1990), soil-dwelling insects at the Finnish archipelago of Åland (Niemelä et al. 1985, or mycorrhiza-forming fungi in the Solhomfjell forest area in S Norway (Bendiksen et al. 2004), studies of variation in species composition by ordination methods usually fail to extract more than three gradients in species composition that are interpretable in terms of environmental complex-gradients (e.g., Økland & Eilertsen 1996, T. Økland 1996, Økland et al. 2001). The term major complex-gradient is used for these few, usually one, two or three, complex-gradients that account for most of the variation in species composition that can be explained environmentally. Environmental gradients are concrete in the sense that gradient positions can normally be quantified by measurements of soil pH, soil calcium concentrations, soil water content, photon fluxes, or other variables. Complex-gradients, on the other hand, are abstractions. No obvious choice of a representative variable that can be used, e.g., to scale complex-gradients, therefore exists. Operationalisation of complex-gradients is usually accomplished by way of indirect indicators, e.g.: by the main structure axis extracted from a set of measurements of relevant environmental variables, extracted by PCA ordination; by use of one, selected, environmental variable as a proxy; or by use of a gradient in species composition, e.g., extracted by an ordination method, which is interpreted as conditioned on this complex-gradient (Økland 1992, Ejrnæs 2000, Rydgren et al. 2003).
- 3. *Species occur within a restricted interval along each major complex-gradient.* The range of genetic variation that can be maintained in a population or a set of populations, within which individuals shall be able to exchange genes by normal mating mechanisms, is limited. Accordingly, one of the most important ecological consequences of

natural selection is that trade-offs are continuously made between traits that are, as such, all beneficial, but that cannot be combined. Examples of such traits are low and high growth rates, small and large seeds, etc. (Tilman 1990). Trade-offs restrict the tolerance of every species to a narrower or broader interval along each major complex-gradient. If a sufficiently broad range of variation along a major complex-gradient is taken into consideration, each species will be able to survive, or occur, or have positive **fitness**, in a restricted interval along the complex-gradient only. The term 'fitness' is here defined demographically, as the average number of descendants in the next generation per individual in the current generation (Caswell 2001). Outside this interval the species will normally be absent or have negative fitness.

I consider the gradient analytic perspective (GAP) as a 'theory', just as evolution of species through natural selection is a theory (Lawton 1999, Dawkins 2009). Several definitions of 'theory' exist, of which one reads: 'a scheme or system of ideas or statements held as an explanation or account of a group of facts or phenomena; a hypothesis that has been confirmed or established by observation or experiment, and is propounded or accepted as accounting for the known facts; a statement of what is held to be the general laws, or causes of something known or observed' [Oxford English Dictionary, cited from Dawkins (2009)]. The gradient analytic perspective makes up a theory according to this definition because it comprises a coherent system of ideas. However, like other biological 'theories', it hardly meets the demands for a scientific theory in the strict sense of Popper's (1959, 1989), which requires falsifiability of appropriate alternative hypotheses.

THE ECOLOGICAL AND GEOGRAPHICAL CONCEPTUAL SPACES

The three fundamental insights of the gradient analytic perspective address patterns of variation in the 'degree of presence' of species along major complex-gradients. Three basic geometric representations ('conceptual spaces') are useful for conceptualising these patterns. From the second insight it follows directly that the low-dimensional **ecological space** with the major complex-gradients as axes is particularly appropriate as a conceptual geometric space for representation of variation in species' quantities, i.e., what is referred to as their 'degree of presence'. Most often, the ecological space is conceived as a an orthogonal space although non-orthogonal axes may in many cases be more realistic, accounting for the fact that major complex-gradients often are not fully independent. This is exemplified by the water-table and lime richness gradients in boreal mires (Malmer 1962, Tyler 1981, Økland 1990b). The complex-gradients, i.e., the axes of the ecological space, are abstract ideal combinations of environmental variables that maximise variation in species' 'degree of presence' (Økland 1990a).

Several categories of variables can be used as proxies for axes in abstract ecological space:

- 1. *Single environmental variables* (Austin & Gaywood 1994); the conceptual geometric space with selected, measurable, environmental variables as axes are referred to as the **environmental variables space** (Økland 1990a).
- 2. *Combinations of environmental variables*, for instance obtained as axes in constrained ordination (CO; ter Braak 1987, Palmer 1993). The most popular constrained ordination methods, redundancy analysis (RDA) and canonical correspondence analysis (CCA; e.g., ter Braak 1987), find axes that are linear combinations of environmental variables,

but methods also exist that search for other functional relationships (Makarenkov & Legendre 2002). It is the 'linear combinations', 'LC scores' of ter Braak (1987) and 'maximally constrained' site scores of Palmer (1993), that represent true linear combinations of environmental variables, while the 'weighted average' scores, 'WA scores' of ter Braak (1987) and 'minimally constrained' site scores of Palmer (1993), fail to have an explicit interpretation in terms of concrete environmental variables and are irrelevant in this context (McCune 1997). Furthermore, it should be noted that all environmental measurements are noisy in the sense that they are subject to recording or measurement error and natural variability, and that the magnitude of this stochastic variation affects the performance of environmental variables as proxies for axes of the ideal ecological space (McCune 1997).

3. *Environmentally interpreted gradients in species composition* (**coenoclines**; Whittaker 1967), e.g., identified by ordination methods (Økland 1986a, 1990a, Ejrnæs 2000, Rydgren et al. 2003).

The concept of the **ecocline** (Whittaker 1967, Økland 1990a, Halvorsen et al. 2009), i.e., the parallel, more or less gradual, co-variation of species composition, i.e. a coenocline, and a major complex-gradient, is central to the gradient analytic perspective. Thus, R. Økland (1996) maintains that identification of ecoclines is a major goal of general-purpose ecological studies in the gradient analytic tradition, i.e., studies which aim at modelling relationships between species and the environment within a study area (Whittaker 1967, Gauch 1982a, Økland 1990a). The ecocline concept can be used to rephrase the aim of general-purpose gradient analytic studies as follows: 'identification of the most important ecoclines, i.e., gradients in species composition and the complex-gradients responsible for this variation, in a study area'. Having identified the major ecoclines, variation in properties of single species, species richness, biomass, productivity, etc., along identified ecoclines can be studied.

The gradient analytic (GA) tradition primarily addresses relationships in ecological space, i.e., without taking the geographic positions of observation units into account. Access to georeferenced observation units opens for visualising coenoclinal or ecoclinal patterns on maps (e.g., Pedersen 1990) as well as for analyses of spatial patterns, e.g., by geostatistical methods (e.g., \emptyset kland et al. 2001, Edvardsen & \emptyset kland 2006). Distribution modelling (DM) starts, and may also end, with patterns of variation in species' 'degree of presence' and/or variation in explanatory variables in a concrete, two- or three-dimensional **geographical space** (e.g., Legendre & Fortin 1989), with geographical co-ordinates *x*, *y* and eventually also *z*, as its dimensions (Guisan & Zimmermann 2000). Every georeferenced site can be represented by a point in geographical space, regardless if it is considered as a dimensionless sampling point or as occupying a fixed area (e.g., a 1-m² vegetation quadrat) or volume (e.g., a 1-m³ volume of sea water). In the latter cases, the observation unit can be represented in geographical space by the position of the centroid or by the range it occupies along each axis.

The geographical space, or a subset of this space, can be divided into contiguous quadrats (grid cells) of equal size by the process of rasterisation or gridding, to give a rasterised geographical space. The term discrete environmental variables space is used for an environmental variables space in which characteristics of grid cells are shown, while the term continuous environmental variables space is used for a space in which other observation units than grid cells are shown. A *set* of grid cells, which corresponds to a specific rasterisation of geographical space, is referred to as units in abstract geographical space when their collective properties are addressed without taking geographical co-ordinates into account.

SAMPLING

Species, as well as other categories of observable object of relevance for distribution modelling, comprises a finite number of individuals. This number can, however, be extremely large and for many natural phenomena, species included, defining individuals is difficult. This is exemplified for species by the dichotomy between ramets or clonal fragments, and genets, i.e., offspring from the same zygote (cf. Harper 1977). All individuals that belong to the same cetegory make up a population according to the statistical definition of the term (all potential sampling units for a phenomenon), while in a biological context a population is defined as individuals belonging to the same species, likely to exchange genetic material or interact with each other in some way. One 'statistical population' may thus make up several 'biological populations'. Each individual present at a given time-point occupies a discrete volume of space. The population, statistical or biological, can therefore be characterised by properties such as number of individuals, mean size of individuals, size variation, and mean distance between neighbouring individuals (e.g., Hutchings 1997). In the real world, recording all individuals in a population is possible only in exceptional cases and estimation is needed to infer properties of the phenomenon studied. Estimation requires access to a representative data set, obtained from the population by sampling, followed by modelling of the relationship between response and explanatory variables. In accordance with Dungan et al. (2002) I define **sampling** as the methods and procedures used to acquire information about the phenomenon under study, i.e., the modelled target. Regardless of which sampling procedure is chosen, sampling inevitably implies filtering of information about the studied phenomenon and, hence, imposes restrictions on the properties of the studied phenomenon that can be inferred from subsequent analyses of the sample (Økland 1990a, 2007). Therefore, as pointed out by Dungan et al. (2002), a clear distinction needs to be made between the properties of a studied phenomenon as such, e.g., a species' distribution or the environmental conditions at a locality, and properties inferred by analysis of a **sample** of observations of this phenomenon.

Natural sampling units can be used in exceptional cases when clones or individuals are observation units (Dungan et al. 2002). In all other cases, sampling is carried out by collecting data for observation units, i.e., (de)limited areas or volumes in a field site or in the laboratory for, or within which, information about a phenomenon is collected. In most cases, observation units are standardised with respect to temporal and spatial coverage. As pointed out in an extensive literature on the 'modifiable area unit problem' (MAUP; e.g., Openshaw & Taylor 1979, Dungan et al. 2002, Wu 2004) the choice of observation-unit dimensions fundamentally influences the properties of the phenomenon that can be inferred from results of subsequent analyses. However, the sample of observation units does not necessarily have to be subjected to analysis (modelling) as it is. We therefore distinguish between the sample of observation units as such, the raw observations, and samples (there may be more than one) of units subjected to analysis. An example of a study in which units subjected to analysis were different from raw observation units is that of Mathiassen & Økland (2007): observation units searched for epiphytic pyrenomycetes in the field were individual Salix shrubs or trees, while multivariate analyses were carried out on total species lists for sets of 10 Salix individuals of the same species, situated in the same bioclimatic zone and section.

Each observation unit can be represented by a point, an area, or a volume, in any of the three conceptual spaces (or variants thereof; see above). Co-ordinates in environmental variables space are given by the values recorded for single environmental variables that span the space; co-ordinates in ecological space are given by values for combinations of environmental variables or environmentally interpreted gradients in species composition; and co-ordinates in geographical space are given by geographical co-ordinates such as longitude and latitude, or east-

ing and northing as given by projected UTM (Universal Transverse Mercator) grid references.

SPATIAL AND TEMPORAL SCALES

The concept of 'scale' is essential in all branches of science that deal with the geographical distribution of spatially explicit entities (Wiens 1989, Legendre & Legendre 1998). The term 'scale' is, however, used with so many different meanings that it was considered a nonconcept by Dungan et al. (2002), who proposed its replacement by other, more precise terms in order to avoid confusion. So far, their proposal has not been approved by the research community. I have therefore retained the term 'scale' in this essay review for description of spatial and temporal patterns of variation, in accordance with current practice. In order to maximise clarity, I define scale-related terms explicitly.

In principle, scale and associated terms can be used to address categories of three different kinds (Dungan et al. 2002): the sample of observation units; a sample of units subjected to analysis, and natural units of the studied phenomenon (e.g., individuals of a species). For each of these three categories, two 'dimensions', or independent variables, are needed to describe the spatial dimension, the 'spatial scale', and two dimensions are needed to describe the temporal dimension, the 'temporal scale' (Dungan et al. 2002).

The two variables that characterise the spatial dimension, both defined in geographical space, are (Wiens 1989, Dungan et al. 2002):

- 1. The **spatial grain**, mostly referred to only as **grain**, is the size, in geographical space, of *one* observation unit. The grain can be expressed as a linear measure, as an area, or as a volume. Custom practice is to express grain in linear terms. For quadratic observation units such as grid cells, the length of the edge is typically taken to be the grain, e.g., 1, 5, and 10 km for the grid-cell observation units used in the study of biogeoclimatic variation in Norway by Bakkestuen et al. (2008), and 1 m for 1-m² vegetation plots (e.g., Økland et al. 2001). Strictly speaking, however, the largest linear dimension of quadratic or rectangular observation units is the length of the diagonal. For observation units with a circular shape, such as the pitfall traps with an aperture diameter of 65 mm as used by Niemelä et al. (1985) for collecting ground-dwelling beetles, the aperture diameter can be taken as the grain.
- 2. The **spatial extent** of the study area, mostly referred to only as **extent**, is the size, in geographical space, of the area within which observation units that make up a sample were collected. As for grain, the extent of quadratic or rectangular study areas is typically recorded as the length of the longest edge, although the diagonal is the largest linear dimension of the area. For study areas with irregular shapes, the longest distance across the area is typically recorded as the extent. Study areas can be naturally delimited (e.g., islands; Niemelä et al. 1985, Preston et al. 2011), they can be delimited by political boundaries (e.g., a country; Pedersen 1990), or they can be delimited by other, e.g., practical, criteria (e.g., the boundaries of a nature reserve; Økland et al. 2001).

Similarly, the temporal dimension is characterised by **temporal grain** and **temporal extent**. Temporal grain is exemplified by recording vascular plants in vegetation plots, which is normally completed within 24 hours. Temporal extents vary from typical values of months, e.g., one summer (Økland et al. 2001), two summers (Bratli et al. 2006), or even five summers (T.



Fig. 2. Terms related to spatial scale and distribution. (a) Map of a land area, delimited by continuous thick line, with localities for a hypothetical species represented by dots. The shaded region delineated by a broken line is the extent of occurrence of the species. The study area from which a sample of observations of the species is obtained is indicated by the large quadrat, delineated by a continuous line. The linear dimension (size) of this study area is the extent of the sample. The study area is rasterised into a regular hexadecadal grid, i.e., a grid with $16 \times$ 16 grid cells, of which each grid cell is taken as an observation unit. The length of the edge of one grid cell is the grain of the sample. (b) Raster map of records of the hypothetical species in the 256 observation units; presence (filled grid cells) or absence (open grid cells). The species is recorded as present in 43 out of the 256 grid cells and, accordingly, has a prevalence in the sample of 0.168. If the edge of each grid cell is 10 km and, hence, the area of each grid cell is 100 km², the area of occupancy of the species within the extent of the sample is 4,300 km².

Økland 1996) for large sets of vegetation data, to decades or even centuries for long-term studies of vegetation dynamics such as the 60-year study of forest understorey vegetation at Karlshaugen, SE Norway (Nygaard & Ødegaard 1999), or the exceptional Rothamstead Park Grass Experiment, initiated in 1856 (e.g., Silvertown et al. 2006). In each of the 10 observation units in the study of Niemelä et al. (1985), beetles were trapped during four periods of five days each, between May 22 and August 24, 1982. Both the temporal grain and the temporal extent of this study are therefore 94 days.

The meaning of grain and extent is illustrated in Fig. 2 by a sample of observations units of a hypothetical species, but the terms apply equally well to any other modelling targets. All known localities for the species, the study area, and observation units used for recording presence or absence of the species, are illustrated on a map in Fig. 2a. Sampling in each observation unit is accomplished by rasterisation of vectorised locality data, whereby points, lines or polygons in (continuous) geographical space is converted to raster data with reference to the rasterised geographical space. The data set consisting of binary observations of recorded presence or absence in the 256 observation units (Fig. 2b) can be subjected to analysis, in which case the set of units subjected to analysis is the same as the set of observation units. An alternative sample of units

subjected to analysis is the set of 16 units, each consisting of 4 × 4 cells of the original 256-cell grid, with presence or absence scored for each. The linear grain size of units in this sample is 4 times larger than in the original sample while the extent of the samples are the same.

When the grain and the extent of the study area are allowed to vary independently of each other, which is normally the case, two independent variables, one for the extent and one for the grain, are needed to characterise the *linear* spatial dimension and two independent variables are needed to characterise the temporal dimension of any sample of observation units or units subjected to analysis (Fig. 3). Nevertheless, common practice is to characterise the spatial 'scale' of a study by terms such as 'fine' or 'small' vs 'large', 'coarse' or 'broad'; 'micro' vs 'macro'; 'local' vs 'regional'; or 'site', 'landscape' and 'continental' vs 'global', with reference to one linear scale in metric units (e.g., Willis & Whittaker 2002, Pearson & Dawson 2003). Fig. 3 shows that the use of one number to characterise 'spatial scales' is generally inappropriate and that more precise definitions of scale-related terms are needed. The statement 'large spatial extents are associated with coarse data resolutions, and small extents with fine data resolutions' of Pearson & Dawson (2003), does, however, indicate that these authors use one linear scale in metric units to characterise 'spatial scales' based upon an implicit, but unspoken, assumption of a more or less fixed relationship between extent and grain. This relationship is characterised by the extent-grain ratio, which is defined as the linear dimension of the extent divided by the linear dimension of the grain. A related term is spatial domain (Wiens 1989) which is defined as the range, along the scale of metric units, that can be addressed by analysis of a given sample. The spatial domain is the interval bounded below by the linear dimension of the grain, e.g., grid-cell edge length, and above by the linear dimension of the extent. The spatial domain of the sample of presence/absence data for hypothetical species in Fig. 2 is 10–160 km. The extent-grain ratio expresses the width of the spatial domain in grain-size units. The extent-grain ratio of the regular hexadecadal grid in Fig. 2, i.e. the grid with 256 grid cells in a 16 × 16 pattern (cf. Conlisk et al. 2009), is 160/10 = 16.

A sample of observation units can be characterised by one number on one scale of metric units if and only if the extent-grain ratio is fixed. This is illustrated for two series of nested, regular hexadecadal grids in Fig. 3. Two options therefore exist for precise definition of terms for 'spatial scales': characterisation by two attibutes, grain *and* extent, or characterisation with reference to a fixed extent-grain ratio. The second option is chosen for defining the terms for characterising spatial scales in this essay review: the term **spatial scale** refers to the linear grain size in samples with extent-grain ratio of 16, typically exemplified by regular hexadecadal grids (Figs 2–3). I define seven terms for spatial scales (Fig. 4), which can be grouped into **broad scales** (linear grain > 1 km) and **fine scales** (linear grain < 1 km). Broad scales include **global scale**, **coarse regional scale**, and **fine regional scale**; fine scales include **coarse local scale**, **medium local scale**, **fine local scale**, and **micro scale**. These terms are to some degree comparable with the terms used by Pearson & Dawson (2003), originally proposed by Willis & Whittaker (2002), see Fig. 4.

Of these spatial scales, the global scale as here defined, which includes the 'continental scale' and 'global scale' of Willis & Whittaker (2002), is mostly outside the range of scales at which environmental factors, recordable today, can explain distributions of species and other relevant targets for modelling. Instead, variation at the global scale is the results of actions of fundamental geophysical processes such as continental plate movements, sea-level changes, mountain-chain upfolding, and repeated glacial cycles, over millions of years (Willis & Whittaker 2002). The spatial distribution of these geological processes themselves and their imprints on the distribution of landforms, ecosystems, and taxonomic groups (see, e.g., Qian & Riclefs 2000, Qian et al. 2007, Riclefs 2007, 2011, Whittaker & Kerr 2011), is outside of the scope of this essay review, the focus of which is therefore restricted to spatial scales from the coarse



extent (m), log₁₀ scale

Fig. 3. The spatial scale of samples (data sets), characterised by the spatial extent (horizontal axis) and the spatial grain (vertical axis). Characteristics of samples used in four published studies are indicated by black symbols: Niemelä et al. (1985) who studied ground-dwelling beetles in the Åland archipelago, Finland, by use of pitfall traps with a diameter of 65 mm; Pedersen (1990) who studied the distribution of vascular plants in the Nordic countries using grid cells of 50 ×50 km as observation units; Økland et al. (2001) who studied the species composition of vascular plants, bryophytes and lichens of swamp forests in Østmarka nature reserve, SE Norway, using 1-m2 vegetation quadrats; and Bratli et al. (2006) who studied the vascular plant species composition of land cover-class patches varying from 3 m2 to 801 000 m2 in SE Norwegian agricultural landscapes. Open and filled red symbols denote two sequences of nested, regular hexadecadal grid samples, i.e., samples with all cells of a regular 16 × 16 grid as observation units. Nestedness is obtained by taking one cell of one grid as the extent of a new regular hexadecadal grid, the cells of which are used as observation units in the sample at the next lower nesting level, and so on. The linear grain size of regular hexadecadal grids are used to define terms for spatial scales in this study (see Fig. 4). Gray, dotted lines are used to indicate 1 m (log10 1 = 0), 1 km (log10 1 000 = 3) and 1 000 km (log10 1 000 000 = 6) along both axes. A linear grain size of 1 km in regular hexadecadal grids marks the limit between fine and broad spatial scales.

Linear grain (extent- grain ratio = 16),	Linear extent, m	Terminology used in this essay review	Terminology of Pearson and Dawson (2003)
10 ⁶	10 ^{7.2}	global	global
	10 ^{6.2}	coarse	continental
10 ⁵			regional
10 ⁴	10 ^{5.2}	fine regional	
10 ³	10 ^{4.2}		landscape
10 ²	10 ^{3.2}	coarse local	local
		medium local	
10 ¹	10 ^{2.2}	fine local	site
10 ⁻¹	10 ^{0.2}	micro	micro

Fig. 4. Terminology for spatial scales, defined as the linear grain size in samples with extent-grain ratio of 16 such as regular hexadecadal (16×16) grids (see Fig. 1). Intervals on the linear scale in metric units that correspond to each term are shown on the vertical axis. Scale-related terms of Pearson and Dawson (2003), which are defined by these authors primarily with reference to study-area extent, are incorporated in the figure by assuming a fixed extent-grain ratio of 16, in accordance with the statement 'large spatial extents are associated with coarse data resolutions, and small extents with fine data resolutions'. An extent-grain ratio of 16 corresponds to a difference between grain and extent of 1.204 units on the log10 scale.

regional to micro.

The term spatial scale interval in which variation is large is defined as the range of spatial scales, within which, by analysis of samples with extent-grain ratio of 16 such as regular hexadecadal grids, the variation in a variable of interest is distinctly larger than in samples with smaller or larger grain sizes. There are good reasons to assume that the spatial scale interval in which variation is large, estimated from samples of empirical data, will be much more strongly influenced by the grain than by the extent. Regardless of how small grain size is used in a study, there will be environmental variation and, most often, also variation in the performance of most species, within each observation unit. Only between observation-unit, i.e., between-grain, variation can normally be 'explained' by analysis of data while within-grain variation is left unexplained (Wiens 1989, Økland 1990). Patterns emerging from analyses, such as coenoclines identified by ordination methods, will therefore remain more or less unaffected by changes of extent as long as the relative frequency of different combinations of fundamental properties, such as important environmental conditions, does not change. The frequency of fundamental properties will change when the study area is extended into areas with different climate, different topography, different bedrock, different land-use history, and/or broader range of variation along important other important environmental gradients.

DISTRIBUTION, PERFORMANCE, AND THE OVERALL ECOLOGICAL RESPONSE

The term **distribution** is used in this essay review to address the physical arrangement of objects of that belong to a specific type category, in general. Analysing distributions requires a more precise and specific terminology for 'characteristics of species' areal occupancy in geographical space' [definition of 'distribution' by Hengeveld & Haeck (1981)]. A fundamental property of distributions is the **extent of occurrence** (Fig. 2a), defined as the 'area which lies within the outermost geographic limits to the occurrence of a species' (Gaston 1991, Gaston & Fuller 2009). Commonly used, but less precise, terms for 'extent of occurrence' are 'geographical range' and 'distributional range'. The extent of occurrence is a property of distributions that is essentially unaffected by rasterisation.

The term performance (van der Maarel 2005) is used as a collective term for what has so far been referred to as the 'degree of presence' of a natural phenomenon within one observation unit, i.e., its quality (presence or absence) and, eventually also, its quantity. I avoided the commonly used term 'response', which is often used for the performance of species ('the species' response'), for two reasons: (1) potential confusion with the term 'response variable'; and (2) the term 'response' is less appropriate for modelled targets such as landforms and nature types which do not respond mechanistically to the environment in the same way as species. Care should be taken not to confound 'performance' as defined above with the predictive performance of a model. Variables used to record performance are termed performance measures. Performance can be recorded qualitatively, as **presence** (= occurrence), the opposite of which is **absence** (Fig. 2b), or, quantitatively. Examples of measures of quantitative performance are: abundance, number of individuals of a species or, for other modelled targets, discrete units, or, for clonal organisms, organismal units (van der Maarel 2005); density, abundance per unit area (van der Maarel 2005); cover, vertical projection of biomass (Du Rietz 1921, Wilson 2011); and subplot frequency, fraction, or percentage, of subplots into which an observation unit is divided, in which a species is present (Økland 1988) in the observation unit. For modelled targets such as nature types, the term **fractional area** is used for the fraction, by area, of an observation unit that is occupied. An index obtained by combining two or more quantitative performance

measures is termed importance value (e.g., Curtis 1959, Økland 1986).

The term aggregated performance is used as a collective term for performance, recorded by some performance measure, aggregated for sets of observations units of a modelled target. Often used aggregated performance measures are (e.g., Økland 1990a): frequency of presence, the fraction, or percentage, of observations units in a set, in which the modelled target is present; and **mean abundance**, the average of abundance values for observation units in the set. The mean abundance can be calculated by taking all observation units in the set into account, or only by using observation units in which the modelled target is present. Aggregated performance is typically estimated by use of a representative sample of observation units in which a performance measure, e.g., presence or absence, or abundance, is recorded. Technically, the frequency of presence can also be calculated for samples of observation units in which observed presence is recorded for some observation units while nothing is known about presence or absence in the remaining, uninformed background observation units. These two fundamentally different types of data are referred to as presence/absence data, or P/A data, and presence-only data, or PO data, respectively. The term frequency of observed presence is used for the fraction of observed presences in a PO data set. The frequency of recorded presence is a characteristic of the data set that can be strongly or weakly related to the real frequency of presence.

A specific set of terms are often used for performance aggregated to, or estimated for, the entire study area, e.g., over all grid-cell observation units in a rasterised study area. The term **prevalence** (e.g., Hirzel et al. 2006), which is used for the modelled target's frequency of presence in a study area, is synonymous with occupancy (Conlisk et al. 2009). The meaning of prevalence is exemplified by the hypothetical species in Fig. 2 which occurs in 43 out of 256 grid cells in the study area and therefore has a prevalence of 0.168. The **area of occupancy**, i.e., the total area of grid cells in which a species, or another modelled target, is recorded as present, is an alternative way to express occupancy in sets of raster data. The area of occupancy is the number of presence grid-cells × the area of each grid cell (Gaston 1991, Gaston & Fuller 2009), All characteristics of distributions that are estimated from rasterised observational data depend strongly on the choice of grain and extent (Dungan et al. 2002, Gaston & Fuller 2009). In general, prevalence decreases with increasing extent-grain ratio.

Knowledge of variation in aggregated performance along an environmental gradient, i.e., of patterns of variation in the modelled target's response to environmental complex-gradients, is an essential element of the gradient analytic perspective. The term **overall ecological response** is used to denote variation in aggregated performance with respect to any variable that may be used as axis in the discrete or continuous ecological variables spaces or in ecological space. The word 'response' is used here in a statistical sense, without any allusion to causal or other functional relationships between the environmental complex-gradient and the modelled target. Typically, aggregated performance is estimated for intervals of fixed width, e.g., one unit, along an axis in environmental variables space, ecological space or geographical space. Examples of intervals and axes in the respective spaces are one pH unit, 1 S.D. unit along an ecologically interpreted DCA ordination axis, and a latitudinal band of width 0.1°. The overall ecological response is exemplified in Fig. 5 which shows variation in frequency of presence of a hypothetical species in response to two explanatory variables.

A model for a modelled target's overall ecological response with respect to a gradient is the target' **response curve** with respect to that gradient (Ellenberg 1953, Whittaker 1956, 1967, Austin 1976). Two examples of **species response curves** are given in Figs 5d–e. Examples of parameters that may be useful for characterising the overall ecological response are: the modelled target's **tolerance** with respect to the gradient, i.e., the range along the gradient in which the modelled target occurs; and its **optimum** along the gradient, i.e. the gradient position at which the response curve peaks (Gauch & Whittaker 1972, Minchin 1987, Austin 2005).





Fig. 5. The overall ecological response of the hypothetical species in Fig. 2. (a) Observations of the species are made in a regular hexadecadal grid sample of 256 observation units, i.e., with extent-grain ratio 16. Species' performance is recorded as presence (filled grid cells) or absence (open grid cells) in each grid cell. (b, c) Recorded values for two explanatory (predictor) variables; explanatory variable 1 (b) and explanatory variable 2 (c). (d, e) Overall ecological response of the species to each of the two explanatory variables, calculated by use of frequency of presence as measure of aggregated performance. Smooth species response curves are indicated by red lines in (d) and (e).

Furthermore, response curves can be characterised by descriptive statistics such as skewness and kurtosis [see Sokal & Rohlf (1995) for definitions]. I use the term **fractional amplitude** for tolerance, expressed as the ratio of the species' amplitude along a gradient and the length of the entire gradient, expressed in relevant units. The fractional amplitude is the difference between the maximum and minimum values for gradient position, recorded on some scale, between which aggregated performance of the modelled target is expected to be > 0, divided on the length of the gradient. Gradient length is normally estimated as the difference between the maximum and minimum value encountered for gradient position for observation units in a sample, disregarding if the species is present or not. The fractional amplitude depends on the 'size' of individual sampling units (grain) and, most notably, of the 'extent of the study area in environmental space' (not in geographical space). Figs 5d–e show overall ecological responses of a hypothetical species with respect to two explanatory variables, visualised by species response curves drawn onto barplots of frequency of presence for each of the four levels of each explanatory variable.

A VARIATION PARTITIONING APPROACH TO QUANTIFYING NATURAL VARIATION

Adequate description of patterns of natural variation requires that the concept of 'variation' can be operationalised and appropriately quantified. For this purpose, I adopt the principles of the variation partitioning (VP) approach, which have been developed as a part of gradient analysis (GA) through a series of publications starting with the influential paper of Borcard et al. (1992). In the GA context, VP mostly implies use of constrained ordination methods to partition variation in a multivariate response variable onto sets of explanatory variables, i.e., to quantify unique and shared components of variation among explanatory variables or sets of explanatory variables (Økland 2003). The approach also applies to single response variables, i.e., the univariate case (Venables & Ripley 2002, Crawley 2007). Explanatory variables appropriate for VP are single environmental variables, groups of environmental variables (Borcard et al. 1992, Økland & Eilertsen 1994, Raatikainen et al. 2007, Stevens et al. 2011), historical variables (Graae et al. 2004), geographical co-ordinates (Borcard et al. 1992, Økland & Eilertsen 1994, Raatikainen et al. 2007, Stevens et al. 2003), hierarchically nested generalisation levels (e.g., land-cover types; Økland et al. 2006), and time intervals (Svenning & Skov 2005, Pellerin et al. 2008).

The VP approach is most often used for identification, for given species groups in given ecosystems, of the explanatory variables that 'best explain' variation in species composition. Multivariate VP approaches thus assist identification of major ecoclines. Examples of studies in which the VP approach is used for assessment of ecocline importance, are the study of freshwater zooplankton by Pinel-Alloul et al. (1995), of forest understorey vegetation by Qian et al. (2003), of bird communities by Miller et al. (2004), of freshwater algae by McGowan et al. (2005), and of terrestrial arthropodes by Schweiger et al. (2005).

A desirable property of **variation components**, i.e. the variation associated with each unique source of variation in a variation partitioning analysis, is that they can be combined in a multifactorial manner (Anderson & Gribble 1998, Økland 2003). The variation partitioning approach therefore not only enables identification of which explanatory variables are important for variation in species composition, but also of spatial scale intervals at which variation is large (e.g., Økland & Eilertsen 1994, Wagner 2004, Økland et al. 2006, Raatikainen et al. 2007). Furthermore, the VP approach can be combined with descriptive geostatistical methods like semivariance analysis (Rossi et al. 1992, Burrough & McDonnell 1998) for further analysis of

spatial patterns.

The reliability of results of variation partitioning analyses, like the results of all other statistical modelling, depends on choice of an appropriate statistical model. However, most species show non-linear overall responses to the main complex-gradients (the third insight of the gradient analytic perspective) while the statistical model implicit in the constrained ordination methods most often used for VP basically assumes a linear relationship. This applies to both RDA and CCA, as evident from the 'linear aspect of correspondence analysis' demonstrated by Wagner (2004). This reduces the precision of variation components estimated by constrained ordination and, notably, inflates the estimated 'total variation' in species data to such extents that only relative amounts of variation explained by different sets and combinations of sets of variables normally can be trusted (Økland 1999).

The main reason for problems with model inappropriateness in multivariate studies is the large between-species variation in the shape of overall responses to main complex-gradients (Økland 1999). With only one response variable, however, VP reduces to analyses of variance components within a generalised linear modelling framework (e.g., Venables & Ripley 2002). In the univariate case, more specific and more complex models can be fit to the species in question, e.g., by allowing for non-linear relationships between response and explanatory variables. Estimates of variation components obtained for single species should therefore, in general, be expected to be more reliable than estimates of variation components for the entire species composition.

The variation partitioning approach allows re-formulation of the purpose of gradient analysis (GA) in the broad sense, including distribution modelling (DM), in terms of maximisation of the explained variation in the response variable (cf. Legendre & Legendre 1998). In the multivariate case, with species composition as response-variable set, indirect GA (ordination) aims at maximising the variation in species composition extracted on the lowest possible number of axes. Thus axis 1 is the latent, or constructed, variable that, with respect to the chosen statistical model, explains the maximum variation that can possibly be explained by any single variable, axis 2 is the constructed variable that explains the maximum residual variation after the variation explained by axis 1 is accounted for, possible to explain by any single variable, etc. Direct multivariate GA and univariate GA, including DM, aim at explaining as much of the variation in the response as possible by the supplied set of explanatory variables.

The variation in performance (presence/absence) of a modelled target can be quantified for all grids, and several measures of the total variation are available. Perhaps the simplest of these is the sum of squared differences between observed binary presence values in *n* grid cells and the mean, which equals the prevalence *p*, i.e. the sum of squares, given as:

$$SS = n \cdot p \cdot (1 - p).$$

SS depends only on *p* and *n*, is proportional with *n*, and peaks for p = 0.5 [for further information, see Crawley (2007)]. A derived measure of variation, which is comparable between grids of unequal size, is obtained by expressing variation as the fraction of the theoretical maximum variation in the grid. This measure, relative variation, which is given on a 0–1 scale, is given by

$$SS_{rel} = p \cdot \frac{1-p}{0.5 \cdot 0.5} = 4 \cdot p \cdot (1-p).$$

I use data for the hypothetical species in Figs 2 and 5 to exemplify how the variation partitioning principle can be used to quantify variation (see Fig. 6). The full set of observations of presence or absence of the species in the 256 cells of the 16 × 16 grid, the Fine sample, was

used to construct a Coarse sample with 16 large observation units, each with grain = 4 grid cells of the hexadecadal grid. Furthermore, observation units of the Coarse sample were used as extents of 16 subsamples of the Fine sample. The extent-grain ratio of the Fine sample is 16, while that of the Coarse sample and of Fine subsamples are 4. This facilitates comparability of explained variation between the spatial scales represented by the Coarse sample and the Fine sample, respectively.

For our hypothetical species, which is present in 7 out of 16 cells in the coarse grid, $SS_{rel,Coarse} = 0.984$. This value is comparable with the mean of SS_{rel} values for the 7 Fine subsample grids in which the species is present, which is $SS_{rel,Fine} = 0.757$ (the mean of SS_{rel} values of 0.234 in the grid with one presence, of 0.750 in the three grids with 4 or 12 presences, and of 0.938 in the 3 grids with 6 or 10 presences).

By use of an appropriate statistical model, the variation in species occurrence can be partitioned on variation explained by explanatory variables and unexplained variation. This is exemplified by generalised linear modelling with presence (or absence) of the hypothetical species as the response variable, modelled with respect to explanatory variables, e.g., variables 1 and 2 of Figs 5b and 5c, respectively, for the Coarse sample and the Fine subsamples. A linear model, for which the SS is an appropriate measure of variation, cannot be used with binary observations because predicted values for the response below 0 or above 1 make no sense. Instead, we may use deviance in a logistic regression model (a generalised linear model with logit link and binomial errors; Venables & Ripley 2002) to obtain appropriate measures of variation. The total deviance of such models is:

$$DEV = n \cdot p \cdot \ln p + n \cdot (1-p) \cdot \ln(1-p).$$

The deviance function for binomially distributed variables closely follows the sum of squares, peaking for p = 0.5 and having a value of 0 for p = 0 or p = 1 (Fig. 7). Like the sum of squares, the deviance can be turned into a relative measure of variation comparable between grids of unequal size, the fraction of the theoretical maximum deviance for the grid, by the following equation:

$$DEV_{rel} = \frac{[p \cdot \ln p + (1-p) \cdot \ln(1-p)]}{0.5 \cdot \ln 0.5 + 0.5 \cdot \ln 0.5} = \ln 2 \cdot [p \cdot \ln p + (1-p) \cdot \ln(1-p)].$$

For our example data, $DEV_{rel,Coarse} = 0.989$ and $DEV_{rel,Fine} = 0.805$. The best logistic regression model for observations of the species in the coarse grid, with explanatory variable 1 (EV1) as the only independent variable, is given by the equation

$$\ln\left(\frac{p}{1-p}\right) = -2.259 + 0.782 * (\text{EV1}) \,.$$

The explained deviance of this model is 2.610 out of a total of 21.930 units, i.e., a fraction of 0.119 which amounts to a fraction of 0.117 of the theoretical maximum deviance in this sample. It should be noted that the explained deviance depends on the variables in the model. By including (EV1)² in the model for the coarse grid, as suggested by the unimodal overall response of the species to this variable (Fig. 5d), the explained deviance increases to 6.1891 units, or 0.278× the theoretical maximum deviance in this sample. Explanatory variable 2 explains no variation in the coarse grid because the average value for this variable does not vary among observation units (grid cells).



Fig. 6. The variation partitioning principle, exemplified by analysis of two different samples of observations of recorded presence (filled grid cells) or absence (open grid cells) of the hypothetical species in Figs 2 and 5. The study area is a regular hexadecadal grid sample of 256 observation units, i.e. with extent-grain ratio 16. (a) Distribution of the species in two samples of observation units: Fine = 256 small units with grain = 1 grid cell of the hexadecadal 16 × 16 grid; and Coarse = 16 large units with grain = 4 grid cells of the hexadecadal grid. A thick, continuous line is used to separate large observation units. The extents are the same for both samples: the entire hexadecadal grid. Black and gray cells indicate presence in small and large observation units, respectively. (b) Variation in species performance in the two samples, expressed as fraction of the theoretical maximum deviance of an appropriate logistic regression null model, shown by the height of entire bars. The maximum variation is obtained when the species is present in 50 % and absent from 50 % of the observation units. The black parts of the columns show the fractions of variation in the Coarse and Fine samples, respectively, which are explained by explanatory variables 1 of Fig. 5b and 2 of Fig. 5c, respectively. The fraction of variation explained by variable 2 in the Fine sample is calculated as the average of variations explained in each of the seven subsets of the Fine sample, with extents equal to the observation units of the Coarse sample of 4×4 grids, in which the species occurs.

Similarly, we find that a fraction of 0.215 of the total variation, or a fraction of 0.173 of the theoretical maximum, is explained, on average, by explanatory variable 2 in the Fine sample (Fig. 6b). Within this scale domain, no variation is explained by explanatory variable 1 which has the same value for every grid in all of the 16 fine-extent grids.

The example in Fig. 6 illustrates the general principle that the tendency for patterns to differ among scales is the rule rather than the exception (Wiens 1989, 2002, Wu 2004).

The operationalisation of the variation partitioning principle exemplified for two nested, regular 4×4 grids in Fig. 6 can be extended to quantify the variation expressed at several spatial scales and, hence, to assess the spatial scale interval in which variation of explanatory variables of all kinds (environmental variables, coenoclines used as proxies for ecoclines etc.) is large. Most variables that are relevant for such analyses can be recorded on continuous scales, and can therefore be analysed by linear models using sum of squares as measure of variation. Variables with skewed distributions should be appropriately transformed before analysis, e.g., by the zero-skewness transformation (\emptyset kland et al. 2001).



Fig. 7. Variation in a sample of binary (presence or absence) observations of a species, expressed as a function of the prevalence (p) of the species. Variation is calculated as the fraction of the theoretical maximum (which is obtained for p = 0.5), averaged over all observations. Two measures of variation are used: red line = sum of squares; blue line = deviance for binomially distributed variables.

REDEFINING DISTRIBUTION MODELLING IN GRADIENT ANALYTIC TERMS

THE DISTRIBUTION MODELLING PROCESS

The explanation of distribution modelling given in the introduction, 'research with the purpose of modelling the distribution of observable objects of a modelled target, as a response to supplied explanatory variables', defines DM very broadly with respect to the specific type of natural phenomenon targeted, the modelling method used, types of explanatory variables used in the modelling, and intended uses of models. Three examples illustrate that most definitions of DM and related terms given in the literature are narrower than the DM definition given above: the definition of a 'species distribution model' by Elith & Leathwick (2009: 678) as 'a model that relates species distribution data (occurrence or abundance at known locations) with information on the environmental and/or spatial characteristics of those locations'; the operational definition of 'species distribution modelling' by Franklin (2009: xv), 'to model, or, in some way, spatially interpolate species distributions, and other biospatial variables'; and the definition of 'ecological niche modelling' by Peterson et al. (2011: 2), 'application of niche theory to questions about real and possible spatial distributions of species in the past, present, and future'.

The large diversity of DM-related approaches is, in my opinion, an argument for of a broad circumscription of the field: exchange of ideas among 'researcher guilds' is important to prevent school formation. Furthermore, and more importantly, a broad circumscription of DM is motivated by the fact that the gradient analytic perspective can serve as theoretical platform for the whole spectre of approaches encompassed by the broad definition of DM.

DM is often described as a four- or five-step procedure, of which some steps consist of multiple tasks (Guisan & Zimmermann 2000, Hirzel et al. 2002, Franklin 2009, Peterson et al. 2011). I here describe DM as a process with 12 steps (Fig. 8). These steps are normally, but not always, carried out in sequence according to the ordered list. In this chapter I briefly describe each step and provide definitions of relevant terms. In the discussion chapter, implications of the gradient analytic perspective for development of theory, methods and best practice will be discussed separately for each step.

- 1. *Problem formulation and specification*. All scientific investigations should start with an explicit formulation and specification of a problem, by use of well-defined terms. This requires a solid theoretical platform (cf. Guisan & Zimmermann 2000, Austin 2002, 2007).
- 2. *Collection of raw data for the modelled target.* DM requires georeferenced observational data for the modelled target. Typical sources of raw *species* data are museum collection databases (Loiselle et al. 2008, Mateo et al. 2010, Robertson et al. 2010) and inventory databases (Edwards et al. 2005), while other data sources may be relevant for categories of modelled targets other than species (e.g., see Franklin 2009). In some cases, several alternative response variables can be used to represent one modelled target (e.g., Wollan et al. 2011).
- 3. *Collection of explanatory data*. DM also requires data for explanatory variables, i.e., variables that may potentially account for some variation in the distribution of the modelled target. All explanatory variables used in DM have to be relevant for the purpose of the modelling (Step 1) which, among others, implies that they have to reflect variation at appropriate spatial and temporal scales. Furthermore, only variables that are avail-



Fig. 8. Overview of the distribution modelling process, emphasising interdependencies between the 12 analytic steps. Steps are grouped into three composite steps, 'ecological model' (red background), 'data model' (orange background), and 'statistical model' (yellow background), in accordance with Austin (2002). Steps that are mandatory for a study to be distribution modelling, are indicated by thick borders. Steps involved in re-iteration of the model are indicated by gray lines. Broken lines indicate optional pathways.

able for the entire study area can be used. Potentially relevant variables include those with a hypothesised or confirmed, direct functional relationship with the performance of the modelled target, those for which a correlative relationship with the modelled target is suspected, as well as all other variables that are available in an appropriate format. Appropriateness of formats may depend on the modelling method. Most DM methods treat all variables as either **continuous variables**, i.e., variables that can take every value in the real domain, or **categorical variables**, i.e., variables that can take a finite number of positive integer values, each of which indicate affiliation to a class, type, etc. Discrete, e.g., count, and ordered factor variables are typically treated as continuous variables while binary variables are treated as categorical variables with two levels. Collection of explanatory data contains two tasks:

- i. *Provide an updated overview of available explanatory variables*, i.e. variables that have previously been operationalised for DM.
- ii. Collection of data for new explanatory variables.
- 4. Conceptualisation of the study area. DM methods require rasterised input data for the modelled target as well as for all explanatory variables. Rasterisation, which is preceded by conceptualisation of the study area as a rasterised geographical space, implies fixing extent and grain, i.e., delimiting the study area and deciding the size of observation units. These important choices should, in principle, be guided by the problem formulation and specification (Step 1) alone. However, availability of appropriate raw data for the modelled target (Step 2) and, in practice, even more importantly, availability of data for relevant explanatory variables (Step 3), tend to dictate conceptualisation of the study area. The main reason for this is that preparation of explanatory variables with 'wall-to-wall coverage' for study areas with large extent-grain ratio is resourcedemanding. Often, therefore, is the grain size of practical DM studies set equal to that of relevant accessible data sets. A 'standard' grid-cell size of 1 × 1 km is used in many studies (e.g., Bombi et al. 2011, Jarnevich & Reynolds 2011, Marino et al. 2011), e.g., because the publicly available WorldClim data set (Hijmans et al. 2005) has this grain size. The set of two biogeoclimatic variables prepared for Norway by Bakkestuen et al. (2008) by PCA ordination of 54 climatic, geological and topographical variables, is available for 1 × 1 and 5 × 5 km grid cells (e.g., Wollan et al. 2008, Edvardsen et al. 2011, Stokland et al. 2011). Extents are often bound to follow administrative borders because data sets, both for modelled targets and explanatory variables, are national or developed for smaller administrative units. The demand for an overview of available data before the final decision about grain and extent is made, explains why conceptualisation of the study area is inserted in the DM process as a separate step after Steps 2 and 3.
- 5. *Preparation of independent variables*. Each explanatory variable collected in Step 3 is prepared for modelling by a two-step procedure, of which step (i) is mandatory:
 - i. *Rasterisation*, by which one value is assigned to each of the *n* observation units in the rasterised geographical space representation of the study area. Rasterisation is normally accomplished by use of geographic information systems (GIS; Burrough & McDonnell 1998, O'Sullivan & Unwin 2003). Most raster data are prepared by **spatial interpolation**, i.e., use of models to estimate unknown variable values from observations in georeferenced points. Accordingly, most explanatory variables used in DM are model predictions. The terms 'environmental layer' and 'GIS layer' are often used for rasterised variables. Rasterised explanatory variables can be qualitative (continuous) or categorical (i.e., factor-type or binary).
 - **ii.** *Transformation* is the mathematical operation by which one or several variables are derived from each raw explanatory variable. These **derived explanatory vari**

ables are in then used to parameterise the model (Step 8,iii). The terms 'explanatory variable', 'predictor variable', and 'independent variable' are mostly used in the literature interchangeably for (i) variables that may, potentially, account for some variation in a response, i.e., in general, without reference to a particular model; and (ii) input variables to parameterisation of the model (see Step 8,iii). In this essay review, I consistently use the term **explanatory variable** for (i) and the term **derived variable** for (ii), while the term **independent variable** is used collectively for the two. Independent variables may therefore include raw explanatory variables and/or variables derived from raw explanatory variables by transformation, i.e., derived variables.

- 6. *Preparation of response variable(s)*. SM requires that raw data for the modelled target is also rasterised to the grid chosen i Step 4. Like independent variables vectors obtained in Step 5, the response variable(s) vector(s) shall have length *n*, the number of grid cells within the extent. The response variable can be quantitative or qualitative, expressing the quantitative performance of the modelled target or its mere presence. Qualitative response variables can be of the presence/absence (P/A) or presence-only (PO) types. Synonyms for the term 'response variable', much used in the literature, are 'dependent variable' and 'training variable'.
- 7. *Statistical model formulation*. DM is mostly accomplished by univariate modelling methods, i.e., methods by which *one* response variable is modelled as a response to the independent variables [but see, e.g., Guisan et al. 1999)]. If the modelled target is represented by more than one response variable (Step 2), each of these is modelled separately. Modelling proceeds in two steps: In Step 7 a framework for the modelling process is set up, while in Step 8 this framework is used to find a model. Setting up the modelling framework (Step 7) consists of two tasks, of which both are mandatory in all statistical modelling:
 - i. *Choice of modelling method*, i.e. to decide which *category* of method to use [reviews of DM methods are found in papers and textbooks such as Guisan & Zimmermann (2000), Elith et al. (2006), Austin (2007), Franklin (2009), and Peterson et al. (2011)]. Methods currently in use for DM can be divided into **group discriminative methods**, i.e., methods that contrast environmental characteristics of presence data points with properties of absence, random or pseudo-absence points, and **profile techniques**, i.e., methods that make predictions from properties of presence data points alone.
 - ii. *Model specification*, i.e., specification of a mathematical function that expresses how the response variable is related to the independent variables. A statistical model typically has two elements, the systematic part and the error part, both of which need to be specified (Sokal & Rohlf 1995). Model specification is exhaustively discussed in standard statistical textbooks (e.g., Pinheiro & Bates 2000, Venables & Ripley 2002, Crawley 2007, Zuur et al. 2007, Hastie et al. 2009).
- 8. *Modelling of the overall ecological response*. In this step, a model, as specified in Step 7, ii, is fit to the sample of recorded values for the response and independent variables. Fitting a model normally involves three tasks, which are performed sequentially or as one integrated process, depending on the method. Operationalisation of modelling results is included in Step 8 as the fourth task.
 - i. *Model selection*, i.e., application of procedures that assist choice among alternative models, is normally accomplished by means of explicit criteria for model comparison based upon internal model performance assessment, i.e., by incorporating Step 8,ii directly into the model selection process. Two principally different approaches to model selection can be discerned (Hastie et al. 2009):

- a. *Subset selection methods*, by which a discrete subset of independent variables is selected and the rest discarded, typically by omission of independent variables that do not contribute significantly to the performance of the model. The explicit criteria for model comparison mentioned above are used in subset selection.
- b. *Shrinkage methods*, by which model coefficients are shrunk by imposing a penalty on their magnitude, rather than left out fom the model (also see Reikeking & Schröder 2006).
- ii. Internal model performance assessment, i.e., calculation of model performance statistics directly by the same data that are used to parameterise the model, e.g., by use of measures of variation explained such as variance, deviance, or loss (e.g., Hastie et al. 2009). The term 'verification', which is sometimes used for what is here termed 'internal model performance assessment' (e.g., Araújo & Guisan 2006), should be avoided because verification of numerical models in the strict sense of the word is not possible (Oreskes et al. 1994). Because internal model performance assessment makes direct use of one set of corresponding values for response and independent variables to find and assess the performance of models (compare with model evaluation procedures of Step 11), results of internal model performance assessment are liable to influence by all kinds of biases and errors in the data (Guisan & Zimmermann 2000, Austin 2007).
- iii. Model parameterisation, i.e., estimation of model parameters. A parameterised model summarises the overall ecological response of the modelled target to the explanatory variables, the latter represented by the set of derived variables. 'Model estimation', 'model calibration', and 'model training' are frequently used synonyms of what is here termed 'model parameterisation'. Note that the term 'model calibration' is used in this essay review in a different meaning (see Step 8,iv).
- iv. Extraction of model predictions. Predictions of the modelled target's aggregated performance in rasterised geographical space, as well as in discrete environmental variables space, are obtained as the fitted values of the parameterised model (Fig. 9b). If the response variable is of the presence/absence type (presence or absence in each grid cell), the prevalence of the modelled target in the study area can be estimated from the data, and model predictions are interpretable as predicted probability of presence (PPP) in each grid cell. This is the case for the example species in Fig. 9, which has a prevalence of 0.168 in the study area (Fig. 2). With presence-only (PO) data, however, the prevalence remains unknown, the probability of presence in each cell cannot be estimated from the data (Phillips et al. 2006, Ward et al. 2009), and the modelled quantity is therefore the relative predicted probability of presence (RPPP). The term 'relative' here indicates that model predictions can be compared among grid cells, but that their absolute values cannot be interpreted in terms of probabilities of presence of the modelled target (Ferrier et al. 2002). RPPP values can be reported in several 'output formats', e.g., 'raw values' that sum to unity over all pixels, and 'cumulative values' (Phillips & Dudík 2008, Halvorsen in press).
- 9. *Collection of presence/absence data for model calibration and evaluation*. A sample of presence/absence observations of the modelled target, preferably collected independently of the sample used to parameterise the model (cf. Step 2), is required for two unrelated purposes; model calibration (Step 10) and model evaluation (Step 11).
- 10. *Model calibration*, i.e., assessment of the numerical accuracy of model predictions (Harrell et al. 1996, Vaughan & Ormerod 2005), in the DM context calibration implies assessment of the degree of correspondence between model predictions and true probabilities of presence of the modelled target. Model calibration implies that



Fig. 9. Steps in the distribution modelling process, exemplified by logistic regression of rasterised presence-absence data for the hypothetical species of Figs 2, 5 and 6 (modelled target, response variable) with respect to the two explanatory variables of Figs 5b (EV1) and 5c (EV2), both recorded in each of the 256 grid cells that make up the study area. (a) Distribution of the hypothetical species in rasterised geographical space: black cells indicate presence and white cells indicate absence. (b) Model of the overall ecological response in continuous environmental variables space (Step 8,iv), obtained as the back-transformed values (predicted propability of presence, PPP) from the logistic regression model PPP = $\exp(g)/(1+\exp(g))$ where g = -5.543619 + 0.9484586*EV1 + 0.6100511*EV2. The model explains 16.95% of the deviance in the response variable (F-test: p < 10–8). (c) Map representation of model predictions in rasterised geographical space (Step 12,i).

the relationship between observed presence or absence (response variable in the calibration model) and predictions from a distribution model (Step 8,iv) is modelled. For distribution models parameterised by use of presence-only data for the response variable, calibration is the only way to bring the predicted RPPP values onto a true probability scale (Pearce & Ferrier 2000b, Phillips et al. 2006, 2009). Model calibration can be accomplished by use of presence/absence data (Step 9) or by use of prior knowledge of the prevalence of the modelled target (Pearce & Ferrier 2000b). Note that the term 'model calibration' is often used in the meaning of what is here termed 'model parameterisation' (Step 8,iii). The term **calibration model** is used to denote a model which is used in model calibration. A graph of frequency of presence plotted against model predictions, typically with subsets of observation units in the calibration data set (Step 9) as data points, is termed **calibration plot** (Chatfield 1995).

- 11. *Model evaluation*, i.e., assessment of model performance by use of data not *directly* used to parameterise the model (Guisan & Zimmermann 2000). The term thus addresses methods for external model performance assessment (compare with definition of 'internal model performance asssessment' in Step 8,ii). The term 'validation', which is often used for what is here termed 'model evaluation' (e.g., Araújo & Guisan 2006), should be avoided because 'model results may or may not be valid, depending on the quality and quantity of the input parameters and the accuracy of the auxiliary hypotheses' (Oreskes et al. 1994: 642). The term 'model evaluation' is often used in a broader sense, also including internal model performance assessment. I have adopted a more strict definition of the term 'model evaluation' because of the fundamental differences between model assessments that use the entire set of response-variable data *directly*, and assessments based upon data *derived from* this set orf more or less independent data (see, e.g., Guisan & Zimmermann 2000, Elith et al. 2006, Raes & ter Steege 2007, Veloz 2009, Edvardsen et al. 2011). Several model performance, or 'goodness-of-fit', statistics are available (e.g., see Fielding & Bell 1997, Pearce & Ferrier 2000b), of which the area under the receiver operating characteristic (ROC) curve, AUC, is one of the most popular (e.g., Franklin 2009). Several strategies exist for evaluation of distribution models. These can be ordered from less to more rigorous, e.g., by their vulnerability to observer bias, etc. (see Guisan & Zimmermann 2000, Elith et al. 2006, Hirzel et al. 2006), as follows:
 - i. *Model evaluation by data-splitting*, whereby *one* sample of observations of the modelled target is split into one subset that is used to parameterise the model and one set that is used to estimate model performance statistics.
 - ii. *Model evaluation by data resubstitution*, whereby model performance statistics are calculated by bootstrapping, jackknifing or crossvalidating procedures. *One* sample of observations of the modelled target is used both for parameterisation and evaluation, but performance statistics are estimated from data not used to parameterise the model.
 - iii. Model evaluation by repeated resubstitution of data, i.e., a combination of (i) and (ii) whereby one sample of observations of the modelled target is randomly split m times into subsets, and the m single values for a model performance statistic are combined into one representative value for the model (e.g., Riordan & Rundel 2009, J. Williams et al. 2009, Weber 2011).
 - iv. *Model evaluation by independent data*, i.e., calculation of model performance statistics by use of presence/absence data for the modelled target, collected independently of the data used to parameterise the model (Step 9).

Several other strategies for model evaluation also exist, which do not fit into the 'gradient' from (i) to (iv) above. Examples of these strategies are the use of predictions from another distribution model, e.g., obtained by other methods, as a reference with which models are compared (Bryn et al. 2012, Hemsing & Bryn 2012); comparison of model predictions with a known distribution that is used as a reference (e.g., Bombi & D'Amen 2012); and comparison with expert knowledge (Mellert et al. 2011). Use of different modelling methods in parallell to check models for consistency accords with the practice in ordination analysis, to use two different ordination methods in parallell and to accept as reliable structure ordination axes identified by both ordination methods (R. Økland 1996).

- 12.*Applications*. Predictions from distribution models can be used for several applied purposes [e.g., see Franklin (2009) and Peterson et al. (2011)], of which two should be specifically mentioned:
 - *Map representation of predictions in geographical space*, i.e., the use of GIS and/ or other software to visualise the modelled ecological response in rasterised geographical space. If the grain is very fine compared to the extent, i.e., if the number of pixels, n, is high, smoothing of predictions may be required for the map representation to be readable. The map representation of predictions for the hypothetical species in Fig. 9c reflects the tendency for the species to be present more often in cells with high, than in cells with low, values for both explanatory variables (see Fig. 9b). While values for explanatory variable 1 increases from 'north' to 'south' in the hexadecadally rasterised study area, showing no systematic variation between 16-cell units, explanatory variable 2 shows no systematic variation between 16-cell units but increases from 'northeast' to 'southwest' within each unit (Figs 5d–e). The pattern of variation in model predictions in rasterised geographical space (Fig. 9c) thus reflects the patterns of variation in both explanatory variables and the species' response to them.
 - *Transfer of modelling results (spatial or temporal extrapolation)*, i.e., use of the model for prediction outside the study area, to other time-points, or to other scenarios. Transfer of modelling results is explained and discussed in an extensive literature, e.g., Araújo et al. (2005), Pearman et al. (2007), Thuiller et al. (2008), Elith et al. (2010), and Peterson et al. (2011).

The 12 steps of the DM process are grouped into three composite steps ('components needed for statistical modelling') in accordance with Austin (2002: 101) as follows (see Fig. 8): Step 1 belongs to 'ecological model', i.e., 'theory to be used or tested'; Steps 2–6, and 9, belong to 'data model', i.e., 'collection and measurement of ... data', however, Steps 4 and 7 also benefit strongly from being informed by basic theory; and Steps 7, 8, 10, and 11 belong to 'statistical model', i.e., 'the statistical theory and methods used'.

Steps 1–8 are essential for a study to belong to distribution modelling (DM) as defined in this essay review, i.e., as a study in which the primary response variable describes a distribution (Steps 2, 4 and 6), with explanatory variables that represent explanatory gradients and are recorded or estimated for all grid cells within the extent of the study (Steps 3–5), and in which the modelled property is the overall ecological response (performance in ecological variables space; Steps 7–8). *It is Step 8, modelling of the overall ecological response, that places DM unambiguously among gradient analysis techniques* as defined by ter Braak & Prentice (1988), and *it is because of Step 8 that a gradient analytic perspective on distribution modelling should be adopted*. More specifically, DM belongs to the sub-category 'direct gradient analysis' of GA techniques, 'in which each species' abundance is described as a function of measured environ-
mental variables', and to the sub-subcategory 'regression', or univariate modelling methods, to which direct gradient analysis techniques for one response variable belong.

Distribution models can be improved iteratively, by incorporating new data for the modelled target (Steps 2 and 9) as well as by using results of one modelling cycle to improve choices made in the next step [Fig. 8; also see Guisan et al. (2006a) and Stokland et al. (2008)].

DISTRIBUTION MODELLING AS AN INDUCTIVE SCIENTIFIC APPROACH

Two main research paradigms are relevant for ecology: (1) the hypothetico-deductive approach, by which knowledge is gradually built from first principles by acceptance or rejection (verification and falsification), or by falsification only (Popper 1959, 1989), of scientific hypotheses; and (2) the inductive approach, by which knowledge accumulates by a two-step procedure: (i) extraction of patterns from empirical data, and (ii) search for general trends in patterns derived from comparable empirical data sets (Økland 2007). Ecology has a long tradition for research by inductive (Lawton 1996), or correlative (Shipley 2000) approaches, but has also, at times, been criticised by strong proponents of the hypothetico-deductive paradigm for being 'subjective' or 'unscientific' (e.g., Murray 2000, 2001). This criticism has sometimes been raised with such an emphasis that concern has been expressed for loss of diversity in ecological research (Noss 1996, Weber 1999, Økland 2007). However, for the last ten years (or so) there has been a shift from insistence on experiments and hypothesis testing to acceptance of, or even preference for, more or less formal modelling approaches (e.g., Shipley 2000, Hastie et al. 2009, Zuur et al. 2009, Grace et al. 2010) as part of a growing consensus that ecology needs hypothetico-deductive as well as inductive approaches (Lawton 1996, 1999, Økland 2007). This paradigm shift occurs because an increasing number of ecologists realise that ecology deals with disentangling complex patterns in search for even more complex causal relationships, and that the complexity of the studied systems far exceeds what can be addressed by simple, testable hypotheses (Wilson 2003). DM is basically a correlative approach (Peterson et al. 2011): tests of effects of single variables or combinations of variables will never account for the complexity of factors and interactions between factors that shape distributions of natural phenomena. In addition to challenges related to the complexity of natural variation, DM has to face the additional challenge that many explanatory variables needed for adequate representation of the distribution-limiting factors, the proximal factors in the terminology of Austin (2002), will be unavailable. Reasons for that include, e.g., difficulties in quantifying, and obtaining areal-covering data for, decisive extreme events such as the one-hundred-year flood or the fifty-year drought spell. Other reasons are costs in terms of labour and other resources of making thousands or millions of measurements, and lack of knowledge of which environmental factors are most important. In practical DM, proximal or otherwise potentially causal factors have to be approximated by surrogate variables that are more or less appropriate for the purpose (Austin 2002). However, even if we were able to record all relevant environmental, historical and other factors, reconstructing the multitude of events (evolutionary, historical, demographic, etc.) that resulted in the specific distribution pattern observable at a given time-point would be in vain. The 12-step DM process described above therefore, in general, accords with the inductive paradigm and the proliferation of DM methodology after year 2000 has occurred as part of the paradigm shift from insistence on hypothesis testing to acceptance of modelling as a useful tool. One distribution model may, though, be used as a reference with which other models are compared (e.g., Bryn et al. 2012, Hemsing & Bryn 2012), i.e., for testing weak hypotheses.

PURPOSES OF DISTRIBUTION MODELLING

Many authors recognise that important choices of methods, options and settings (Step 7 in the DM process; Fig. 8) should be guided by the purpose of the DM project (e.g., Guisan & Zimmermann 2000, Araújo & Guisan 2006, Jiménez-Valverde et al. 2008). Araújo & Guisan (2006: 1679) therefore encourage modellers to make the purpose of their modelling clear at the outset, stating 'that [distribution] modellers should make a clearer distinction between niche models and the modelling of spatially explicit features'. Franklin (2009: 207) points to the importance of purpose for choice of modelling strategy by stating: 'evaluation of species distribution models ... has tended to focus on the predictive performance as the most important measure of model validity' while 'predictive power is really only one aspect of model evaluation' and 'ecological realism ... (model credibility) [is] also important'. She thus indicates a potential conflict of interest between ecological interpretability of modelling results, i.e., good representation of the overall ecological response in environmental variables space, and predictive performance in geographical space. In the discussion chapters 'Implications [of the gradient analytic perspective] for choice of data model' and 'Implications [of the gradient analytic perspective] for choice of statistical model', I will discuss this conflict of interest in greater detail and show that modelling purpose dictates the appropriateness of different types of response-variable data, different explanatory variables, and different modelling methods. An explicit distinction between DM purposes along these lines is, however, normally not made in the DM literature. An exception, however, is the statement of Peterson et al.'s (2011: 2) that '... what has been termed "species distribution modelling" ..., as well as the related (but by no means equivalent) endeavor called "ecological niche modelling" ...', which suggests that the two terms are used, at least partially, for DM approaches with different purposes.

I recognise three main purposes of DM, which represent nodes in a continuum of purposes:

- 1. **Ecological response modelling** (ERM), which comprises DM with the main purpose of modelling the relationship between a target, typically the performance of a species, and a set of explanatory variables. The focus in ERM is to find and understand *general patterns* in the overall ecological response of the modelled target to explanatory variables; with or without reference to a particular study area or point in time. ERM thus addresses relationships in environmental variables (or ecological) space. ERM purposes can be divided into two sub-categories:
 - a. **Specific-purpose ecological response modelling**, i.e., to describe and understand distributional variation at relevant scales, with regard to a specific set of explanatory variables.
 - b. **General-purpose ecological response modelling**, i.e., to describe and understand distributional variation at relevant scales, without regard to a specific set of explanatory variables.
- 2. **Spatial prediction modelling** (SPM), the distribution of a modelled target in a specific study area in a specific time interval, modelled by use of a set of explanatory variables, with the main purpose of optimising the fit between model predictions and the true distribution of the modelled target's performance in this area at this point in time. SPM thus addresses relationships in geographical space.
- 3. **Projective prediction modelling** (PPM), the distribution of a target, modelled by use of a set of explanatory variables, with the main purpose to transfer model predictions to a spatiotemporal setting different from the one at which the data used for modelling were collected, i.e., other areas and/or time intervals or scenarios. PPM can ad-

dress relationships in geographical space or environmental variables (or ecological) space.

The three purposes differ with respect to which Step in the 12-step DM process that is focused most strongly and, accordingly, which conceptual geometrical space is relevant for use and interpretation of results. In ERM, the modelled target's overall ecological response to specific explanatory variables is modelled in order to improve the modeller's insight into the mechanisms and processes behind observed relationships, as such. The focus of ERM is entirely on relationships in environmental variables (or ecological) space, i.e., on Steps 7–8 in the DM process. Examples of research questions addressed in ERM are the ranking of environmental factors according to importance for the species in question (e.g., Wollan et al. 2008); in addition to exploratory analysis of response-curve skewness with respect to a specific environmental variable for a set of species (e.g., Austin et al. 1994). ERM is brought to the extreme by 'mechanistic niche modelling' (Kearney & Porter 2009) by which environmental variables with documented physiological impact on the modelled species are used are used as explanatory variables in the modelling. Provided that the focus of the study is on the species' response to explanatory variables 1 and 2 *as such*, as illustrated by environmental variables in Fig. 9b, the model in Fig. 9 exemplifies ERM. In an ERM context, the predicted distributional consequences of relationships in environmental variables (or ecological) space (Fig. 9c) are considered unimportant.

The above-mentioned examples illustrate specific ERM purposes, i.e., the modelled target's relationship to a specific set of explanatory variables. In general-purpose ERM, on the other hand, the aim is to identify the environmental complex-gradients which are most important for the modelled target in order to improve our understand of its relationship with the environment. The definition of the general-purpose ERM conforms to the definition of the general-purpose ecological study (R. Økland 1990a, 1996), which for vegetation as study object is formulated as follows: 'to summarize the main structure in a species-by-sample data matrix, to relate structure in vegetation to external factors, and to generate hypotheses about vegetation-environment relationships' (R. Økland 1996: 289).

Prediction modelling, which can be used as a collective term for PPM and SPM, on the other hand, has as its main focus to construct the model that gives the best spatial predictions in a time perspective that is either synchronous (SPM) or asynchronous (PPM), and/or a geographic area of interest that is either coincident with (SPM), or differs from (PPM), the spatiotemporal setting at which the set of units subjected to analysis were collected. The focus of SPM and PPM is on relationships in geographical space, exemplified by Fig. 9c. SPM and PPM studies do not necessarily have the spatial predictions *as such* as their focus, these purposes also include DM studies that address questions that require predictions from SPM and PPM models.

PPM differs from SPM by its focus on projections into geographical space under scenarios of temporal environmental change (most often, climate change; Guisan and Zimmermann 2000, Guisan et al. 2006b, Elith & Leathwick 2009) or into other geographical spaces (Randin et al. 2006, VanDerWal et al. 2009, Thompson et al. 2011). Specific challenges associated with PPM as compared with SPM (or ERM) are defined outside the scope of this essay review. Discussions of PPM can be found in a number of studies, e.g., Pearson & Dawson (2003), Guisan & Thuiller (2005), Araújo et al. (2005), Araújo & Guisan (2006), Baselga & Araújo (2009), Diniz-Filho et al. (2009), Franklin (2009), Kriticos & Leriche (2010), and Peterson et al. (2011).

EXPANDING THE GRADIENT ANALYTIC PERSPECTIVE: PATTERNS OF NATU-RAL VARIATION IN TIME AND SPACE AND THE PROCESSES AND MECHA-NISMS RESPONSIBLE FOR THESE PATTERNS

Empirical GA studies have revealed many strong patterns that can be generalised over regions, ecosystems and species groups. In particular, strong and generally valid patterns have been found for: (1) the spatial scale intervals in which variation along important environmental variables is large (Økland 1990a, Halvorsen et al. 2009); (2) the spatial scale interval in which these variables are important for explaining variation in species performance (e.g., Rydgren et al. 2003); and (3) properties of species' overall ecological responses and the processes responsible for these patterns. These general patterns, which are summarised in this part of the essay review, expand the gradient perspective into a broad theoretical basis for DM. Particular emphasis is given to assessment of the spatial and temporal scales at which patterns of natural variation can be recognised and at which scales the processes responsible for these patterns operate.

Many examples in this section are taken from studies of patterns of natural variation in Norway (which I know by own field experience). The mainland of Norway covers only 323,802 km², but comprises an exceptional range of nature-type variation, its moderate size taken into account (Halvorsen et al. 2009). The main reasons for this are: wide range of climatic variation (Moen 1999, Bakkestuen et al. 2008); high mineral and bedrock diversity (Ramberg et al. 2007); high diversity of land forms (Anonymous 1984, Sulebak 2007); and considerable variation in traditional land use systems throughout the country (Sømme 1954, Christensen 2002, Almås et al. 2004). The range of variation in natural conditions found in Norway includes most of the variation that can be found in the circumboreal zone. My main focus in this essay review is on vegetation (plants), but the theoretical considerations and its implications are relevant also for other organisms with low mobility (including fungi and many groups of invertebrates).

PATTERNS OF NATURAL VARIATION

Regional, local, and condition or impact ecoclines

Gradient analysis assists identification of the most important ecoclines in a study area. Being axes of the ecological space, ecoclines are abstract ideals. Although empirical studies show that patterns of co-variation between environmental variables, and between species composition and environmental variables, often can be generalised, such patterns are never *fully* consistent among regions (T. Økland 1996), over time intervals (Gunnarsson et al. (2002), or across spatial scales (Økland et al. 2006). Spatial inconsistency, recognised as the modifiable areal unit problem (MAUP) by Openshaw & Turner (1979), is extensively discussed in the literature, e.g., by Jelinski & Wu (1996) and Wu (2004); see Økland et al. (2006) and Bakkestuen et al. (2008) for practical examples. The different abilities of explanatory variables 1 and 2 (in Fig. 5) to explain variation in the occurrence of the example species rasterised to different spatial domains (Fig. 6) is a simple example of spatially inconsistent patterns.

Despite temporal and spatial inconsistencies, the ecocline concept has proven useful for generalising patterns of natural variation. Thus Halvorsen et al. (2009) use studies by ordination and other gradient analysis techniques to generalise patterns of variation in species composition

Table 1. Examples of ecoclines recognised as important in Norway according to Halvorsen et al. (2009) and the spatial scale intervals in which variation along them is large. 'Spatial scale at which variation is large' is defined as the range of spatial scales, within which, by analysis of samples with extent-grain ratio of 16 such as regular hexadecadal grids, the variation in a variable of interest is distinctly larger than in samples with smaller or larger grain sizes. Compiled from Halvorsen et al. (2009), but with terms for spatial scales at which variation is large adjusted to fit the definitions adopted in this essay review.

Ecocline	Spatial scale at which variation is large (m)	Category	Importance
bioclimatic zone	10 ³ -10 ⁵	regional ecocline	universally important in terrestrial ecosystems; almost all groups of organisms respond to 'warmth' (e.g., temperature of the growing season)
bioclimatic section	10 ^{3.5} -10 ⁵	regional ecocline	universally important in terrestrial ecosystems; almost all groups of organisms respond to variation in water suply at regional spatial scales
lime richness	10 ¹ -10 ⁴	local ecocline	important in freshwater and terrestrial ecosystems for all except strongly mobile organisms; includes essential resources for growth
particle size (of mineral substrates)	10 ⁰ -10 ⁴	local ecocline	important for sessile aquatic organisms by regulating substrate stability (susceptibility to disturbance by water currents) and for terrestrial organisms by influencing soil drainage and water retention
severity of drought	10 ^{0.5} -10 ^{1.5}	local ecocline	important for plants, fungi and soil-dwelling invertebrates in well-drained non-wetland terrestrial systems; influences ability to survive periods of exceptional drought (important correlated environmental variables are soil depth, terrain shape, topographic position and aspect)
strength of rheogenous water influence	100-101	local ecocline	important for plants and invertebrates that depend more or less strongly on constant physio-chemical conditions (water temperature and supply of water and minerals), in wetlands and terrestrial systems influenced by rheogenous (spring) water
water saturation (of the ground)	10 ⁻¹ -10 ¹	local ecocline	important for plants and invertebrates by determining the degree of water saturation (e.g., measured as the median volumetric soil water content) in non-wetland terrestrial systems and the duration of water saturated topsoils in wetlands
snow-cover stability	10 ^{0.5} -10 ^{1,5}	local ecocline	important for many plants in alpine and arctic regions; plants differ in tolerance for frost and wind disturbance in winter
reduced growing-season due to prolonged snow-lie	100-101.5	local ecocline	important for many plants in alpine and arctic regions, plants differ in the time needed to complete their life cycle

Table 1 (continued).

Ecocline	Spatial scale at which variation is large (m)	Category	Importance
duration of inundation	10-1-101.5	local ecocline	important for sessile organisms which differ in their tolerance of submergence
dune stabilisation	10 ¹ -10 ^{2.5}	local ecocline	important for plants which differ in their ability to colonise bare sand and to withstand burial in mobile sands
long-term agricultural management intensity	10 ^{1.5} -10 ³	local ecocline	important for plants, fungi and soil-dwelling micro- organisms; in each group considerable differences in tolerance for qualitatively different disturbance regimes are found
eutrophication	10 ⁴ -10 ⁶	condition or impact ecocline	important for most organisms in freshwater and terrestrial ecosystems by enhancing the availability of nitrogen, an essential resource for growth
regrowth succession on agricultural land	10 ^{0.5} -10 ^{2.5}	condition or impact ecocline	important for most ground-dwelling organisms by affecting time available for re-colonisation, buildup of organic soil layers etc. after abandonment of farming
regrowth succession of tree stands	10 ^{1.5} -10 ³	condition or impact ecocline	important for most ground-dwelling organisms by affecting radiation and time available for re-coloni- sation after harvesting of trees or natural disturbances

and major complex-gradients in Norway into ecoclines that account for most of the explainable compositional variation [the Norwegian Nature Types (NiN) approach, still only available in Norwegian]. The NiN framework is used as a basis for description of ecoclines recognised as important in Norway (see Table 1).

Halvorsen et al. (2009) sort ecoclines into three groups according to spatial and temporal scales with large variation (Halvorsen et al. 2009):

- 1. **Regional ecoclines**; parallel variation in species composition and macroclimatic factors (bioclimatic variation; Bakkestuen et al. 2008), typically with large variation at spatial scales of 1 km or broader; under the assumption of no change in type or magnitude of human influence, or other condition or impact ecoclines, patterns will remain more or less unchanged for centuries or millennia.
- 2. Local ecoclines; parallel variation in species composition and important environmental factors (edaphic, moisture-related, etc.), typically with large variation at spatial scales of 1 km or finer; under the assumption of no change in type or magnitude of human influence, or other condition or impact ecoclines, patterns will remain more or less unchanged for centuries or millennia.
- 3. **Condition or impact ecoclines**; parallel variation in species composition and important environmental factors, typically with large variation at temporal scales of decades [(6–)10–100 years]

The tripartition into regional, local, and condition or impact ecoclines is based on two criteria; the temporal and spatial scale intervals at which variation is large. The fundamental division of ecoclines is into **basic ecoclines** (regional and local ecoclines) on one hand, with patterns that remain more or less stable over time-scales of centuries, and condition or impact ecoclines on the other, which comprise transient patterns. Accordingly, patterns of species accumulation and establishment of ecosystem-level processes are affected by, and result in, variation along basic ecoclines (e.g., Noss 1990). Variation along condition and impact ecoclines is to a large extent independent of variation along basic ecoclines, because change of state, e.g., with respect to 'trampling and associated erosion', which is a typical example of a condition or impact ecocline, can take place without significant change of 'basic conditions' at the site. The division of basic ecoclines by means of the spatial scale interval in which variation is large into regional and local, or climatic vs. edaphic, or zonal vs. azonal, gradients, follows a long tradition that is motivated by the more or less independent responses of species to the two sets of factors (Schimper 1898, Cajander 1921, Kalela 1954, Ahti et al. 1968, Økland & Bendiksen 1985). Regional ecoclines address patterns on regional spatial scales, while local ecoclines address patterns on fine, i.e., local and micro, spatial scales (Fig. 4).

Local and condition or impact ecoclines do not correspond to undisturbed and undisturbed sites, respectively, nor to stable and successional sites. To the contrary, examples of ecoclines with degree of impact by disturbance as the main responsible factor, are found both among local ecoclines and among condition or impact ecoclines. Typical examples are the local ecocline 'flooding in an alluvial site', which is conditioned on long-term predictable water-induced disturbance, the intensity of which varies along the ecocline, and the condition or impact ecocline 'trampling and associated erosion', which is conditioned on impacts that are more unpredictable and therefore likely to give rise to variation in species composition on finer time-scales. Successional ecoclines which result from slow, natural, ecological processes such as primary successions after glacier retreat or 'severity of drought', belong to the local ecoclines because patterns tend to be invariant over centuries. Variation in 'severity of drought' results from primary successions having different speeds on different substrates, depending on topography, climate and several other factors. However, the successional ecocline 'regrowth succession on agricultural land' is typified as a condition or impact ecocline because it mostly displays variation over time scales of decades.

Regional ecoclines. For more than half a century, two regional ecoclines, or 'bioclimatic gradients'; Table 1) have been recognised as important by Fennoscandian vegetation geographers, for Norway (Sjörs 1963, Ahti et al. 1968, Tuhkanen 1980, Moen 1999) as well as for the entire circumboreal area (Tuhkanen 1984): a 'sectional ecocline' that runs from oceanic climates in the west to slightly continental inland climates in the east, and a 'zonal ecocline' that runs from temperate climates in the south and at low altitudes to cold climates in the north and at high altitudes. According to Fennoscandian tradition, the former is divided into 'vegetation sections' of which five occur on the Norwegian mainland, and the latter is divided into 'vegetation zones' of which 5-8 are recognised in Norway (Moen 1999). High importance of these and only these ecoclines at regional scales has been corroborated in a large number of studies, e.g., Moen (1987) and Aune & Holten (2011). Two examples of multivariate studies in which regional ecoclinal patterns are identified, are Pedersen (1990) and Myklestad (1993), who studied distributions of 722 vascular plant species and 24 Salix species, respectively, in Fennoscandia. Both of these studies were based upon samples of species observations, rasterised to a grain size of 50 × 50 km, subjected to ordination. The samples of units subjected to analysis consisted of 522 and 558 grid cells in the two studies, respectively. The two main compositional gradients recognised in both of these studies closely parallelled the expert divisions into 'vegetation sections' and 'vegetation zones'. Bakkestuen et al. (2008) found similar patterns of variation when a set of 54 climatic, topographical, hydrological and geological variables recorded for all of Norway, rasterised to grain sizes of 1, 5, and 10 km, was subjected to PCA ordination: patterns along the first two PCA axes coincided with variation along the 'sectional' and 'zonal' gradients of Moen (1999). Bakkestuen et al. (2008) demonstrated that this geographical pattern was invariant over grain sizes in the interval 1–10 km.

The finest spatial scales at which substantial variation in species performance can be explained by regional ecoclines is strongly influenced by the broad-scale topography (relative relief; Anonymous 1984), which is an important determinant of the distribution of temperatures and precipitation (Førland 1979, 1993, Aune 1993, Moen 1999). In parts of the world with lower relative relief and less steep climatic gradients variation along bioclimatic, or regional, ecoclines may be negligible below spatial scales of 10 km or even more (cf. Metzger et al. 2005).

Local ecoclines. While variation at broad scales, i.e., at spatial scales typically addressed by samples with extent-grain ratio of 16 and linear grain > 1 km (Fig. 4), can be efficiently summarised into two bioclimatic gradients (Bakkestuen et al. 2008), exhaustive description of variation at fine scales (< 1 km) require a multitude of 'factors', or local ecoclines. The number of local ecoclines recognised as important in at least one type of ecosystem at the ecological system level in the first version of NiN (Halvorsen et al. 2009) is 30. Types at this level are defined with respect to spatial scale so that a patch of one specific type *normally* covers 100 m² or more (Halvorsen et al. 2009). Some local ecoclines are recognised as important within type of ecological system only, while others are important over a broad range of types. Among the latter, variation in species composition related to 'lime richness' holds a key position because this ecocline is important in freshwater systems and wetland systems as well as non-wetland terrestrial systems, and because variation related to lime richness can be observed over a considerable range of spatial scales. Many terms have been used for this ecocline, e.g., 'soil reaction' (Ellenberg et al. 2001), the 'rich-to-poor edaphic gradient' (Du Rietz 1949, Sjörs 1967, Arnesen et al. 2007), 'the acid, calcium-poor to alkaline, calcareous and carbonbate-rich gradient' (Wheeler & Proctor, 2000), and 'the differentiation into acidic vs calcareous sites' (Walker et al. 2001). Properties of the bedrock such as chemical composition, hardness, and structure (e.g., layering), which influence weathering rates, determine the input of essential elements to the ecosystems and are the primary causes of variation in lime richness (hence the term 'geological richness'; cf. Sjörs 1967). Occurence of mosaics of bedrock types with size of individual patches ranging from centimeters to hundreds of kilometers (e.g., Solli & Nordgulen 2007) contributes to the wide interval of observed spatial scale intervals in which variation in lime richness is large. However, most organisms do not live in direct contact with the bedrock itself but in, or on, the topsoil and/or in the ground water. For most organisms, properties of the bedrock are therefore just one, often minor, set of determinants of the environmental conditions experienced by the organisms. The most important modifiers of direct bedrock influence are glacial, glaciofluvial and fluvial processes. These processes bring about redistribution and weathering of parent material and, subsequently, in interaction with terrestrial and soil-dwelling biota, topsoil development (Romell 1935). These processes depend, directly or indirectly, strongly on terrain shape (e.g., Økland & Eilertsen 1993), which influences soil depth (Skyllberg 1990) and other variables associated with the complex-gradient component of the lime richness ecocline. The complex dependencies between factors responsible for patterns related to lime richness are described in detail, among others, for boreal forests by Økland & Eilertsen (1993) and T. Økland (1996), for 'swamp forests' by Økland et al. (2001), and for mires by Sjörs (1948), Malmer (1962), and Økland (1989b). The distinction between regional and local ecoclines is not always sharp. Thus, the spatial scale intervals in which variation along lime richness is large and in some areas also include fine regional scales (e.g., Økland 1989a, Wollan et al. 2008). Similar patterns are also shown by other ecoclines that are categorised as local, such as the dominant

particle size of abyssal plains, which may be homogeneous over many kilometres (Thorsnes et al. 2009). This and other local ecoclines do, however, primarily display large variation at finer spatial scales (linear grain; < 1 km). On the Norwegian mainland, which is dominated by landscapes with moderate or coarse relative relief (Anonymous 1984, Etzelmüller et al. 2007, Sulebak 2007), particle size tends to vary over short distances due to the fine-scaled action of geophysical processes.

Even though all organisms are dependent, at least to some extent, on water, many organisms do not tolerate extensive periods of submergence. Thus, unless specific adaptations to aquatic environments have been developed, vascular plants depend on aeration of below-ground parts to survive waterlogging (Metsävainio 1931, Bannister 1964). The moisture regime of a site is influenced by several geophysical processes that interact with each other and with other important environmental factors in complex ways. This results in existence of several, more or less independent, 'moisture-related', local ecoclines that differ with respect to the spatial scale interval in which variation is large and with respect to which ecosystems they are relevant for. Boreal forests provide a typical example. Økland & Eilertsen (1993) demonstrate existence of two independent ecoclines related to soil moisture, termed 'severity of drought' and 'water saturation' (Table 1). For 'severity of drought', which is conditioned on variation in soil depth and topographic position, variation is large in the spatial scale interval 5-25(-100) m. Nevertheless, the response of many species to this ecocline seems to be regulated by die-back during periods of particularly severe summer drought, as demonstrated by Erkamo (1956, 1958) for Trientalis europaea in Finland and by Økland & Bendiksen (1985) for Calluna vulgaris in Norway. This exemplifies a situation where a factor, temperature, with large variation on coarse regional scales, bring about patterns on fine to medium local scales by interaction with local factors such as topography and soil depth. The spatial scale interval in which variation along the water saturation ecocline is large, is (0.5-)1-10 m. This ecocline reflects variation in forests from 'normal' or 'median' soil moisture from well-drained ground to moist, i.e., slightly paludified, ground in forests, often dominated by Sphagnum spp. (Økland & Eilertsen 1993, T. Økland 1996), and extends into peatlands (mires) in which surface microtopographic patterns with large variation at spatial scales as fine as 10 cm directly determine depth to the water table, the factor which determines degree of water saturation (Økland 1989b, Ohlson & Økland 1998, Økland et al. 2001, 2008).

With increasing altitude, i.e., towards the boreal-alpine forest limit, and northwards, i.e., towards the boreal-arctic forest limit, temperatures decrease and rainfall often increases (Sjörs 1948, Førland 1979). Summer drought severity is not likely to be an important factor in cold, treeless, alpine and arctic ecosystems. Instead, a distinct zonation of vegetation from wind-exposed ridges to snowbeds in depressions has since long been recognised (Vestergren 1902, Fries 1913, Nordhagen 1928, 1943) as typical of these systems. This zonation, which mimics the variation related to drought severity in boreal forests (Økland & Bendiksen 1985), can be described in terms of two ecoclines that are both conditioned on snow cover: 'snow-cover stability', i.e., the variation above snow-beds from wind-exposed ridges to lee sides, and 'reduced growing-season due to prolonged snow-lie', i.e., the variation from moderate to extreme snow-beds. Both of these ecoclines are conditioned on topography and on dominant wind directions being the same over years. Together these factors cause locally uneven, but temporally predictable, snow distribution patterns (Dahl 1957, Baadsvik 1971, Odland & Munkejord 2008, Odland 2011). The spatial scale interval in which variation is large, is the same for the two ecoclines, 1-10(-25) m (Table 1), mostly reflecting spatial scales of the local topography. The zonation splits into two ecoclines because an important shift of factors responsible for species' performance takes place in the middle part of the gradient: from tolerance to frost and wind disturbance in winter at the wind-exposed ridge end of the zonation to tolerance to short growing seasons towards the

extreme snow-beds (Resvoll 1917, Gjærevoll 1956, Dahl 1957, Halvorsen et al. 2009).

Other important local ecoclines include variation on tidal and freshwater shores related to flooding (in coastal ecosystems also to salinity), for which large variation is observed for spatial scale intervals in the range 1–100 m (e.g., Fremstad 1981, Elven et al. 1988), and variation in coastal dune ecosystems related to 'dune stabilisation' (Lundberg 1987) for which large variation is mostly found for spatial scale intervals between 5 and 50 m.

Species compositional differences due to variation in 'long-term agricultural management intensity' also satisfy the definition of a local ecocline. This ecocline does not reflect the 'intensity of current agricultural use', which is a condition or state ecocline, but rather the 'intensity of total management impacts associated with exploitation for agricultural purposes, that has given the ground its ecological characteristics and its species composition' (Halvorsen et al. 2009). Variation in species composition and fundamental ecosystem properties along this ecocline is large, as demonstrated in many studies (e.g., Norderhaug et al. 2000, de Blois et al. 2001, Myklestad 2004, Bratli et al. 2006, Hamre et al. 2010): from ecosystems with no indication of management to high-intensity management systems such as farmland dominated by crops. These two extremes hardly have any species in common. Between these extremes several 'management intensity levels' can be distinguished: very low intensity management, e.g., forests managed for forestry but also used for cattle or sheep grazing; low intensity management for agricultural purposes without artificial fertilisation, ploughing or seeding, typically resulting in semi-natural grassland sites; and from moderate to high intensity management which all imply ploughing, artificial fertilisation, seeding and/or pesticide application. Shifts along the 'longterm agricultural management intensity' ecocline in direction of lower management intensity are slow and typically take more than hundred years (e.g., Aasetre & Bele 2009). Semi-natural grasslands develop from forest ecosystems over centuries or millennia of low-intensity management (Emanuelsson 2009). Shifts in direction of increased management intensity are effected immediately by strong sudden impacts such as applying artificial fertiliser to a semi-natural hay-meadow.

Local ecoclines that express variation on fine scales related to warmth or moisture may, to some extent, interact with regional (bioclimatic) ecoclines. This is exemplified by the increasing fractional area of snow-beds, slightly paludified forests below the tree line and moist coastal and alpine heaths, with increasing climatic humidity (Nordhagen 1943, Økland & Bendiksen 1985, T. Økland 1996). Another example is the shift in species' overall ecological responses to topographic (ridge-to-slope) gradients from oceanic to continental climates, as expressed in the 'bio-geoecological law' of Boyko's (1947) and the 'law of relative site constancy' (Walter & Walter 1953).

Even though many local ecoclines are needed to account for all environment-related variation in species composition at the ecological system level, the number of major complexgradients accounting for variation in species composition and, hence, the number of important ecoclines within *each specific major type* at the ecological system level, is low. This is expressed in the second fundamental insight of the gradient analytic perspective, a corrollary of which is that ecological systems differ, more or less strongly, with respect to which local ecoclines are important for explaining within-system variation. The extent to which ecological systems differ with respect to which ecoclines are important, also expresses the degree to which they differ with respect to important structuring processes and mechanisms. This is exemplified by open (non-woodland) systems on rock outcrops and on shallow soils. The ecocline 'lime richness' is important in both of these ecological systems, while 'water saturation' and 'danger of severe drought' are relevant only for the two last-mentioned ecoclines because a soil layer is normally needed to create moisture gradients that persist long enough after rainfall to give rise to species compositional gradients. In summary, some ecoclines are relevant for many ecological systems, such as 'lime richness', others are relevant for one major type only, e.g., 'reduced growing-season due to prolonged snow-lie', which is only relevant for snow-beds.

Condition or impact ecoclines. Three examples of condition or impact ecoclines are given in Table 1, of which two operate on local and one on regional spatial scales. Typically, the spatial scale interval in which variation along condition or impact ecoclines is large reflects the scale of the factor responsible for this variation, e.g., management, natural or man-made disturbance, or other impacts. Thus, shorter-term variation in species composition and environmental conditions resulting from abandonment or change to a less intensive management regime (e.g., Vandvik & Birks 2002, Bratli et al. 2006, Hamre et al. 2007, Potthoff 2007) can be recognised as variation along the condition or impact ecocline 'regrowth succession on agricultural land' (Table 1). This ecocline typically displays large variation in the spatial scale interval 10–100 m (medium local scale) in landscapes formed by the low intensity, labour-intensive management regimes which were typical for most of Europe before World War II, and typically on coarse local scale, (50–)100–500(–1000) m, in landscapes formed by modern, machinery-intensive agricultural practices (cf. Robinson & Sutherland 2002, Emanuelsson 2009). Similarly, the spatial scale interval in which variation is large along the condition or impact ecocline characteristic of boreal forests, 'regrowth succession of tree stands', is large and depends on the logging scheme (Östlund et al. 1997, T. Økland et al. 2003). Other examples of condition or impact ecoclines associated with large variation mostly at local spatial scales are 'watercourse regulation' (Jansson et al. 2000), 'all-terrain vehicle impact' (Harper & Kershaw 1996), and 'trampling and associated erosion' (Arnesen 1999, Willard et al. 2007).

Eutrophication, brought about by human-induced emissions and subsequent deposition of nitrogen compounds (e.g., Bobbink et al. 1998, 2010), exemplifies a condition or impact ecocline that is associated with large variation in species composition at spatial scales broader than 10 km (Henriksen et al. 1995, Odell & Ståhl 1998). Other condition or impact ecoclines along which species composition changes over time intervals of few decades but that are associated with large variation at regional scales, include acidification due to emission and deposition of long-distance airborne pollutants (e.g., sulfur; Hesthagen et al. 1999) and, currently subject to great concern, human-induced climatic change impacts (Frahm & Klaus 2001, van Herk et al. 2002, Aerts et al. 2006).

Resource, direct, and indirect gradients, or proximal and distal factors

Many categorisations other than the division into local, regional, and condition or impact ecoclines have been proposed for environmental complex-gradients and ecoclines. Of these, the two which are most often referred to in the DM literature are the division of environmental factors into resource, direct, and indirect gradients (Austin 1980, Austin & Smith 1989) or, alternatively, into **proximal factors** and **distal factors** (Austin 2002). The terms 'proximal' and 'distal' refer to the role of the environmental factor in question in a conceptual model of processes that determine variation in a species' performance; the environmental factor that ultimately brings about variation in species' performance is the most proximal one (Austin 2002). Distal factors, on the other hand, do not *as such* impact species' performance, but serve as surrogates, or proxies, for more proximal factors. The terms resource, direct, and indirect are used to characterise environmental gradients by the nature of their impact on the target organism: resource gradients, e.g., nitrate concentrations in soil, are consumed by the organism; direct gradients, e.g., temperature in the growing season, have direct physiological influence on the organism but (unlike resource gradients) are not depleted; while indirect gradients, exemplified by altitude, have no direct influence on organisms but may be useful as proxies for resource or direct gradients. Obviously, resource and direct gradients are more proximal than indirect gradients, hence the terms 'distal' and 'indirect' are used more or less as synonyms (Austin 2002).

Austin (e.g., 2005) emphasises that no absolute limits exist between these categories, and that one gradient may have characteristics of several categories. This is exemplified by the water-table gradient in boreal bogs (Økland 1992). The water table (or more precisely, the depth from the peat surface to the water table) does not, *as such*, affect plants and the gradient is therefore indirect according to Austin's definition. However, the vertical position of the water table determines water availability, which is an essential resource for plant growth, as well as the duration of anaerobic, reducing conditions which have direct physiological effects on the plants. The water-table gradient thus combines properties of resource, direct, and indirect gradients.

The divisions into resource, direct and indirect gradients, and into proximal and distal factors, do not take into account the spatial and/or temporal scales at which large variation is found. No correspondence therefore exists between categories of ecoclines (regional, local and condition or impact) according to Halvorsen et al. (2009) and the division into resource, direct and indirect gradients of Austin (1980).

Hierarchies of spatial and temporal variation

A basic assumption often made in ecology, DM included, is that strong correlations exist between the level of biological diversity, i.e., organism, population, community, and landscape (Allen & Starr 1982, Noss 1990), and the temporal and spatial scale intervals in which variation is large. Implicit in this assumption is that patterns recognisable on fine local spatial scales result from processes that operate on fine temporal scales and that affect low, e.g., within-population, levels of organisation, while patterns recognisable on regional spatial scales result from processes that operate on long temporal scales and that affect the ecosystem or higher levels of organisation (e.g., Mackey & Lindenmayer 2001, Willis & Whittaker 2002, Pearson & Dawson 2003, Franklin 2009, Hortal et al. 2010). These assumptions are, however, challenged by several authors, including Allen & Hoekstra (1990) and van der Maarel (2005), who argue that very intricate relationships may exist between these three hierarchies of natural variation: the hierarchy of spatial scale intervals in which variation is large, the hierarchy of temporal scales, and the level of biological diversity. Examples that illustrate this point are easily found. Firstly, ecoclines that are relevant both for the population (species) and community organisation levels occur both among local and condition or impact ecoclines, as exemplified by the 'lime richness' and 'eutrophication' ecoclines, respectively (Halvorsen et al. 2009). Furthermore, the regional ecoclines 'bioclimatic sections' and 'bioclimatic zones' are both relevant for explaining variation at several levels of organisation. Secondly, variation brought about by processes operating on temporal scales of millennia occurs along regional as well as along local ecoclines. Thus, both of the regional ecoclines 'bioclimatic sections' and 'bioclimatic zones' contribute to explaining postglacial migrations towards a dynamic equilibrium with climatic conditions (Huntley et al. 1989, Birks 1993a, Giesecke et al. 2007, Giesceke et al. 2010). Similarly, variation along the local ecoclines 'water saturation' and 'drought severity', partly also 'lime richness', in boreal forests, is determined by a hierarchy of factors of which one of the most important in the circumboreal zone, to which most of Norway belongs, is glacial erosion and deposition of glacial and glacifluvial sediments. Over thousands of years, these processes create topographic patterns at fine and medium local spatial scales. Local topographic variation does not impact the understorey species composition of boreal forests directly, but acts via control over variation in soil development and soil characteristics like pH and organic content. Soil development throughout the entire postglacial period is responsible for present-day patterns recognisable at fine local, and

even micro, spatial scales (Troedsson & Tamm 1969, Troedsson & Lyford 1973). Finally, strong variation also occurs between condition or impact ecoclines with respect to the spatial scale interval in which variation is large (see Table 1 for examples).

These examples show that species' distributions are determined by 'factors', or ecoclines, which freely combine temporal and spatial scale intervals in which variation is large, and that the importance of different factors varies greatly among ecosystems. Explicit knowledge about which ecoclines are the most important determinants of variation in the area of interest for modelling a target phenomenon, e.g., a species, and the spatial and temporal scale intervals in which variation along these ecoclines is large, is therefore imperative for good decisions to be made in all phases of a DM study. Most notably, such knowledge is essential for data collected for the modelled target and explanatory variables (Steps 2–3 in the 12-step DM process; see Fig. 8) to be appropriate, for appropriate specification of the statistical model (Step 7,ii), and for appropriate interpretation and use of modelling results (Step 12).

Characteristics of overall ecological responses of modelled targets

Gradient analysis in general, and distribution modelling in particular, require careful choice of statistical model (Austin 1976, 1987, 2007, Økland 1990a, 2007). Perhaps the most critical task in statistical model formulation is model specification (Step 7, ii in the 12-step DM process; see Fig. 8), in which assumptions about the shape of the modelled target's overall ecological response are translated into mathematical functions. The overall ecological response expresses how aggregated performance varies along gradients. According to the third insight of the gradient analytic perspective, species occur within a restricted interval along each major complexgradient. This holds true in the theoretical situation where complex-gradients can be conceived as axes that extend to infinity in both directions. However, within the physically delimited study areas of real DM projects, variation along all complex-gradients will be bounded above and below. To apply to such practical situations, the third insight of the GAP needs a clarifying statement as follows: a species occurs within a restricted interval along each major complexgradient provided that the range of variation along this gradient, encountered in the study area, includes at least one of the species' tolerance limits. If both tolerance limits are included in the range of variation encountered in the study area, the species' overall ecological response will be unimodal, with maximum for aggregated performance corresponding to the species' optimum along the complex-gradient (e.g., Økland 1990a). At this point, the reader is asked to recall that complex-gradients are abstractions which have to be approximated by a proxy, a representative variable (see discussion under the second insight of the GA perspective).

Unimodal functions can be parameterised in many different ways. The shapes of overall ecological response curves for species have therefore been debated by ecologists for more than fifty years. Initially, the main focus was on species' responses to local complex-gradients (Whittaker 1967, Austin 1976, 1980, Økland 1986, Minchin 1989, Oksanen & Minchin 2002), although responses to regional complex-gradients have also been addressed in several studies (e.g., Hengeveld & Haeck 1982, Austin et al. 1984, Brown 1984, Økland 1989a, Brown et al. 1996, Thuiller et al. 2003, Austin 2007). Properties of overall species responses to gradients have been reviewed by Økland (1990a), Austin et al. (1994), and Austin (1999a, 2005) and are discussed, among others, by Økland (1992), Ejrnæs (2000), Oksanen & Minchin (2002) and Rydgren et al. (2003). Several consistent patterns emerge from this literature, which can be summarised as follows:



Fig. 10. Influence of the sampled range of variation along an explanatory (predictor) variable on the shape of a hypothetical species' overall ecological response to this variable. (a) The distribution of the hypothetical species in rasterised geographical space: black cells indicate presence and white cells indicate absence. The study area is rasterised into a regular hexadecadal (16 × 16) grid which is sampled by taking each grid cell as an observation unit (the grain of the study). Species' performance is recorded as presence (filled grid cells) or absence (open grid cells) in each grid cell. (b) Recorded values for the explanatory variable. (c) Overall ecological response of the species, with frequency of presence as measure of aggregated performance, modelled by generalised additive modelling (GAM). The red line is the species response curve, obtained be smoothing fitted values from the GAM. (d) Overall ecological response in the subset for which the value of the explanatory variable is less than 12.5, with species response curve fitted by linear regression (LM).



Fig. 11. Dependence of shape of the overall ecological response to an explanatory variable on the range of variation along the gradient that included in the sample. The explanatory variable can be a single environmental variable, a coenocline, or any other variable used as proxy for a complex-gradient or an ecocline that is important for the species in question. (a) Unimodal response in a sample of observation units that spans the entire tolerance of the species. (b) Asymmetric (truncated unimodal) response in a sample that includes the species' optimum and one of the species' tolerance limits. (c) Hinge-shaped response in a sample that includes one tolerance limit but not the species' optimum. (d) Near-linear response in a sample that neither includes the optimum nor any tolerance limit. Inserts show which part of the species' tolerance that is masked by the sampling (gray).

1. Most species have unimodal overall ecological responses to environmental complexgradients, provided that: (i) the variable is linearly related to, and strongly correlated with, a complex-gradient that is important for the species; and (ii) the sampled range of environmental variation includes the entire tolerance of the species (Figs 10c, 11a). Complex, bi-, tri- or multimodal responses occasionally occur, most often due to taxonomic heterogeneity, uneven or irregular sampling, or interference from other gradients (Økland 1986a). For instance, deviant response curves may result from existence of an additional gradient that influences a species' aggregated performance in one part of the focal gradient only (Økland 1986a, Austin et al. 1984, 1994).

- 2. Truncation of species response curves occur frequently. The overall ecological response curve is truncated when the range of environmental variation included in the sample does not include the entire tolerance of the species (Figs 10d, 11b–d). Three different response-curve shapes, resulting from truncation, are shown in Fig. 11b–d. An asymmetric unimodal response curve results if the sample includes the species' optimum and one of its tolerance limits (Fig. 11b). A 'hinge-shaped' curve, i.e., a function that is near linear for values of the explanatory variable larger than ('forward hinge'), or smaller than ('reverse hinge'), the tolerance limit *l* and 0 otherwise (Phillips & Dudík 2008), results if the sample includes one tolerance limit but not the species' optimum (Fig. 8c). Finally, a more or less linear curve results if the sample neither includes the optimum nor any tolerance limit (Fig. 11d). Truncation of response curves frequently occurs in real data sets (e.g., Økland 1986a, Rydgren et al. 2003).
- 3. Response-curve shapes are determined primarily by the amount of compositional turnover in the sample. The relative frequency of unimodal, truncated unimodal, hinge-shaped, more or less linear, and deviant or indeterminate response-curve shapes to an explanatory variable in a specific data set is determined primarily by the amount of compositional turnover in the sample (Gauch & Whittaker 1972, Økland 1990a, Vellend 2001, Rydgren et al. 2003). However, response-curve shapes are also influenced by the way the gradient is scaled. Measures of compositional turnover, which are often used to express positions along gradients (e.g., Økland 1986b) are, however, influenced by the performance measure used, and, notably, the relative weighting of high versus low performance values (Eilertsen et al. 1990); the extent-grain ratio of the study (Økland et al. 1990), which determines how the variation in species performance is partitioned on between observation-unit and within observation-unit variation; and the method used to quantify compositional turnover (Oksanen & Tonteri 1995). Only variation between observation units can normally be 'explained' by analysis of a sample, as explained in the chapter 'Spatial and temporal scales'.
- 4. Response-curve symmetry is influenced by the scaling of the variable. The relative frequency of more or less symmetric versus more or less skewed unimodal response curves does not only depend on properties of the species and of the variable to which responses are studied, as such, but also on the way the gradient variable is scaled (Økland 1986a, 1992, Minchin 1989, Austin 1990, Austin et al. 1994). Every unimodal response curve can be turned into a symmetric curve, or vice versa, by choice of an appropriate non-linear transformation of the variable (Økland 1990a, 1992). Although no single transformation can be found that turns response curves for all co-occurring species into symmetric curves (Økland 1986a), rescaling of gradients in units of compositional turnover may tend to make response curves for a set of species on average slightly more symmetric [Økland (1986b), but see Rydgren et al. (2003)]. It has been argued (e.g., Minchin 1989) that the way gradients are scaled is essentially arbitrary and, thus, that all scalings are equally valid. Most authors do, however, agree that response-curve shape, including degree of symmetry or skewness, are important properties of the species (Austin 1990, 2005, Økland 1990a, Austin & Gaywood 1994, Oksanen & Minchin 2002). Økland (1990a, 1992) argues that response-curve skewness is most meaningfully considered with respect to gradients scaled in units of compositional turnover, because with respect to such scalings the steepness of each species' response curve, i.e., the rate of change in the species' aggregated abundance per unit along the gradient, is related to the average species turnover along the gradient.
- 5. *Response-curve shape is influenced by relevance of the variable for the species.* In a given data set the frequency of species with determinate responses to a gradient variable,

i.e., species with unimodal or monotonous response models that explain significantly more variation than appropriate null models, increases with increasing appropriateness of the variable as proxy for a major complex-gradient, and with increasing importance of the complex-gradient itself for the species. With reference to the first insight of the gradient analytic perspective, that species respond to environmental complex-gradients and not to single environmental factors, it can be argued (Økland 1986a, 1990a, 1992) that species' overall responses should be studied with respect to the best possible proxies for important complex-gradients. The argument for scaling of gradients in units of compositional turnover, mentioned in point 4 above, also applies here: Ejrnæs (2000) and Rydgren et al. (2003) show that species responses to environmentally interpreted DCA ordination (Hill & Gauch 1980) axes scaled in units of compositional turnover more often tend to be determinate than responses to measured explanatory variables. However, the use of ordination methods for scaling of gradients in units of compositional turnover, has been critisised by e.g., Minchin (1989) and Oksanen & Tonteri (1995), for possible artifacts due to shortcomings of the ordination method.

The recent search for 'macroecological rules' (Lawton 1999) or 'ecogeographical rules' (Gaston et al. 2008) has brought renewed interest in the shape of overall ecological responses of species to regional ecoclines, although in a new context and disguised in new terminology. The hypothesised 'positive abundance-occupancy relationship' (AOR) and the 'peak model for intraspecific patterns' (Gaston et al. 2008, Conlisk et al. 2009, Köckemann et al. 2009, Leuschner et al. 2009, Buckley & Freckleton 2010) more or less exactly correspond to the unimodal overall ecological response, applied to regional gradients: a positive AOR implies that species' aggregated performance in a subset of observation units appropriate for analysing variation in the regional spatial domain increases from the periphery to the centre of the species' total extent of occurrence (e.g., Hengeveld & Haeck 1981, Brown 1984). The study of 65 species of vascular plants, bryophytes and lichens on 76 mires in SE Norway by Økland (1989a) is an example of empirical support for a positive AOR: aggregated performance of the species in the 1000-km² study area (recorded as frequency of presence in the 76 investigated mires) increased from an average of 5 % for species for which the study area was close to their distributional limit to 28 % for species for which the study area was situated near the distribution centre. Also the number of mire site-types in which each species was recorded, i.e., the 'habitat breadth', increased from 'marginal' to 'central' species (Pearson's product-moment correlation coefficient: r = 0.69, P > 0.0001, n = 65). This indicated a strongly positive relationship between aggregated performance and 'habitat breadth'.

The unimodal relationship applies to variation in aggregated performance, but not necessarily to other traits, along regional (or local) ecoclines; see reviews by Sagarin & Gaines (2002) and Sagarin et al. (2006).

General features of the relationships of other types of observable targets for DM – such as 'nature types' in a wide sense, including types of communities, ecosystems, and landscapes; land-cover types; and landforms, minerals, and bedrock types – to environmental gradients, are hardly at all discussed in the literature. Reasons for this may be: (1) that relationships between nature types and environmental gradients are outside the primary interests of researchers with nature classification as their main focus; (2) lack of tradition for gradient-based approches among phytosociologists until recently, regardless of affiliation to 'school' (cf. Økland 1990a); (3) that distributions of most geological phenomena are explored from the perspective of geophysical processes rather than with reference to present-day environmental conditions, because the latter are irrelevant for the formation and present-day distribution of these phenomena; and (4) that relationships of modelled targets other than species tend to be idiosyncratic, with few or no properties that can be generalised, even over groups of such phenomena.

There is, however, a general recognition that 'nature types' of most kinds represent overlapping or discrete intervals along environmental gradients, as expressed for 'communities' by Whittaker (1962: 128): 'Natural communities are related to one another along many, complexly related gradients of environment; and along these environmental gradients community properties form gradients which, to a considerable extent, are continuous rather than step-like. Relations of communities may consequently be understood, in the abstract, in terms of a complex, multi-dimensional, and largely continuous pattern; in this pattern community-types represent areas or points defined by given criteria'. This may indicate that points 1 and 2 above, that aggregated performance is more or less unimodally related to important gradients, applies to of 'nature types' as well as species. Furthermore, exceptions to point (iii) exist, as exemplified by patterned ground resulting from periglacial processes (e.g., Luoto & Seppälä 2002, Luoto & Hjort 2006, Hjort & Marmion 2009), which depend directly on present-day environmental, notably climatic, conditions and are in danger of disappearing as a result of climate change (Luoto et al. 2004). The close relationship with regional as well as local complex-gradients demonstrated for these landforms indicate that the unimodal response model may also apply to some geological targets for DM. Based on these considerations, I hypothesise that for most natural phenomena targeted by DM, intervals exist along at least some environmental gradients, outside of which these phenomena fail to occur.

STRUCTURING PROCESSES

Overview of structuring processes

The overall ecological responses of *species* to important environmental complex-gradients result from the action of structuring processes (Økland 1990a), which can be categorised in several ways. Evolution, i.e., gradual or abrupt changes in the frequency and/or distribution of genotypes due to natural selection, provides the background for understanding how all processes that are currently active in structuring of species-environment relationships came into being. The importance of evolutionary processes is illustrated by the positive relationship between species richness on coarse regional spatial scales (the regional species pool; Taylor et al. 1990, Eriksson 1993) and the length of the time span in which evolution has proceeded in a favorable environment without interruption (Zobel 1992, Eriksson 1993, Nekola & White 1999). The *fundamental* role of evolution, for all aspects of biological diversity, past and present, can hardly be overstated [e.g., see Murphy & Lovett-Doust (2008) and Franklin (2010)]. Snapshots of species' distribution patterns, which are the typical targets for DM and a main focus of this essay review, are also results of evolutionary processes. However, a complementary way to understand distributions is in terms of processes that actively shape and maintain species' current overall ecological responses, operating on ecological rather than evolutionary time scales. These processes can be divided into three main categories with sub-categories as follows:

- 1. *Limited physiological tolerance* comprises two main extrinsic processes which reduce the performance of a species compared to its physiological potential:
 - i. *Stress* (*sensu* Grime 1979: 21) comprises 'external constraints which limit the rate of dry matter production of all or a part of the [community]' (note that Grime refers to 'vegetation' in his definition of 'stress'). One example of a stressor is suboptimal

temperatures, the importance of which increases towards the cold end of the regional ecocline 'bioclimatic zones'. Another example is extended snow-lie, which increases in importance along the local ecocline 'reduced growing-season due to prolonged snow-lie' towards extreme snow-beds. The limits of most vascular plant species towards extreme snow-beds in arctic and alpine ecosystems are set by demands for growing seasons of a certain length to complete the life cycle (Resvoll 1917, Gjærevoll 1956).

- ii. **Destabilising processes** (Økland 1990a), which correspond to disturbance *sensu* Grime (1979: 39), comprise 'mechanisms which limit the [plant] biomass by causing its partial or total destruction'. Destabilising processes act by increasing the density-independent mortality of the focal species. Grime (1979) included in his 'disturbance' concept not only wind, frost, drought, erosion and wildfires but also herbivores, pathogens and all kinds of human activities. Økland (1990a) recognises two sub-categories within destabilising processes:
 - a. **Disturbance** sensu stricto, which comprises sudden and unpredictable events leading to biomass destruction. An example of disturbance, recognisable at fine local spatial scales, is the creation of forest-floor gaps by tree uprooting (Schaetzl et al. 1989a).
 - b. *Fluctuations*, which comprise more or less predictable events leading to biomass destruction, such as extended dry and rainy periods. An example of an effect of fluctuations is the die-back of plants from shallow-soil ridges in dry years, the mechanism responsible for variation in species composition along the 'drought severity' ecocline in boreal forests (Økland & Eilertsen 1993).
- 2. **Interspecific interactions** comprise interactions between individuals of different species that bring about change in the performance of one or both species relative to their physiological potential. Types of interactions are often characterised by notations like '(a,b)', where 'a' and 'b' are indicators of the outcome of the interaction, seen from the point of view of each of the two organisms: + indicates a positive outcome, indicates a negative outcome, and 0 indicates a neutral outcome. Five types of interspecific interactions are commonly recognised (Goldberg 1990):
 - i. *Competition* (-,-) comprises interactions, the outcome of which is negative for both organisms. Depending on the relative magnitude of the outcomes for each of the interacting organisms, competitive interactions can be ordered along a gradient from symmetric (equal outcomes for both species) to asymmetric. The classic example of competition is resource competition by which individuals of two different species share a depletable mineral resource in short supply (Tilman 1982).
 - ii. Amensalism (0,-), a term which dates back to Burkholder (1952), comprises interactions, the outcome of which is neutral for one and negative for the other organism. The negative impact of trees on understorey plants (such as bryophytes) in forests is a typical example of amensalism, demonstrating how amensalism by an indirect mechanism modifies the effect of forest trees on the radiation, rainfall and litterfall at ground level [see Økland & Eilertsen (1993) and references quoted therein]. Typically, amensalistic interactions occur independently of the identity of any of the interacting species and rather result from the morphological characteristics of the larger species. Amensalism is an *unspecific* type of interaction which can often, with equal right, be interpreted as background stress due to unfavourable environmental conditions brought about by the presence of a living organism. Amensalism is the end-point of the gradient from a completely asymmetric to a completely symmetric interaction between two species. As pointed out by Økland (2000), amensalism is

often, intentionally or unintentionally, included in a broad 'competition' concept.

- iii. Commensalism (0,+), or facilitation, comprises interactions, the outcome of which is neutral for one and positive for the other organism. Commensalism is typically exemplified by the relationship between epiphytes and their host trees. A more specific example of commensalism is the occurrence of single shoots of Sphagnum balticum among S. fuscum in tall bog hummocks where the former species is unable to grow in pure patches due to low physiological tolerance to drought (Rydin 1985). However, with scaffolding and water supplies provided by densely growing S. fuscum, S. balticum is able to extend its tolerance limit towards bog hummocks (Økland 1989b).
- iv. *Mutualism* (+,+) comprises interactions to the benefit of both organisms. Mutualism can be obligate (obligatory) or facultative. Mycorrhizas are typical examples of obligate mutualisms (e.g., Smith & Reed 2008).
- v. *Parasitism and contramensalism* (+,-) comprise interactions, the outcome of which is negative for one and positive for the other organism. The term **parasitism** is used for symbiotic relationships by which one organism (the parasite) is dependent on another (the host) for nutrient supply and the outcome for the host is negative but not lethal. The term **contramensalism** is used for other (+,-) interactions, i.e., without existence of direct dependence between the interacting organisms. Mitchell & Arthur (1998) exemplify contramensalism by the interaction between small bryophytes growing at the base of a rock ledge and the large, thallose liverwort *Conocephalum conicum*. Establishment of *Conocephalum* is facilitated by the presence of the small bryophytes, while the latter are negatively affected by being overtopped by the large *Conocephalum* thalli.

Most cases of documented **allelopathy**, the mechanism by which plants release chemicals that affect other plants (Wardle et al. 1998), reveal a negative effect on receivers of allelochemicals, to the benefit of the releaser (Inderjit et al. 2011), i.e., a (+,-) relationship. Well-documented cases of allelopathy in boreal forests include inhibition of tree seedling growth by secondary metabolites, typically phenolic compounds (e.g., Nilsson 1994), released from ericaceous species such as *Empetrum nigrum* (Nilsson & Zackrisson 1992, Zackrisson & Nilsson 1992), *Vaccinium myrtillus* (Jäderlund et al. 1996, Mallik & Pellissier 2000), and *Ledum groenlandicum* (Inderjit & Mallik 1997). Allelopathy is an *unspecific* interaction between individuals of different species; a system of complex interactions that is best understood on the ecosystem level (Wardle et al. 1998, Inderjit et al. 2011). Allelopathy may also involve the microbial community and mycorrhizal interactions (Inderjit et al. 2011).

3. *Demographic processes* comprise processes, often with a strong stochastic element, that cause variation in a species' performance not possible to explain as the response to environmental-complex gradients, contemporary or historical, or as the outcome of interactions with other organisms. The term 'demographic process' (e.g., van Groenendael et al. 2000) is used to highlight the fact that the processes in question bring about changes in the demography of the focal species. Botanical examples of demographic processes are diaspore production, dispersal of diaspores into new sites, germination and establishment. The alternative term 'apparent random factor' could have been used to highlight two properties of demographic processes: that the exact sequence of events leading to the present pattern can mostly not be reconstructed, at least not without molecular genetic studies (e.g., Brochmann et al. 2003, Alsos et al. 2007, Tollefsrud et al. 2008); and that results of demographic processes may seem erratic and inexplicable in a snapshot when no information about the history is avail-

able. What is here referred to as demographic processes are important causes of 'noise' (Poore 1956) in ecological data sets, a term much used in early GA literature (e.g., Gauch 1982a, 1982b) for variation not possible to explain by a model. [The complement of 'noise' is 'structure', which pertains to explained variation (Gauch 1982a)]. I prefer the value neutral term 'demographic process' over 'noise', which implicitly conveys a negative attitude towards this kind of variation.

Three sub-categories are recognised within demographic processes:

i. Dispersal into new sites, i.e., transportation and successful establishment of propagules, vegetative or sexual, in sites previously unoccupied by the species in question. Dispersal into new sites is treated as a separate sub-category of demographic processes because of the important difference in effect on distributions of dispersal to new sites compared with dispersal to sites already occupied by the species. Dispersal into new sites is directly responsible for changes in performance patterns on spatial scales much broader than the normal population patch size.

Dispersal into new sites may, over time, contribute substantially to geographical patterns of species' performance that are recognisable on a wide range of spatial scales, regional scales included (van Groenendael et al. 2000). The term **migration**, i.e., massive and/or long-term dispersal into new sites which brings about changes in a species' extent of occurrence, addresses instances of dispersal into new sites with important distributional consequences. Examples are migration of species groups or entire floras or faunas, occurring when large, new land areas are laid open for colonisation, e.g., following deglaciation. Migration is the result of many events that take place on local scales (e.g., Fægri 1934, Elven 1980, Blaalid et al., in press) and that add up to patterns on regional scales (e.g., Skov & Svenning 2004, Birks 2008). Migration is typically, but not necessarily, facilitated by environmental change (Birks & Birks 2008). Examples of migrations in which environmental change has not played an important part, are biological invasions facilitated by man as dispersal vector (e.g., Lambdon et al. 2008), and the gradual migration of the key tree species in boreal forests, Picea abies, westwards in Europe after the last glaciation (Hafsten 1992, Tollefsrud et al. 2008, Seppä et al. 2009).

Theories of gap dynamics (Pickett & Thompson 1978), seed and microsite limitation (Eriksson & Ehrlén 1992), metapopulation dynamics (Hanski 1982, 2004, Hanski & Gilpin 1991) and source-sink population dynamics (Pulliam 1988, 2000) emphasise different aspects of the stochasticity involved in dispersal into, or establishment in, formerly unoccupied sites. An important role of dispersal into new sites, which is often recognised in DM contexts (e.g., Soberón 2007, Hirzel & Le Lay 2008, Franklin 2009), is the occurrence of newly established sink populations outside the species' normal tolerance limits, maintained by recurrent influx of diaspores from persistent source populations. Sink populations may be ephemeral or persist for a long time as stable remnant populations, a term defined by Eriksson (1996) as populations established after successful reproduction, dispersal and establishment events (e.g., under exceptionally favourable climatic conditions), that are unable to persist by own sexual reproduction (Eriksson 1996), but that survive by clonal growth for decades, centuries or even millennia. A classical example of stable remnant populations is provided by Tilia cordata in northern England where this tree species occurs ca. 200 km north of its current reproductive limit (Pigott & Huntley 1978, 1981). Palynological evidence indicates survival of remnant Tilia populations for up to 5 000-7 000 years by clonal growth (Pigott & Huntley 1980). Other examples of remnant populations include occurrences of clonal mire plants in

mires (bogs) with ombrogenous surface peat, e.g., *Carex pauciflora, Erica tetralix* and *Sphagnum papillosum* in SE Norway (Økland 1989b, 1990d). Most probably, these populations established under minerogenous conditions centuries ago. Dispersal into new sites corresponds to 'biogeographic', or 'movement-related' processes in the terminology of Hortal et al. (2010).

ii. Within-population demographic processes, i.e., processes which determine the fate of individuals, which give rise to occurrence patterns at spatial scales finer than the normal patch size of populations of the species in question. This subcategory comprises all demographic processes, including diaspore dispersal, germination and establishment, growth, clonal branching, sexual reproduction and death as far as they result in changes in the structure (Hutchings 1997) of existing populations. Synchronous dieback of larger parts of populations is mostly, but not necessarily, caused by limited physiological tolerance to adverse external factors (e.g., Gauslaa 2002) or impacts by herbivores or other organisms. The latter is typically exemplified by local dieback of *Betula pubescens* in northern boreal forests of Fennoscandia due to herbivory by larvae of the autumnal moth, *Epirrita autumnata* (Tenow & Bylund 2000, Karlsson & Weih 2003).

Almost all instances of growth, clonal branching and death, and most instances of dispersal and establishment, bring about change in the number of individuals within existing populations. The importance of demographic processes for performance variation within existing populations is well documented in an extensive literature on plant population ecology (e.g., see textbooks and reviews by Harper 1977, Silvertown & Charlesworth 2001, Rydgren & Økland 2002, Rydin 2008). The importance of random, within-patch, 'movements' for plant distributions at micro spatial scales is highlighted in the 'carousel model' of van der Maarel & Sykes (1993, 1997), which emerged from observations of low persistence of vascular plants, both clonally and sexually reproducing species, at micro spatial scales in an alvar limestone grassland. What is here termed 'within-population demographic processes' is contained in the broader concept of 'occupancy dynamics' of Hortal et al. (2010), which also includes the destabilising processes that bring about within-population demographic variation.

The term **extinction debt** (Tilman et al. 1994), i.e., expected future extinction of species due to events in the past, addresses a within-population process typically resulting from former changes of environmental conditions which turns populations of many species into sink populations. Extinction debt is well documented for vascular plants in semi-natural grasslands after cessation of management and/ or fragmentation (e.g., Cousins 2006, 2009, Hamre et al. 2010), and for vascular plants (Vellend et al. 2006) and lichens in forests after fragmentation (Berglund & Jonsson 2005, Öckinger & Nilsson 2010).

iii. Space limitation covers stochastic effects brought about by limitations on the number of individuals, of the same or different species, that can co-occur in an observation unit of a given, small, size (Oksanen 1996). Space limitation becomes increasingly important towards spatial scales at which the size of the observation unit approaches the average size of plant units (van der Maarel et al. 1995). This follows directly from the positive species (richness)-area relationship (SAR; Arrhenius 1921, He & Legendre 1996, M. Williams et al. 2009), which predicts that the number of individuals, and hence also the number of species and the fraction of the local or regional species pools, that are present in an observation unit, decrease when the size of this unit decreases. The modus operandi of space limitation as a structuring process is by combination of two mechanisms: (a) low availability of sites that open

for colonisation at any given time point; and (b) stochasticity of establishment in vacant sites.

Stress and destabilising processes influence species' overall ecological responses in two different ways:

- 1. **Background stress or disturbance** is a collective term for processes that reduce the performance of a species compared to its physiological potential, without variation in the magnitude of effects along the complex-gradient. Background stress or disturbance is exemplified by vascular plants in the middle alpine bioclimatic zone, in which low temperatures restrict growth also when local environmental site conditions are favourable (Nordhagen 1943).
- 2. *Gradient-dependent stress or disturbance* addresses processes that reduce the performance of a species compared to its physiological potential situations, with variation in the magnitude of effects along the complex-gradient. Typically, the magnitude of performance reduction increases from the species' optimum towards the tolerance limits as exemplified by vascular plants along the local ecocline 'reduced growing-season due to prolonged snow-lie' along which density-independent mortal-ity increases monotonously towards extreme snow-beds (e.g., Resvoll 1917).

Effects of gradient-dependent stress or disturbance on a species' overall ecological response can be described along (at least) two dimensions:

- 1. **Resistance** (Pimm 1984); i.e., the magnitude of change in a species' performance in response to a certain amount of perturbation of environmental conditions, e.g., measured as the unit displacement of a site in environmental variables, or ecological space. Resistance, which can be quantified by the slope of the response curve over a unit interval along axes in the conceptual space, varies from high when the response curve is flat (species inert to perturbation) to low when the response curve is steeply ascending or descending. One extreme along this response gradient is the **threshold response**; the more or less theoretical situation by which a small change in an environmental factor triggers a large but predictable response.
- 2. **Reversibility**; i.e., the tendency for a species' performance to return to the initial magnitude when a former perturbation of environmental conditions is reversed. The concept of reversibility combines stability and resilience (Pimm 1984, Ives 1995) into one dimension. Pimm (1984) defines **stability** as a binary variable: a system is stable if initial values of the response are restored when former perturbation of environmental conditions are reversed, and unstable if initial values are not restored. Resilience is defined as the rate of restoration. Reversibility thus makes up a gradient from stable and resilient, i.e., reversible, systems that rapidly return to initial values; via lowresilient stable systems with slow return; to unstable or irreversible systems, which do not return to initial values. Irreversibility may result from removal (e.g., Hörnberg et al. 1999) or introduction (e.g., Hörnberg et al. 1995, Ehrenfeld 2010) of key species or from ecosystem degradation to initial conditions dominated by inorganic or naked soils (e.g., Feagin et al. 2005, Feldmeyer-Christe et al. 2011). Typically, irreversibility involves feedback mechanisms, as exemplified by the effect of moisture reduction and litterfall from a growing pine tree on peat-moss growth and abundance in boreal bogs (Ohlson et al. 2001).

Legacies from structuring processes in terms of changes in species performance patterns may last long after the process ceased to be active. Unfortunately, however, in most cases the imprints of structuring processes are not sufficiently specific to allow identification of the specific process(es). Much of the variation in species performance that can be observed in a snapshot in time, will remain unexplained. Disentangling the different processes and their relative importance requires long time-series of demographic and environmental data for the target species, typically obtained from permanent observation units (Austin 1981). This is exemplified by the 20-year demographic study of *Hylocomium splendens* in boreal forests which shows that litterfall, rodent grazing and uprooting, micro-landslides and frost and water damage are all important for the distribution of this species at micro scales (Økland 1995, 2000, Økland & Bakkestuen 2004, Bakkestuen et al. 2009).

The *Hylocomium* example also shows that no definitive limit can be drawn between environmental processes such as limited physiological tolerance, e.g., to disturbance processes, biotic processes such as interspecific interactions, and demographic processes: both the environment and other species influence the performance of the target species *via* demographic effects. The division into structuring processes therefore needs to be applied in a pragmatic way, e.g., by considering a hierarchy of processes with limited physiological tolerance on top, followed by interspecific interactions, and ending with demographic processes. In such a hierarchical framework, limited physiological tolerance comprises all effects on species performance that are directly predictable from position along the complex-gradient in question, including effects of interactions with species that normally vary in performance along this gradient. Furthermore, interspecific interactions comprise all residual effects predictable from the presence of other species. Accordingly, what is here referred to as demographic processes only comprise demographic changes which are not brought about by environmental or biotic processes.

Importance of structuring processes at different spatial and temporal scales

Just like ecoclines differ with respect to temporal and spatial scale intervals in which variation along them is large, the contributions of different structuring processes to patterns of variation in species performance and, hence, species composition, depend on the grain and extent chosen for the study (Økland 1990a). The DM literature rarely goes beyond very general statements about scales of variation, as exemplified by the summary of 'scale relationships' of four types of 'factors' that affect species distributions in the recent paper by Hortal et al. (2010): (1) dispersal into new sites, i.e., 'movement-related', or 'biogeographic' factors in the terminology of Hortal et al. (2010), is important at spatial scales from the fine regional to the coarse regional; (2) limited physiological tolerance to environmental factors, i.e., 'scenopoetic' factors in the terminology of Hortal et al. (2010), is important at spatial scales from the coarse local to the regional; (3) interspecific interactions, i.e., 'bionomic factors' in the terminology of Hortal et al. (2010), are important at spatial scales from micro to coarse regional but with decreasing importance from the coarse local towards regional scales; and (4) within-population demographic processes, included in 'occupancy dynamics' (He & Gaston 2000) in the terminology of Hortal et al. (2010), are important at spatial scales from micro to fine regional but with decreasing importance from the coarse local scale towards coarser scales. [Note that Hortal et al.'s terminology for scales, which is based upon Pearson & Dawson (2003), is here translated into the terminology explained in Fig. 4.] More or less similar opinions on relationships between processes and the scales on which they operate, are often expressed in the DM literature, regardless of which organism group is focused (e.g., Pearson & Dawson 2003, Franklin 2009, Soberón 2010). The large diversity of environmental complex-gradients with respect to spatial and temporal scales at which variation is large (Table 1), and of structuring processes responsible for species' responses to these gradients, motivate for a more nuanced view on the relationship between process and scale.

Limited physiological tolerance. Hortal et al. (2010) indicate that the relative importance of 'scenopoetic' factors is high at broad spatial scales, with increasing importance from extents of 10–1 000 m to 10 km, beyond which is large. This is, however, at odds with the many examples of local ecoclines with high importance for species compositional variation at micro, fine and medium local spatial scales (see Table 1), along which tolerance limits are set by limited physiological tolerance. Micro-scale patterns recognisable in observation units of 1 m or smaller, brought about by limited physiological tolerance are exemplified by the epiphytic lichen species composition on forest trees which varies within single trees and even within single branches of each tree (Holien 1997, Coxson & Coyle 2003), by the variation in epixylic species performance between (Høiland & Bendiksen 1997, Heilmann-Clausen 2001), and even within (McAlister 1997, Kushnevskaya et al. 2007), individual logs, and by the epilithic bryophyte and lichen species composition which varies within small rock surfaces (Weibull 2001, Pentecost & Zhang 2006). In all of these examples, water supply is important in some way, resulting in local ecoclines such as 'water saturation', 'air humidity' and 'water supply to bedrock' (Halvorsen et al. 2009). Another example of a micro-scale local ecocline is the extension of the 'water saturation' gradient into boreal mires, in which water supply is basically a function of surface microtopography (Økland et al. 2001). Median depth to the water table is a good proxy for this gradient (Økland 1989b), as demonstrated by Økland (1990b), who found that depth to the water table was the variable which explained the largest fraction of variation in species composition in the boreal mire Northern Kisselbergmosen (SE Norway). Limited physiological tolerance determines species' performances along this ecocline down to spatial detail of centimetres (Økland 1990c). These examples show that ecoclinal variation in species composition, brought about by limited physiological tolerance of species to gradient-dependent stress or disturbance, is an important structuring process at spatial scales down to the size of individual plants. That species' responses to regional ecoclines, the variation along which is mostly expressed on coarse regional spatial scales, are also determined by limited physiological tolerance, to low vs high temperatures, or to arid vs hyperhumid climates, is well documented in the classical biogeographic literature (e.g., Walter 1968, Dahl 1998).

Interspecific interactions are neighbour phenomena (Mithen et al. 1984) and, accordingly, of highest importance at temporal and spatial scales where individuals are in direct physical contact, i.e., near the size of individuals. For the vast majority of low-mobile organisms, neighbour interactions take place on micro or fine local spatial scales.

Increasing amounts of empirical evidence indicate that the high importance for plant species composition often attributed to negative interspecific interactions like competition and amensalism, also at spatial scales much broader that plant unit size, is an overstatement (e.g., Økland 1990a, van der Maarel 2005). For negative interspecific interactions between two species to contribute to patterns at spatial scales broader than the size of individuals, the inferior competitor has to encounter the superior competitor in a large fraction of the sites in which it occurs, i.e., within a major part of its tolerance area in conceptual ecological space and over a large geographical area. Furthermore, the outcome of the interaction has to be highly predictable and more or less invariant of position along major complex-gradients, successional state, order of arrival of the two species at each site, etc. Well-documented examples of negative interspecific interactions between plants that add up to coarser-scale patterns are not many, but some exist. One of the best-documented cases is provided by Leathwick & Austin (2001), who modelled the distribution of tree species in New Zealand. They found that GAM distribution models for 11 out of 12 rare tree species in New Zealand were considerably improved by including density of the dominant tree genus *Nothofagus* as an independent variable in the models. Their results were

thus in accordance with predictions from the hypothesis that many single interaction events with similar outcomes sum to a pattern that is recognisable on spatial scales much broader than the size of individuals (Leathwick & Austin 2001). Another example is provided by Burns (2007), who found that occurrence patterns of the shrub *Sambucus racemosa* on small islands in Canada were nonrandom and consistent with expectations, given that negative interactions from established species were an important process. Further studies are, however, needed before generalisations can be made about the commonness of this phenomenon among plants.

Based upon theoretical reasoning, increasing importance of interspecific interactions, summing up to recognisable patterns at broader scales, is likely to result when organisms are more mobile, have lower density, and compete with other organisms for resources that are more essential and in increasingly short supply. Accordingly, broad-scaled distributional consequences of interspecific interactions should be expected to be more common among animals, particularly among vertebrates. An illustrative case study is provided by Heikkinen et al. (2007), who found that distribution models for four hole-nesting owl species in Finland were improved by including presence data for six woodpecker species as explanatory variables. Model improvement was significant for samples of owl presence in 10-km grid cells, less clearly when 40-km grid cells were used. The spatial scale interval in which large variation in owl performance due to effects of interspecific interactions can be traced thus included the fine regional, but hardly the coarse regional scale.

The literature on biological invasions provides several examples of interspecific interactions that, over shorter or longer time intervals, bring about distributional shifts of indigenous species that are recognisable on local or fine regional spatial scales (Mack et al. 2000, Reinhart et al. 2006, Combs et al. 2011). A well-documented example from Fennoscandia is the westward movement of Norway spruce, *Picea abies*, which has been going on for most of the Holocene and still has not come to an end (Hafsten 1992, Tollefsen et al. 2008, Seppä et al. 2009). Due to its high maximum relative growth rate and its shade tolerance, *Picea abies* is in general a stronger competitor than *Pinus sylvestris*, *Betula* spp. and broad-leaved deciduous forest trees in this region, over a wide range of environmental conditions (cf. Linder et al. 1997, Dehlin et al. 2005). This explains why *Picea* locally replaces other tree species (Seppä et al. 2009). However, within their extent of occurrence the other tree species are still more or less constantly present in observation units of 1 km² or larger within their extent of occurrence (e.g., Hultén 1971). This indicates that results of negative interspecific interactions among plants are mostly detectable at spatial scales finer than the fine regional scale.

Like negative interactions, positive interspecific interactions, i.e., commensalism and mututalism, also basically affect species' performance on spatial scales near the size of individuals. Typical examples of patterns on micro and fine local spatial scales that are brought about by positive interactions, are the facilitation of the rare vascular plant *Delphinium uliginosum* by the moss *Didymodon tophaceus* in serpentine wetlands of the U.S. (Freestone 2006), the associations observed between specialised pyrenomycetous epiphyte species on *Salix* in N Norway (Mathiassen & Økland 2007), and the enhanced performance of some vascular plant species in alpine heaths in the presence of shelter-providing bryophytes and/or other vascular plants (e.g., Carlsson & Callaghan 1991, Callaway 1995, Choler et al. 2001). In general, the importance of facilitation increases towards more stressful environments (Callaway et al. 2002).

Like negative interspecific interactions, effects of positive interspecific interactions are expected to result in single-species patterns, and patterns in species richness, recognisable at fine local spatial scales (Cavieres & Badano 2009). Conditions necessary for positive neighbour interactions to sum to patterns recognisable on coarser scales, are generally the same as for negative interactions, but with opposite sign. However, with increasing strength of the dependence of one species on another species, i.e., along the gradients from neutral interactions to

obligate mutualistic or parasitic interactions, respectively, the probability for the interaction to give rise to patterns recognisable at coarser scales increases. One example is obligate mycorrhizal fungi, which are restricted to the extent of occurrence of their mycorrhizal partners, on local (Bendiksen et al. 2004) as well as regional (Eckblad 1981) spatial scales. Such dependence is carried to the extreme by rare animal species with strong dependence on specific plants or plant groups, e.g., for food and shelter at larval stages (Araújo & Luoto 2007, Preston et al. 2008). Consequences for DM are exemplified by Araújo & Luoto (2007), who found significant improvements of spatial predictions for the butterfly *Parnassius mnemosyne* when known presences of species of the herb genus *Corydalis* spp. were included among independent variables in the modelling, even if grid cells of 50 × 50 km (in the coarse regional domain; Fig. 4) were used: *Parnassius* larvae are monophagous on *Corydalis* species (Luoto et al. 2001). Patterns recognisable on coarse regional spatial scales have been demonstrated for fungal plant pathogens with narrow food-plant preferences and/or their hosts [e.g., Alexander et al. 2007; also see see van Andel (2005) for review].

One reason why distributional consequences of interspecific interactions are difficult to assess (e.g., Franklin 2009), is that negative and positive interspecific interactions typically occur together in complex ways in plant communities (Callaway & Walker 1997). This is exemplified by the experimental study of alpine vegetation by Mitchell et al. (2009): strong negative as well as strong positive interactions were found between pairs of species, but neither type of interaction was considered important for the structure of the community as a whole.

Demographic processes. Within-population demographic processes and space limitation first of all affect the fate of individuals and, hence, manifest themselves as patterns at micro and fine local spatial scales. Rare instances of long-distance dispersal into new sites may, however, extend a species' extent of occurrence considerably (Alsos et al. 2007, Nathan et al. 2008, Pedersen 2009) and give rise to distributional patterns with large variation on spatial scales up to the coarse local and fine regional (e.g., Hovstad et al. 2009, Moore 2009, Jacobson & Peres-Neto 2010) or, in extreme cases, even the coarse regional (Nathan et al. 2008, Pedersen 2009) or perhaps also the global. Dispersal is therefore important at all spatial scales, from the finest to the broadest. Svenning & Skov (2002) demonstrated that dispersal affects the distribution of plants on fine to medium local spatial scales in Danish deciduous forests by analysing a sample of observation units with linear dimension of grain 5–14 m and of extent < 1 km: poor dispersers had a more clumped distribution than species with good dispersal capabilities. Decreasing probability for a diaspore to reach a site with increasing distance from the source is the main mechanism behind reduced compositional similarity of ecologically similar sites with increasing inter-site distance, as expressed in the important but not universally applicable 'rule' referred to as 'distance decay of floristic similarity' (Nekola & White 1999). Thus R. Økland et al. (2003) demonstrated considerable variation in species composition among 11 boreal swamp forests that could be explained neither by any of the 53 recorded environmental explanatory variables nor by between swamp-forest distances. The linear dimensions of grain and extent in this study were 10–100 m, and approx. 2 000 m, respectively, corresponding to medium local spatial scales. These results indicated that the observed pattern was not mainly due to recent successful dispersal and establishment events. Instead, R. Økland et al. (2003) hypothesised that the distinctness of each swamp forest was due to a combination of processes among which stochasticity of establishment in gaps, 'windows of opportunity', and persistence of established clonal species are both important. Variation at fine spatial scales due to randomness in demographic processes is exemplified by Økland (1989b) who, in a detailed study of a boreal bog, found about 15 small species of *Cladonia* spp. that were able to colonise naked peat patches in hummocks, apparently without differences in microsite preferences. These examples show that dispersal into new sites and other demographic processes bring about large variation in

species performance over a wide range of spatial scales, although with decreasing importance from finer to broader scales. By definition, space limitation is important only at fine, i.e., micro and fine local, spatial scales.

Assessment. Table 2, which summarises the ranges of spatial scale intervals in which variation is large for each of the structuring processes, shows that existing empirical data for plants and other organisms with low mobility do not support the generalisations about 'scale relationships' expressed by Hortal et al. (2010) and elsewhere in the DM literature. Two discrepancies are particularly important: (1) 'environmental factors' that operate via limited physiological tolerance are important on all spatial scales from micro to the coarse regional; and (2) 'biotic factors', of which competition is most strongly focused in the literature although amensalism, commensalism, and facultative mutualism, are likely to be at least equally important, are primarily important on micro and fine local spatial scales, although noticeable exceptions to this exist. Furthermore, two more points should be noted: (3) that dispersal to new sites contributes to performance variation over a wide range of spatial scales; and (4) that the importance of 'occupancy dynamics', i.e., within-population demographic processes and space limitation, increases strongly towards spatial scales near the size of individuals of the species in question.

My conclusion from the review of structuring processes is that a more balanced view of the relationship between structuring processes and spatial scale is urgently needed. In particular, plants and other immobile organisms have to be recognised as fundamentally different from strongly mobile organisms, and there seems to be a strong tendency for patterns of performance variation to be idiosyncratic, i.e., to depend on properties of the species and characteristics of the study area.

Dependence of species' overall ecological responses on structuring processes

Regardless of spatial scale interval in which performance variation of a species along a major complex-gradient is large, the species' overall ecological response to an important complex-gradient is expected to follow a unimodal curve because of limited physiological tolerance to extrinsic processes, i.e., stress and destabilising processes, the intensity of which depends on position along the complex-gradient (see the chapter ' Characteristics of overall ecological responses of modelled targets' and Fig. 12). Background stress or disturbance, and demographic processes, influence aggregated performance at all spatial scales, without systematic variation in intensity of the process along the complex-gradient (Fig. 12). The importance of each subcategory of demographic process depends on the spatial scale addressed. While lack of dispersal into new sites is important at regional spatial scales (Fig. 12a), within-population demographic processes are most important at local spatial scales (Fig. 12b) and space limitation is most important at micro, perhaps also fine local, spatial scales (Fig. 12c, Table 2).

The response models in Figs 12a–c agree with the model of Austin's (Austin 1990: Fig. 12) in two important respects: (1) by predicting an increasing role of physiological tolerance to stress and disturbance from the optimum towards gradient ends; and (2) by accounting for higher potential importance of negative interactions on aggregated performance near gradient midpoints where many species tend to have their physiological optima. In accordance with Austin (1990), I have termed gradient extremes in Fig. 12 'deficient end' and 'toxic end', respectively. The models in Fig. 12 do, however, differ from Austin's model in five important respects:

- 1. By allowing for variation in the importance of structuring processes among spatial scales, in accordance with Table 2.
- 2. By allowing for variation in the kurtosis of the overall ecological response curves among

low, moderate and high - based upon expert judgement by the author of the fraction of variation in performance of this species in each scale Table 2. Importance of different structuring processes for explaining variation in the performance of a 'typical' plant species, i.e., a species for which the process is relevant, at different spatial scales. Spatial scales intervals are defined with reference to linear grain sizes in samples with extent-grain ratio of 16, such as regular hexadecadal grids (see Fig. 4). Importance is reported on an ordinal scale with four levels – negligible, interval, that is explained by the process in question.

Process Spa	atial scale interval	(m)					
	Micro (< 10 ⁰)	Fine local $(10^0 - 10^1)$	Medium local (10 ¹ –10 ²)	Coarse local (10 ² –10 ³)	Fine regional (10 ³ –10 ^{4.5})	Coarse regional (10 ^{4.5} –10 ⁶)	Global (> 10 ⁶)
Limited physiological tolerance (to environmental factors in a broad sense) Interspecific interactions	high	high	high	high	high	high	moderate
competition and amensalism commensalism and facultative mutualism obligate mutualism and parasitism	moderate moderate high	moderate moderate high	low moderate high	low low high	negligible low high	negligible negligible moderate	negligible negligible low
dispersal into new sites* within-population demographic processes* space limitation	not relevant high high	low moderate moderate	moderate low low	moderate not relevant negligible	moderate not relevant negligible	moderate not relevant negligible	low not relevant negligible
		:		-		-	

*these two sub-categories of structuring processes are partly defined with reference to spatial scale interval in which variation is large, and are therefore 'not relevant' in some spatial domains



Fig. 12. Hypothetical contributions from different structuring processes to explaining variation in species' aggregated performance along environmental complex-gradients at different spatial scales. Spatial scale is defined as the linear grain sizes in samples with extent-grain ratio of 16 such as regular hexadecadal grids (see Fig. 4). Aggregated performance is recorded on a scale from 0 (absence) to 1 (maximum). LPT = limited physiological tolerance; Δ = contribution from limited physiological tolerance to factor that is dependent on position along the complexgradient, shown for gradient position xk; Δ +, Δ - = increase and decrease, respectively, of aggregated performance, relative to the situation in which the net contribution from interspecific interactions is 0. (a) Micro scale (grain size = 25 cm, extent = 4 m), e.g., corresponding to the local ecocline 'water saturation' (= depth to the water table) in a boreal mire. (b) Medium local scale (grain size = 25 m, extent = 400 m), e.g., corresponding to the local ecocline 'drought severity' in a boreal forest. (c) Fine regional scale (grain size = 1 km, extent = 16 km), e.g., corresponding to the regional ecocline 'bioclimatic zones' in W Norway. spatial scales, i.e., narrow-peaked vs. flat-topped curves (Oksanen & Minchin 2002).

- 3. By opening for the possibility that negative as well as positive interactions between the target species and other species may influence the shape of the overall ecological response. The effects of positive interactions, i.e., commensalism or mutualism, and negative interactions, i.e., competition and amensalism, contrast each other and may cancel each other out (Fig. 12b–c). The magnitudes of contributions from interspecific interactions, regardless of sign, increase in the models towards finer spatial scales. In Fig. 12b, interspecific interactions influence the value for aggregated performance at each point along the gradient within the tolerance limits of the species, i.e., by a **magnitude response**, while in Fig. 12c an **amplitude response**, i.e., a shift in the species' tolerance limits, is shown near the toxic end of the gradient. There is no *a priori* reason, however, to expect amplitude responses to be restricted to the finest spatial scales.
- 4. By explicitly incorporating contributions from processes that reduce the aggregated performance at the optimum from the theoretical maximum (of 1 in Figs 12a–c). Of such processes, background stress and disturbance, and lack of dispersal into new sites, are the most important at regional spatial scales. Towards finer spatial scales, the importance of within-population demographic processes is expected to increase. Near the size of individuals, space limitation is likely to be most important.
- 5. *By not incorporating systematic variation in curve skewness in the models.* Austin's model predicts response curves to be increasingly skewed with increasing distance of the species' optimum from the mid-region of the gradient, with the skew pointing in direction of this mid-region. Response curves for *Eucalyptus* species in Australia with respect to annual mean temperatures by Austin et al. (1994) accord with this prediction. The result of Økland (1986), that the skewness of response curves depends on the scaling of the gradient, does, however, leave open the answer to the question about the role of choice of scaling of the gradient for curve skewness. Austin et al. (1994) studied response curves with respect to a gradient scaled in physical units (°C). It remains to be seen if more symmetric response curve would be obtained by scaling the gradient in units of compositional turnover, by a method not open to criticism such as the non-linear rescaling option in DCA ordination (Oksanen & Tonteri 1995).

The overall ecological responses in Fig. 12 are models. Empirical overall ecological response curves will be less smooth due to effects of sampling, local idiosyncracies etc.

DISCUSSION: IMPLICATIONS OF THE GRADIENT ANALYTIC PERSPECTIVE FOR DISTRIBUTION MODELLING

ECOLOGICAL MODEL (STEP 1)

Problem formulation and specificiation, Step 1 in the distribution modelling process (Fig. 8), relies on a firm theoretical fundament. The logical choice of a starting point for the discussion of implications of the gradient analytic perspective for DM is therefore the basic concepts of the niche and related concepts, and conceptual models for DM built upon these concepts.

Concepts of the habitat and the environment

The term 'habitat', which is related to the verb 'inhabit', has been used for a long time to address the surroundings of a particular organism, e.g., the environment in which a species can be found (e.g., Tansley 1935) or, as formulated by Whittaker et al. (1973: 328): the 'range of environments or communities over which a species occurs'. Whittaker et al. (1973) also provide a precise definition of the habitat in terms of gradient concepts. Firstly, quoting Goodall (1963), the 'habitat hyperspace' was defined as the *m*-dimensional co-ordinate system with axes that characterise the landscape (or location or site) under study. Secondly, a species' habitat, i.e., the 'habitat hypervolume', was defined (Whittaker et al. 1973: 328) as 'an abstract formulation of this range [of occurence] in terms of extensive environmental variables and the species' limits in relation to them', i.e., the region in the 'habitat hyperspace' in which the species occurs. This abstract concept of the habitat corresponds to the hypervolume in ecological space, occupied by the species. A concrete approximation of this abstract concept of the habitat is the hypervolume in an environmental variables space with axes that are proxies for the axes of the ecological space, occupied by the species. Hutchinson (1978) used the term 'scenopoetic', or 'scene-setting', or 'habitat-structuring', variables, for the axes of the habitat hyperspace. The term 'scenopoetic variable' is interpreted by Soberón (2007) as synonymous with 'direct gradient' in Austin's terminology, while others, e.g., Hortal et al. (2010), use the term 'scenopoetic variable' in a wider meaning.

The definition of 'habitat' proposed by Kearney (2006: 187), as 'a ... physical place, at a particular scale of space and time, where an organism either actually or potentially lives', differs from the more abstract definitions given above because 'in contrast to an environment or a niche, a habitat can exist and be described without reference to an organism' (Kearney 2006: 187). Kearney instead uses 'environment' for 'the biotic and abiotic phenomena surrounding and potentially interacting with an organism', i.e., the 'particular environment experienced by an organism', 'the result of the interaction between the characteristics of that organism and the habitat in which it occur'. In Kearney's terminology two organisms that live together in the same habitat may experience different environments.

Kearney's concept of the habitat corresponds to Hutchinson's (1978) concept of the 'biotope'; a place in 'the physical world ... conceived as a map, each point (or cell) of which is characterized by its geographical co-ordinates and the local values of *n* environmental attributes at a given time' (Colwell & Rangel 2009: 19651) that can be described without reference to organisms, in geographical and/or environmental variables spaces.

The term 'habitat' is also often used as synonymous with 'ecosystem' or 'site', e.g., in EUNIS, the European habitat classification system (Davies et al. 2004). The classical explanation of an 'ecosystem' by Tansley (1935: 299), which reads '... including ... the organism-complex ... [and] also the whole complex of physical factors forming what we call the environment of the biome – the habitat factors in the widest sense' is, however, much broader than Kearney's habitat and Hutchinson's biotope concepts.

Niche concepts

The term 'niche' was first used by Grinnell (1917) and has thereafter been used in many, wider or narrower, meanings to denote the relationship of an organism to the environment and/or other to organisms (Vandermeer 1972, Whittaker et al. 1973, Soberón 2007, Colwell & Rangel 2009). Colwell & Rangel (2009: 19651) point out that Hutchinson's (1978) concepts of 'biotope' and 'niche' both address 'exactly the same *n* environmental attributes [which] define [a conceptual]

space', but nevertheless are fundamentally different: while the 'biotope' is a place in the physical world that exists without reference to organisms, the niche only makes sense as an attribute of [a group of] organisms, e.g., a species. Thus, the environmental variables space is a common arena for the two concepts because both the 'biotope' and the 'niche' can be described by use of environmental explanatory variables, a fact referred to as Hutchinson's duality by Colwell & Rangel (2009). The 'biotope' can also be characterised in geographical space.

Concepts of the 'niche' fall into two groups: the 'Grinnellian niche', which comprises 'the environmental requirements for a species to subsist without immigration' (Hirzel & Le Lay 2008: 1373), and, following Elton (1927), the 'Eltonian niche' which comprises the species' 'relationships to other species' (Hirzel & Le Lay 2008: 1373). While the 'Grinnellian niche' corresponds exactly to their concept of 'habitat', Whittaker et al. (1973) propose a definition of the term 'niche' that parallels their definition of the habitat but addresses the Eltonian niche only. Firstly, they (p. 332) define the niche hyperspace as the *n*-dimensional co-ordinate system the axes of which 'representing other member species of the community as well as more general niche variables such as height above ground, prey size, etc.' Secondly, they characterise the axes of this niche hyperspace as follows: 'Each species in the community utilizes, or occurs in, or is affected by, some range of these axes [which] ... define a multidimensional niche hyperspace interrelating the species of the community'. In the terminology of Whittaker et al. (1973), a species' niche is the region in the 'niche hyperspace' in which the species occurs. Hutchinson (1978) coined the term 'bionomic' for the axes of the niche hyperspace of Whittaker et al.'s (1973). The term 'bionomic variable' was defined by Soberón (2010: 160; also see Soberón 2007) as comprising all variables that 'affect the fitness of the populaton, but [that] can also be consumed or modified and [on which] the population ... therefore ... has an impact', i.e., variables that represent interspecific interactions as well as resource gradients in Austin's terminology. Soberón's (2007, 2010) interpretation of the terms 'scenopoetic variable' and 'bionomic variable' matches his definitions of the Grinnellian and the Eltonian niche: the species' response to scenopoetic variables defines its Grinnellian niche while its response to bionomic variables defines its Eltonian niche. Most authors, as exemplified by Hortal et al. (2010), do, however, treat the terms 'bionomic factor' and 'biotic interaction' as synonymous and do not include resource gradients in these concepts.

Kearney (2006: 187), although in principle accepting Hutchinson's idea of the niche as an 'n-dimensional hypervolume', redefines the 'niche' as 'a subset [my emphasis] of those environmental conditions which affect a particular organism, where the average absolute fitness of individuals in a population is greater than or equal to one.' Including all conditions that affect fitness in his definition of the 'niche', the Eltonian niche as defined above as well as a major part of the Grinnellian niche is included.

The Grinnellian and Eltonian niches are often associated with the terms *fundamental niche* and *realised niche*, defined by Hutchinson (1957). The fundamental niche is the *n*-dimensional hypervolume, i.e., the conceptual space in which all factors of importance for the occurrence of the species, both physical and biological, are included as axes, in which a species in the absence of competition with other species is able to persist indefinitely. The realised niche is defined as the part of the fundamental niche in which the species is able to persist even when exposed to competition from other species.

Why the concepts of habitat and niche are not useful for distribution modelling

Neither the Grinnellian nor the Eltonian, and neither the fundamental nor the realised, niche concepts are clear in themselves. Accordingly, I find the relevance of all of these concepts for

distribution modelling unclear. The main reasons for lack of clarity are:

- 1. Lack of clarity of the fundamental and realised niche concepts.
- 2. Lack of a clear distinction between 'dimensions' of the Grinnellian and Eltonian niche spaces.
- 3. Representation of interspecific interactions as axes ('dimensions') in a conceptual 'niche hyperspace' is inadequate.
- 4. Failure of the niche concepts to take demographic processes, including historical factors, into account.
- 5. Lack of clarity with respect to how to delimit a species' niche.

Lack of clarity of the fundamental and realised niche concepts. This reason for lack of clarity is thoroughly discussed by Araújo & Guisan (2006: 1678), who refer to Hutchinson's original text in which it is stated that 'all...variables, both physical and biological, being considered, the fundamental niche of any species will completely define its ecological properties' (Hutchinson 1957: 416). In their interpretation of this text, Araújo & Guisan (2006: 1678) state that 'limiting factors (e.g., temperature and known presence of mutualist species) and resource factors (e.g., energy and presence of prey) should be part of ... the fundamental niche'. Such an interpretation includes *all* factors that limit the occurrence of a species, regardless of the type of relationship this species has to them, in the definition of the fundamental niche. Furthermore, Araújo & Guisan (2006) interpret Hutchinson's realised niche as the response of the species when competitive interactions with other species at the same trophic level is also taken into account, i.e., as the species' range along axes of the 'ecotope hyperspace' [= the habitat and niche hyperspaces taken together; Whittaker et al. (1973)].

The concepts of the fundamental and the realised niche are only useful if they can be appropriately operationalised. This is extensively discussed by Araújo & Guisan (2006) and Soberón (2007, 2010), neither of whom draw clear conclusions. Several of the other reasons for lack of clarity discussed below are rooted in lack of clarity of the fundamental and realised niche concepts.

Lack of a clear distinction between 'dimensions' of the Grinnellian and Eltonian niche spaces. Several competing definitions of the Grinnellian and Eltonian niche spaces exist, as exemplified by the difference between the commonly applied definition of the Grinnellian niche hyperspace and Soberón's definition (Soberón 2007, 2010). According to the former, all environmental [or, habitat, in the sense of Whittaker et al. (1973)] factors determine the Grinnellian niche. Soberón, on the other hand, transfers factors that can be affected by the organism itself, 'bionomic variables' in his terminology, from the Grinnellian to the Eltonian niche hyperspaces. This difference between the two concepts of the Eltonian niche demonstrates the complexity of interspecific interactions and the fact that no clear distinction can be drawn between interspecific interactions and responses to resource gradients. Lack of a clear distinction between dimensions of the Grinnellian and Eltonian niche spaces also result from the fact that interactions between species are far too complex to be divided into 'competition' which can be represented by 'bionomic variables' and 'other interactions'. In fact, these 'other interactions' represent a problem in themselves because they are not easily sorted on 'Grinnellian' and 'Eltonian' factors, regardless of how these concepts are defined. I will illustrate these points by some examples, the first of which is amensalism, (0,-) interactions, which make up one end-point of a gradual transition from symmetric competition via asymmetric competition to unilateral (one-sided) interaction. By definition, a species that has an amensalistic impact on another species contributes an Eltonian niche dimension for the impacted species while the converse is not true. Furthermore, amensalistic interactions are usually not species-specific: the unaffected species impacts the

other species by its structure, as exemplified by trees which by their mere presence bring about variation along complex-gradients of radiation, throughfall precipitation, water saturation, etc. This environmental variation has a well-documented effect on understorey species composition; see Økland & Eilertsen (1993) and references quoted therein. No definitive answer exist to the question if such amensalistic impacts should be treated as several dimensions of the 'Grinnellian niche hyperspace' or as one dimension of the 'Eltonian niche hyperspace'. Similar arguments also apply to other kinds of interspecific interactions. My second example is parasitism, i.e., (+,-) interactions by which one species (the parasite) is dependent on another species (the host) and the latter is negatively affected by the interaction. With reduced impact on the host and lower benefit for the parasite, respectively, parasitism grades gradually into commensalism, (+,0) interactions, and amensalism. The division into Grinnellian and Eltonian niches breaks down in this case because interactions cannot be divided into 'resources' and 'competition'. Similar arguments apply to the fundamental and realised niches because even these concepts rely on our ability to make a clear distinction between 'competition' and 'other factors'. Positive interspecific interactions, which have proven important in a large number of ecosystems, represent a particularly difficult case: should they be considered as fundamental niche factors or as determinants of a species' realised niche? Araújo & Guisan (2006: 1678) argue that a 'consequence of including both positive and negative interactions within the niche framework is that the clear-cut dichotomy between fundamental and realized niches becomes artificial and its usefulness debatable'. Furthermore, they rhetorically ask: 'If ... the fundamental niche is defined by the resources and limiting factors required for species' persistence, and that the realized niche is defined by the constraints preventing the exploitation of resources, should the absence of mutualists or facilitators (thus preventing the use of resources) be included as part of the factors defining the realized niche?' They conclude their discussion by stating that 'ambiguities concerning the role of biotic interactions within the niche framework need to be resolved in order to allow appropriate integration of these neglected issues into niche models. I rephrase this as follows: If these ambiguities cannot be resolved, which I believe is the case, niche concepts are not useful for DM.

Representation of interspecific interactions as axes ('dimensions') in a conceptual 'niche hyperspace' is inadequate. Resource gradients according to Austin (1980), which are included in Soberón's (2010) concept of 'bionomic variables', are adequately represented as contributors to dimensions in the ecological space. The latter are made up by complex-gradients which may consist of co-varying resource, direct and indirect gradients. The unimodal overall response of species to these complex-gradients is primarily shaped by limited physiological tolerance to stress and destabilising factors, the intensity of which depends on position along the complex-gradient. However, other important structuring processes, including interspecific interactions and demographic processes, do not influence species by adding new, independent 'niche dimensions' but by modifying the shape of species' overall responses to the major complex-gradients. Figs 12b–c show that interspecific interactions influence aggregated performance in two ways, by a magnitude response and by an amplitude response. Therefore, from a conceptual point of view, it is inapproapriate to represent the 'dimensions of the Eltonian niche', or 'bionomic variables', as independent axes of a conceptual space.

Most major complex-gradients combine aspects of Grinnellian *and* Eltonian niche dimensions, as demonstrated by variation in the importance of physiological tolerance *and* interspecific interactions along almost all important ecoclines. The CSR model of Grime's (1977, 1979) is relevant in this respect. Grime defines three main ecological processes, competition, stress and disturbance, and divides species into three primary life strategies, competitor, stress-tolerator and ruderal (C, S, and R, respectively), on the basis of their evolutionary adaptations to environments in which stress, disturbance or none of these are important. Grimes's model, as well as the centrifugal model of Keddy & MacLellan (1990), is based on the implicit assumption that all (or almost all) ecoclines are associated with variation in the intensity and nature of interspecific interactions, that negative interactions are important in benign parts of the gradients and unimportant in the stressful and/or disturbed parts of gradients in which positive interactions may instead be important. Variation in species composition along important ecoclines in many ecological systems has been interpreted within this framework, e.g., semi-natural grasslands (Eilertsen 1991), boreal forests (Økland & Eilertsen 1993), mires (Økland 1989b, 1990b, 1990c) and alpine heaths (e.g., Wijk 1986, Rydgren 1994).

The only conceptual geometric space that is adequate for representing a species' total relationship with its surroundings is the ecological space. To my best judgment, the ecological space allows representation of the entire complexity of a species' overall responses, with or without the effects of interactions with other species and/or demographic processes taken into account.

Failure of the niche concepts to take demographic processes, including historical factors, into account. Pulliam (2000) emphasised the importance of demographic processes, most notably lack of dispersal, for species' realised distributions. Demographic processes have thereafter been discussed much in the DM literature (e.g., Soberón & Peterson 2005, Araújo & Guisan 2006, Soberón 2007, 2010, Hirzel & Le Lay 2008, Barve et al. 2011, Peterson et al. 2011). In particular, demographic processes have been recognised as important in DM studies with a projective purpose (PPM), such as modelling of distributional consequences of climate change (Pearson & Dawson 2003, Dullinger et al. 2004, Guisan & Thuiller 2005, Engler et al. 2009, Meier et al. 2010).

A species may be absent from sites in which environmental conditions allow it to persist (i.e., within its Grinnellian niche) *and* in which it does not face the risk of exclusion by interactions with other species (i.e., within its Eltonian niche). The most obvious reasons for absence in such cases are: (1) that the species has never reached the site, i.e., due to lack of dispersal; (2) that the species is temporarily absent for demographic reasons, e.g., due to mortality after local disturbance events, adverse climatic conditions in the near past, etc.; or, at fine local and micro spatial scales, because of (3) space limitation, i.e., that all suitable sites are temporarily occupied. Eriksson & Ehrlén (1992) refer to lack of dispersal (1) as 'seed limitation', while (3) is included in their concept of 'microsite limitation'. At spatial scales broader that the fine local, successful dispersal into new sites causes range shifts, over decades, centuries or millennia (Pearson & Dawson 2003). At sufficiently fine spatial scales, all species will fail to occupy at least some suitable sites.

Soberón (2007: 1118), also see Soberón (2010), Barve et al. (2011), and Peterson et al. (2011), incorporates demographic processes into a niche framework by defining 'accessible area', i.e., 'the total area that has been or is accessible to the species within a time period of interest'. However, as also pointed out by Soberón (2007), it is difficult to define accessible area because occupancy patterns are fractals, showing patterns on multiple spatial scales, and because space limitation is not explicitly addressed, neither in Soberón's concept of accessible area nor in other concepts of the niche. Niche concepts therefore do not account for the fact that most species occupy only a small fraction of observation units in samples that allow analysis of patterns in the micro and fine local spatial domains.

Lack of clarity with respect to how to delimit a species' niche. Delimitation of the niche in the (fundamental or realised, Grinnellian or Eltonian) niche hyperspace is a problem in itself, in addition to, and separate from, the difficulties with representing all factors of interest as dimensions of this hyperspace. Hutchinson (1957) included in his original definition of the niche *all* conditions under which the species 'is able to persist indefinitely', i.e., where its fitness is positive. Leibold (1995: 1380), in a discussion of difficulties involved in separation of the
Grinnellian and Eltonian components of the niche, argued that '... the niche concept is always meant to be general. ... Grinnell, Elton, Hutchinson, and MacArthur and Levins all conceived that it was meant to summarize either "many" or "uncountable" aspects of the biology of the organisms'. Accordingly, Leibold suggested that a 'total niche' should be defined, which comprises the conditions under which a species has positive per capita growth rate. Leibold's definition of the niche is attractively simple, but fails to apply to practical situations for at least two main reasons: Firstly, because at the time-point sampling is carried out, a species can be expected to be present in many observation units where its long-term fitness is negative (sink populations): short-lasting sink and long-lasting stable remnant populations in which the species is unable to complete its life cycle have been shown to be important contributors to landscape, or gamma (γ), species richness (Eriksson 1996, 2000, Heegaard et al 2007, Kiviniemi 2009) by a mass effect (Shmida & Ellner 1984). Secondly, because a species is often absent from observation units within its 'total niche', i.e., from sites in which its fitness is expected to be positive, for demographic reasons (Fig. 12c). The possibility that a species is present in sites where its fitness is negative and absent from sites in which its fitness might have been positive, implies that a species' distribution does not reflect fitness variation in a simple way: the distribution results from impacts by a large ensemble of processes, recent and historical, that affect, and have affected, the species. In practice, this means that fitness can only be assessed by a mechanistic, i.e., physiologically based, approach that starts with the relationship between fitness-related properties (morphological, physiological, behavioural, demographic or other life-history properties) and explanatory variables (Pearson & Dawson 2003) or by long time series of observations of the fate of individuals in permanently marked observation units (Rydgren & Økland 2002). In the real world, however, the physiological approach to modelling is unrealistic (Austin 2007) and the time needed for reliable assessment of long-term population trends (and, thus, fitness) is most often beyond reach (Bierzychudek 1999). Furthermore, results of analyses are always associated with some degree of uncertainty. Therefore, short-cuts such as inferring mechanims from observations by use of a correlative approach, are open to criticism (Shipley 2000). The complexity of fitness variation makes a full mechanistic understanding of a species' ecology impossible and precludes exact delimitation of a species' niche, even if the dimensions of the niche hyperspace could be unambiguously defined.

Assessment. My conclusion, then, is that the classical habitat and niche concepts, perhaps with exception of a broad concept of the niche as an inclusive term for the total relationship of a species with its surroundings as adopted, e.g., by Colwell & Rangel (2009), incur too many theoretical and practical difficulties to be useful as a platform for distribution modelling. Alternatives to conceptual models for DM based upon niche and habitat concepts should instead be searched for by integrating knowledge of performance variation in environmental variables and ecological spaces over a range of spatial (and temporal) scales with knowledge about the mechanisms by which this performance variation translates into distributional patterns in geographical space. One conceptual modelling framework for DM that accords with these principles is outlined below.

What is really modelled in distribution modelling?

In accordance with the conclusion of the previous section that the classical niche and habitat concepts are burdened with too many difficulties to be useful for DM, I will discuss what is modelled in SDM, i.e., distribution modelling with species as modelled target, in terms of mechanisms and processes that determine species' distributions in geographical space and their responses in ecological (or environmental variables) space. A species' distribution is the realisation, in

geographical space, at a particular time-point or over a short time interval, of the species' response to the totality of 'biotic and abiotic phenomena surrounding and potentially interacting with an organism', i.e., the 'particular environment experienced by an organism' [quoted from the definition of *environment* by Kearney (2006: 187)]. The distribution, as sampled at a given point in time, is the result of the complex interplay between many, fundamentally different, processes: evolution of physiological tolerances which constrain the way individuals of a given species respond to the main environmental complex-gradients, modifying effects of interactions with other species, and demographic processes. The outcomes of all of these processes are stochastic to variable degrees: responses to major environmental complex-gradients are more deterministic, while demographic processes have a stronger stochastic element.

The response data used in SDM to model the overall ecological response to selected explanatory variables are *realised distributional data*. For spatial predictions from a distribution model (Steps 8, iv and 12, i in the 12-step DM process; see Fig. 8) to correspond fully with the real distribution of the modelled species, the following conditions have to be satisfied: (1) the sample of observations of the target species is fully representative for the distribution of the species (Step 2); (2) all 'biotic and abiotic phenomena surrounding and potentially interacting with an organism' (Kearney 2006: 187) are fully adequately represented by the explanatory variables and derived variables obtained from them by transformation (Steps 3 and 5); (3) the modelled species' distribution is in dynamic equilibrium with the environment; i.e., no migration of the species is currently going on; and (4) the systems in which the species occurs are static (Chiarucci et al. 2010); a system without stochastic variation, e.g., due to demographic processes, is necessary to avoid prediction error. Only when all of these conditions are satisfied, will a distribution model potentially summarise all systematic variation in aggregated performance of the modelled species. This distribution model, which summarises all variation in the distribution of the modelled target and thus perfectly predicts its distribution, will be referred to as the **optimal distribution model**. The optimal distribution model is optimal from the points of view of all three DM purposes; ERM (ecological response modelling), PPM (projective prediction modelling), and SPM (spatial prediction modelling). From the ERM perspective, this model is optimal because it provides the best possible summary of relationships in ecological space, including the modifying effects of interactions with other species and demographic factors. From the PPM perspective, this model is optimal because a good summary of relationships in ecological space is an optimal basis for projecting occurrence patterns to other spatial and/ or temporal contexts (Guisan & Thuiller 2005, Chapman & Purse 2011, Webber et al. 2011). From the SPM perspective, this model is optimal simply because it gives the best possible spatial predictions. Because real distributional data are used for DM, DM is modelling of the realised distribution. This is the case regardless of DM purpose; in the ERM setting the realised overall ecological response, i.e., the realised response in ecological space, is focused, in the PPM setting the *realised* overall ecological response is used for projection, while in the SPM setting focus is on the spatial realisation of the overall ecological response.

An apparent difference in opinion can be traced in the DM literature between authors who argue that the realised distribution, often worded 'realised niche', is modelled in DM (e.g., Guisan & Zimmermann 2000, Austin 2002, Thuiller et al. 2004, Franklin 2009) and authors who argue that DM addresses potential distributions (e.g., Araújo & Guisan 2006, Peterson 2006). Although the lack of clarity of many terms used in DM contexts opens for the possibility that such differences are semantic only, a real disagreement is likely to be present among authors with respect to the ability of DM to address the potential distribution (often worded 'fundamental niche'). Araújo & Guisan (2006) and Peterson (2006) argue that an important distinction should be made between distribution models based upon environmental ['scenopoetic' in the terminology of Soberón (2007, 2010)] variables only [such models are termed 'ecological

niche models' by Soberón & Peterson (2005), Peterson (2006), and Peterson et al. (2011)] and distribution models which, in addition, include biotic ('bionomic' in Soberón's terminology) variables [such models are referred to as 'distribution models' by Soberón & Peterson (2005), Peterson (2006) and Peterson et al. (2011)]. Peterson (2006) explicitly states that 'ecological niche models' address fundamental niches while 'distribution models' address realised niches, and Peterson et al. (2011) stress the non-equivalence of these two concepts. Like Elith & Leathwick (2009), I find this relationship between type of explanatory variable and type of 'niche' addressed in DM problematic. With reference to the discussion of applicability of niche and habitat concepts to DM in the previous chapters, there are at least two reasons for this: (1) that no clear distinction can be made between 'scenopoetic' and 'bionomic' variables; and (2) that interspecific interactions contribute to variation in aggregated performance of species along almost all major complex-gradients (Fig. 12). When effects of 'bionomic' variables cannot be separated from effects of 'scenopoetic' variables in models of overall ecological responses to explanatory variables, no distinction between models of the 'fundamental' and models of the 'realised' 'niche' can be made.

Araújo & Guisan (2006) argue that models built with environmental explanatory variables address potential habitats only while models that include variables of all kinds, also biotic, come closer to addressing potential geographic distributions. Their use of the word 'potential' rather than 'realised', which follows Guisan & Zimmermann (2000) and is followed by many other authors as well, including Jiménez-Valverde et al. (2008) and Zafra-Calvo et al. (2010), may, however, be semantic rather than representing a real difference of opinion. The input to DM is a sample of observations of performance of the modelled target, analysed as if it were representative for the phenomenon under study. The filtering of information about the phenomenon under study implicit in the sampling process (Økland 2007) implies that no guarantee can be given that results obtained by analysis of the sample give a correct picture of the properties of the studied phenomenon as such. Thus, the simplification implicit in all modelling implies that model predictions are *estimates* with the *potential* of being close to true values, conditioned on a set of assumptions being met. Four important conditions are listed above. If this set of four conditions listed above were met, predictions from distribution models would represent potential distributions in the meaning of the word 'potential': 'potential realised distribution' = realised distribution under specified conditions. These conditions will, however, never be met by real data, which are inevitably burdened with shortcomings such as sampling bias, identification errors, detection errors, positioning errors, etc. [e.g., see Barry & Elith (2006), Robertson et al. (2010), Wolmarans et al. (2010), Kéry (2011), Niamir et al. (2011) and Rota et al. (2011)]. Furthermore, ecosystems are not static and demographic processes are important on all spatial and temporal scales. Distribution models use real data and therefore address the realised distribution.

Although all distribution models are models of the realised distribution, distribution models based upon different sets of explanatory variables will differ with respect to how close they come to the theoretically optimal model, given the purpose of modelling. Obviously, the explanatory variables, or more precisely, the variables derived from them by transformation, which are used to parameterise the model of the overall ecological response, are the most important single factors influencing how close *one specific* distribution model comes to the optimal model. The statement by Araújo & Guisan (2006), that models with environmental explanatory variables address potential habitats while models that include variables of all kinds come closer to address potential geographic distributions, can be understood in this context.

A model that only includes environmental explanatory variables might, at a first glance, seem to comply with the ERM (ecological response modelling) purpose of DM, i.e., 'modelling the relationship between a target, typically the performance of a species, and *a specific set* of

explanatory variables', because environmental explanatory variables that represent the main ecoclines are more 'fundamental' and invariant over time and in space than other kinds of explanatory variables. However, this is not necessarily true, as pointed out by Austin (2007) and clearly demonstrated in the study by Leathwick & Austin (2001) of the distributions of 12 tree species in New Zealand. For all tree species, models for the overall ecological responses at coarse local spatial scale were strongly dependent on inclusion or exclusion of the density of Nothofagus spp., the dominant tree genus in the region, among the explanatory variables. This clearly shows that interspecific interactions can contribute to responses to environmental explanatory variables in ways that are hard or impossible to predict. In fact, all 'non-environmental factors' that co-vary with environmental explanatory variables that are used in DM will, in a context-dependent way, confound the interpretation of models as representing generally valid overall ecological responses. This is exemplified by a species which is absent from a region due to lack of dispersal while this region is distinctively characterised by explanatory variables included in the model, e.g., climatic variables, which is likely the case for Picea abies in Norway. This tree species has still not reached the oceanic, westernmost parts of the country (Hafsten 1992). Thus, interpretation of the *generality* of distribution models will always have to rely on sound ecological judgement such as understanding of the mechanisms responsible for the observed variation in performance of the studied species with respect to variables included in the model (Austin 2007).

Kearney & Porter (2004, 2009) argue that modelling with the aim of understanding distributions should be based on physiological knowledge, and thereby use the term 'mechanistic niche modelling' (MNM) for approaches by which physiological responses and constraints that determine a species' distribution are analysed using knowledge of the mechanistic relationships between functional traits and environment. MNM is rooted in biophysical animal ecology, by which principles of thermodynamics are used to derive mechanistic models for the relationship of animals to climatic conditions through exchange of energy and mass (Porter & Gates 1969, Porter et al. 1973). Rather than starting with raw and rasterised species data (Steps 2 and 6 of the 12-step DM process; Fig. 8), MNM starts with a model for the species' overall functional (e.g., physiological) response to a performance-limiting variable, which is assumed to describe the relationship well (Step 7, ii in Fig. 8). Using observations of the performance of the focal species as a proxy for fitness, this functional relationship is 'translated into multidimensional environmental space' via a model for variation in the factor in question, e.g., body temperature, as a function of rasterised environmental, e.g., climatic, explanatory variables in an alternative to Step 8 of the 12-step process. The resulting model of fitness in environmental variables space is conceived as 'a mechanistic depiction of a species' fundamental niche which can then be used to infer distribution limits' (Kearney & Porter 2009: 339), e.g., by comparison with known distributional data [the definitions of 'niche' and 'fundamental niche' used by Kearney (2006) and Kearney & Porter (2004, 2009) are discussed above]. Because the response variable in MNM is not derived from distributional data, and because the MNM approach does not include steps 2 and 4 in the DM process, the MNM approach falls outside of the definition of DM adopted in this essay review. Nevertheless, the physiological knowledge on which MNM is based in important for interpretation and for judging the general validity of DM results (Austin 2007). In particular, approaches like MNM are relevant when DM is performed with the purpose of understanding relationships between a distribution and all kinds of 'factors', environmental and biotic, that influence this distribution (the general ERM purpose).

The specific ERM purpose of DM differs from the general-purpose ERM, SPM and PPM purposes by the investigator's *deliberate* interest in the response to the *specific* explanatory variable or variables used in the modelling. The difference between specific-purpose ERM, general-purpose ERM and SPM in this respect is illustrated by the following example: DM performed with

the purpose of modelling the response of a species to annual mean temperature *as such* is ERM. DM performed with the purpose of producing a model of best fit to a set of distributional data, that happens to include annual mean temperature as the only significant explanatory variable, is general-purpose ERM if identification and understanding of the species' relationship with the environment is the main focus of the study and SPM if the main focus is on predictions in geographical space. The general validity of a DM model in the ERM context and transferability of a model to areas outside the study area (i.e., its applicability for the PPM purpose) will depend on the strength of the species' overall ecological response to the explanatory variables in the model. Stronger patterns of more general validity can be expected to be associated with important complex-gradients with large variation at coarse spatial scales (regional gradients) than with less important gradients (local ecoclines and condition or impact ecoclines) with large variation at micro or fine local spatial scales (Table 2, Fig. 12). The different roles of explanatory variables in specific-purpose ERM on one hand, and general-purpose ERM and SPM on the other, can, to some degree, be compared with the roles of fixed and random factors in generalised linear (mixed) modelling, GL(M)M: while explanatory variables in specific-purpose ERM and fixed factors in GL(M)M are included in models because the response to them is in itself of interest (in specific-purpose ERM because a relationship between the fixed factor and a proximal, or causal factor is assumed or inferred), explanatory variables in general-purpose ERM are of interest in an exploratory way and in SPM not of interest in themselves. In SPM, the explanatory variables are relevant only as far as they can explain significant variation in the response. Similarly, random factors are included in GL(M)M mostly to secure appropriate statistical handling of samples of observation units that are not fully randomised. PPM is intermediate in this respect but perhaps, in practice, often closer to ERM than to SPM: good projections depend on the ability of the model to summarise generally valid relationships in ecological space and there is rarely any interest in the *specific* variables included in this model.

The parallel between general-purpose ERM and specific-purpose ERM on one hand and the terms general- and specific-purpose ecological studies, used to characterise studies of species composition (R. Økland 1996), indicates that the DM method has different roles in the two ERM purposes. In general-purpose ERM, the DM method plays an explorative role, parallelling that of indirect gradient analysis techniques, i.e., ordination methods, while in specific-purpose ERM it parallels that of direct gradient analysis techniques, i.e., constrained ordination methods.

While in ERM the purpose is to understand distributions, SPM (and PPM) are directed at the end product, a best possible prediction (or projection) of performance. SPM and generalpurpose ERM mostly make use of all available explanatory variables (see, e.g., Franklin 2009). Typically, the SPM purpose is coupled with intended practical use of the model, e.g., the search for new localities of rare species (e.g., Guisan et al. 2006a, Marage et al. 2008, Parolo et al. 2008) or efficient, model-based placement of sampling units for monitoring rare natural phenomena (Schmieder & Lehmann 2004, Peters et al. 2009, Jones et al. 2010).

The SPM and ERM purposes are not mutually exclusive, but represent a continuum of purposes that range from applied interest primarily in obtaining good spatial predictions of the distribution of a modelled target, i.e., relationships in geographical space, to interest in general aspects of the relationship of the modelled target to specific gradients in ecological space. General-purpose ERM takes an intermediate position on this gradient, although sharing with specific-purpose ERM the main focus being on Steps 7–8 in the 12-step DM process. ERM and SPM may represent different phases in research on distributions, SPM is important in a descriptive, or ' α ', phase, while ERM (and partly also PPM) is important in a ' β ' phase in which understanding of relationships and assessment of their general validity is the main focus. These phases may follow each other within one single DM study, in which DM results from analyses undertaken to obtain good spatial predictions for the modelled target (the SPM purpose) trigger

interest in general patterns of the modelled target's overall ecological response to distributionlimiting factors (the ERM purpose). Even more common is the use of DM with a dual purpose, i.e., to obtain good spatial predictions and, at the same time, get new insights into the distribution of the modelled target and its potential causes.

The 'gradient of DM purposes' from ERM to SPM is discussed by Jiménez-Valverde et al. (2008), who refers to it as 'the potential-realised distribution gradient' (cf. discussion of the terms 'potential' and 'realised' above). According to Jiménez-Valverde et al. (2008) the position of a distribution model along this gradient is determined by characteristics of the data used for DM and the DM approach chosen. In my opinion, the order of these issues should be reversed: the purpose should guide choice of data model and statistical model in DM.

Review of some conceptual models for distribution modelling

Conceptual models are diagrams or, more generally, 'frameworks', that summarise relationships between 'factors' that, mostly in complex ways, influence targeted phenomena such as species. Such modelling frameworks may be informal (Pearson & Dawson 2003) or built according to formalised rules (Grace et al. 2010). Many and widely different conceptual models have been proposed for DM (e.g., Franklin 1995: Fig. 1; 2010: Fig. 3.4; Guisan & Zimmermann 2000: Fig. 3; Pulliam 2000: Fig. 1; Pearson & Dawson 2003: Fig. 4; Guisan & Thuiller 2005: Fig. 1; Soberón 2007: Fig. 1, 2010: Fig. 1; Hirzel & Le Lay 2008: Fig. 1; Barve et al. 2011: Fig. 1; Peterson et al. 2011: Fig. 3.1, Table 3.1). One of the most important roles of conceptual models is to assist development of theory (e.g., Guisan & Zimmermann 2000, Austin 2007, Peterson et al. 2011).

A frequently encountered type of conceptual model, also for DM, is a 'flowchart' with the realised distribution of a species (often termed the 'fundamental niche') as its endpoint. Flowchart models summarise anticipated (mechanistic) relationships between all factors that are assumed to influence the distribution of the target species, directly or indirectly (e.g., Franklin 1995, Guisan & Zimmermann 2000, Guisan & Thuiller 2005). Flowchart models, which are informal parallels to the structural equation meta-models constructed in initial phases of structural equation modelling (SEM), may be useful in initial stages of conceptualisation, but fail to address the *nature* of relationships between explanatory variables and response. SEM is a powerful tool for analysis of complex dependencies among explanatory variables which may influence a response variable, as demonstrated by Grace & Pugesek (1997), Grace (1999) and Grace et al. (2010). However, Austin (2007) concluded that SEM is likely to be of limited relevance for DM; because of its restrictive assumptions of linear relationships between independent variables used to parameterise the model and the response, and multivariate normal distribution of errors; and because large data sets are needed.

Pearson & Dawson (2003) propose a 'hierarchical modelling framework' in which the dependence of a species' distribution on different factors and processes at different spatial scales is conceptualised. Their framework is explicitly built on theories of a hierarchical structure of ecological systems. Pearson & Dawson (2003) illustrate the proposed framework by a hypothetical example species, the distribution of which is determined by 'suitable climate' at regional spatial scales, by 'suitable land-cover' at some finer scale, and by 'reduced biotic competition' at even finer scales. The conceptual model shows idealised distributions in geographical space, visualised at two spatial scales. An essential element of the framework of Pearson & Dawson (2003) is that higher levels constrain lower levels, i.e., that variation at broader spatial scales constrain variation at finer spatial scales. Pearson & Dawson (2003: 369) consider their framework as 'a useful starting point for approaching the extreme complexity of the natural system' and state that 'validating the scale dependencies outlined [and] ... identifying appropriate scales of analysis for different environmental drivers ... should be the focus of further research'. However, except for the obvious that climatic factors impact species distributions on regional spatial scales, Pearson & Dawson (2003) do not elaborate their framework into a more complete conceptual model by incorporating knowledge of responses to other important complex-gradients (or ecoclines) with large variation in finer spatial scale intervals. Pearson et al. (2004) apply this hierarchical approach to practical DM, starting with modelling of broader-scaled response patterns and ending with modelling of finer-scaled patterns nested within the former.

Another conceptual model for DM, first proposed by Soberón & Peterson (2005), has been elaborated step by step, first by Peterson (2006), thereafter by Soberón (2007, 2010) and, finally, by Peterson et al. (2011). This model is described as 'a heuristic representation of factors affecting the distribution of a species' (Soberón 2007: 1118) and as 'a heuristic scheme ... to describe some of the results of the interacting factors determining a species distribution ... [in] an abstract representation of the geographical space' (Soberón 2010: 161). Soberón (2010), Barve et al. (2011), and Peterson et al. (2011) use the name 'BAM diagram' for this model, which is named after the three intersecting regions A, B and M in abstract geographical space, the size of each of which determines the target species' distribution.

A basic assumption of the BAM model is that the fitness of a population is affected by variables of two kinds, 'scenopoetic' and 'bionomic' (Soberón's definitions of these terms are discussed above). A and B denote regions in abstract geographical space, with combinations of scenopoetic and bionomic variables, respectively, in which the species has positive predicted fitness. The BAM diagram visualises relationships in abstract geographical space but relies on knowledge (or models) of relationships in environmental variables space. The region in abstract geographical space in which source populations, i.e., populations with positive fitness (Pulliam 2000), of the species may possibly occur, is A \cap B, the intersection of A and B. The M region is included in the model to account for absence of the species from subregions within A \cap B due to lack of dispersal. Thus, $G_0 = A \cap B \cap M$ is the region in abstract geographical space in which source populations are expected to be found, while $G_1 = (A \cap B)|M$, the intersection of A and B, not included in M, is the region outside the actual distributional area in which new source populations may establish, and M $|(A \cap B)$ is the region in which sink populations may be found.

The BAM model is open to criticism for relying on unclear concepts of the niche, and for untenable divisions into scenopoetic and bionomic factors on one hand and into resource, direct and indirect environmental gradients on the other. Nevertheless, the BAM model represents a novel way to conceptualise the influence of important, principally different, factors on a species' distribution. Soberón (2010) [also see Barve et al. (2011)] uses the BAM model as a conceptual basis for simulation studies, undertaken to show that, at 'coarse resolutions' (corresponding to regional spatial scales, cf. Fig. 4), the effects of bionomic variables are adequately 'explained' by important scenopoetic (environmental) factors. This result, which is in accordance with the empirical evidence for low importance of interspecific interactions at regional spatial scales (see Fig. 12a), demonstrates a need for conceptual models for DM that take spatial scale intervals at which variation is large explicitly into account.

The need for incorporating more of nature's complexity into conceptual modelling frameworks for DM does not stop with scale relationships; much of the knowledge of ecoclines and structuring processes summarised in the 'natural variation' chapter of this essay review is directly relevant for conceptualising major steps in the DM process. For instance, conceptual models should distinguish between effects of interspecific interactions, positive and negative, that vary in a systematic manner along important complex-gradients and, thus, that can be predicted from values for proxies for relevant 'gradients', and other effects of interspecific interactions that can only be predicted from knowledge of the interacting species' performance *as such*. Modelling of the performance of species with strong mutualistic or parasitic relationships to other species exemplifies a case in which modelling results may be considerably improved by incorporation of known presence of the symbiont or the host as explanatory variables. Furthermore, a good conceptual model should account for variation due to demographic processes.

HED: a new conceptual framework for species distribution modelling based upon the gradient analytic perspective

In order to accord with insights of the gradient analytic perspective and the main conclusions in the preceding discussions about ecological models, I argue that a good conceptual model for *species* distribution modelling (SDM) should take the following points into account:

- 1. Variation in species' performance occurs along several environmental complexgradients and is due to the impacts of multiple structuring processes.
- 2. Variation in aggregated performance of a species along each major complex-gradient normally results from the impacts of many structuring processes, of which some influence species' performance in a context-dependent and some in a context-independent manner. Context-dependence here means that variation can be related to each major complex-gradient or differs between complex-gradients, while context-independence means 'background' stress or disturbance, the intensity of which is weakly or not at all related to major complex-gradients. Accordingly, major environmental complex-gradients and ecoclines can therefore not be divided into categories by the structuring processes responsible for the variation in aggregated performance along them.
- 3. Each major environmental complex-gradient and the structuring processes responsible for variation along them can be characterised by the spatial scale interval in which variation in species' performance is large. Although ecoclines cannot be divided into disjunct groups according to scale relationships, there are good reasons to consider a tripartition into:
 - i. regional ecoclines with large variation at regional spatial scales;
 - ii. local ecoclines, with large variation at local or micro spatial scales; and
 - iii. condition or impact ecoclines, with large variation at fine temporal scales.
- 4. Lack of dispersal into new sites explains species' distributions on all spatial scales while other demographic processes, i.e. within-population demographic processes and space limitation, explain absence from otherwise suitable sites mostly at fine local and micro spatial scales.
- 5. The impact of interspecific interactions on the performance of immobile organisms not obligately dependent on other organisms, e.g., mutualism or parasitism, is mostly expressed on moderate or fine local and micro spatial scales.
- 6. Interspecific interactions may enhance (positive interactions) or reduce (negative interactions) the performance of an organism compared to its performance in the absence of interactions with other species.
- 7. Applied to variation in species' performance, the hierarchical principle of natural variation implies that higher levels, such as regional spatial scales, constrain lower levels, such as local and micro spatial scales (Kotliar & Wiens 1990, Wu & Loucks 1995). This calls for a top-down approach to distribution modelling (Whittaker et al. 2001, Pearson & Dawson 2003).



on distribution maps. Figures in each row represent patterns for the same spatial scale interval. Spatial scales are defined as the linear grain sizes in samples with extent-grain ratio of 16, typically exemplified by regular hexadecadal grids (cf. Fig. 4): the coarse regional spatial scale Fig. 13. HED: a conceptual framework for distribution modelling, illustrated by a hypothetical example species. The HED framework consists one model for performance variation along each major ecocline, illustrating responses in ecological space and the way they are modified by the influence of condition or impact ecoclines, and by interactions with other species; and distribution maps (D-map; right column: Figs d, h and I), i.e., the spatial realisation of the response in rasterised geographical space. A map representation of model predictions is also shown (upper row: grain size = 100 km, Figs a-d); the medium local scale (middle row: grain size = 25 m; Figs e-h); and the micro scale (lower row: of three types of diagrams: heuristic factor diagrams (H-diagram; the left column of the panel: Figs a, e and i) which illustrate factors that affect site suitability and accessibility in abstract geographical space; ecological response curves (E-curves; middle column: Figs b, c, f, g, j, k),



and low negative fitness, respectively, on D-maps. Orange lines are used for regional, red lines for local, and green lines for condition or impact or the subsets in the H diagram for the regional scale (a) into which the species has been able to disperse is denoted D, while the subset of maintain stable populations, effects of interspecific interactions not taken into account, are denoted ER+ , EL+ and ES+ (subsets with respect to regional, local and condition and impact ecoclines, respectively); subsets in which the species has low negative fitness but may occur for shorter or longer periods as sink populations are denoted ER-, EL- and ES-; and subsets in which the species has too low negative fitness to establish, even for a shorter period, and hence fails to occur, are denoted ER0, EL0 and ES0. Delimitation of these subsets in H-diagrams and the corresponding extents of occurrence for the conditions they represent, are indicated by continuous and broken lines for positive fitness grid cells from which the species is absent due to lack of dispersal is denoted DC. These subsets and the corresponding extents of occurrence grain size = 10 cm, Figs i–l). Subsets of observation units (grid cells) in H-diagrams in which the species has positive fitness and thus may



are shown on D-maps by brown lines. Subsets with and without species that interact positively (IP) and negatively (IN) with the target species dark and light blue lines, respectively. Light and dark grey shading, respectively, are used to illustrate subsets and the corresponding extents of occurrence in which the species has positive fitness and low negative fitness, respectively, after the impacts of interacting species have been accounted for: These subsets are denoted I(ELTCEST) and I(EL+CES+) and I(EL+) and I(EL -) in H-diagrams for the medium local and micro scales (Figs e and i), respectively. Dots and circles indicate species presences, representing populations with positive fitness and low negative fitness, respectively. Black symbols are used for populations, the fitness of which is conditioned only on positions along ecoclines, while blue dots indicate populations with enhanced fitness due to positive interactions with other species. Light blue crosses indicate sites from which are denoted IP+, IP0, IN+, IN0, respectively. The corresponding extents of occurrence are indicated in H-diagrams and on D-maps by dotted, che species is absent due to negative interactions with other species. A new conceptual modelling framework for DM that takes these points into consideration, the HED framework, is exemplified in Fig. 13. This modelling framework is inspired by previously published conceptual models for GA and for DM, in particular the species response models by Ellenberg (1953), Whittaker (1967) and Austin (1980, 1987, 1990, 2005, etc.), by the scale hierarchical framework for DM by Pearson & Dawson (2003), and by the BAM model of Soberón (2010) and Peterson et al. (2011). However, the HED framework differs from any of those by integrating species' overall ecological responses to major environmental complex-gradients in ecological space over a range of spatial scales with distribution in geographical spaces.

The new conceptual modelling framework makes use of three types of diagrams for each spatial scale interval:

- 1. The *heuristic factor diagram*, or *H-diagram*; a heuristic representation of factors that affect site suitability and accessibility in abstract geographical space [the heuristic factor diagram is a parallel to the BAM model of Soberón (2010)].
- 2. The *ecological response curves*, or *E-curves*; one model for the overall response of the modelled species to each major complex-gradient, i.e., in ecological space, with indication of the relative importance of structuring prosesses.
- 3. The *distribution map*, or *D-map*; the spatial realisation of the response in concrete, rasterised geographical space, upon which model predictions are superimposed.

Coarse regional scales. At coarse regional spatial scales, performance variation is explained primarily by regional, climatic, ecoclines (Fig. 13b–c). This important result from gradient analysis is corroborated by several DM studies which unequivocally point to the climatic variables contributing to the regional ecoclines 'bioclimatic zones' and 'bioclimatic sections' (Table 1) as the only, or the most important, explanatory variables for explaining performance variation in the regional spatial domain (Austin & Leathwick 2001, Pearson et al. 2004, Skov & Svenning 2004, Parviainen et al. 2008, Wollan et al. 2008). The species' long-term average maximum fitness in grid cells of the conceptualised study area (cf. Step 4 in the 12-step DM process; Fig. 8) can, if known, be used to divide the observation units into three subsets that are illustrated in the H-diagram in Fig. 13a:

 \mathbf{ER}_+ : sites in which the species has positive fitness and thus may maintain source populations

ER_: sites in which the species has low negative fitness but may occur for shorter or longer periods as sink populations

 \mathbf{ER}_{0} : sites in which the species has too low negative fitness to establish, even for a shorter period, and hence fails to occurs

The idea of illustrating fitness variation in conceptual geometric spaces is borrowed from Hirzel & Le Lay (2008: Fig. 1), who show variation in the fitness of a hypothetical species in rasterised geographical space, corresponding to the D-map, and in ecological space, corresponding to a map representation of relationships which in the HED framework are expressed by the E-curves.

The important role of dispersal (and lack of dispersal) for the species' access to habitable sites, and hence for occurrence patterns at regional spatial scales, is illustrated in the H-diagram (Fig. 13a) by the division of the abstract geographical space into two compartments: **D** that consists of sites accessible to the target species within a relevant time period, and **D**^c, the inaccessible complement of **D**. Criteria for sorting sites into subsets based upon **ER** and **D** coincide if all habitable sites in the study area are accessible. Fig. 13a illustrates the alternative case of non-coincidence between **D** and **ER**_r where **ER**_r is the union of **ER**₊ and **ER**₋; **ER**₊ \cup **ER**₋. The

intersection between \mathbf{ER}_{T} and \mathbf{D} , $\mathbf{ER}_{T} \cap \mathbf{D}$, is the extent of occurrence of the species. At regional spatial scales, the species may be absent from individual grid cells within the extent of occurrence because of limited physiological tolerance to background factors or lack of dispersal to all accessible and habitable sites (see Fig. 12a). Common species, i.e., species with generally high local abundance, are likely to be present in most observation units (regional-scale grid cells) as a consequence of the positive abundance-occupancy relationship, while rare species are likely to be absent from a higher percentage of grid cells, e.g., due to very specific demands with respect to local ecoclines (e.g., Skogen 1973, Elvebakk et al. 1994) and/or condition or impact ecoclines (e.g., Lennartsson & Svensson 1996, Kruys et al. 1999, Berglund & Jonsson 2001, Oostermeijer et al. 2002). Figs 13b–c show E-curves for a hypothetical species with respect to two regional ecoclines. The shapes of these curves depend not only on the species' relationship with the gradient in question, but also on the extent of the study area. Fig. 13d shows the D-map for a hypothetical, relatively rare species.

Medium local scales. Within the extent of occurrence of the species, regional ecoclines gradually lose importance as explanatory variables for species performance variation when the spatial domain is shifted from the coarse regional to finer spatial scales. At medium local spatial scales (Fig. 13e–h), local ecoclines (EL sets in Fig. 13e) are the major determinants of species' performance. If the species' long-term average maximum fitness in grid cells of an appropriately conceptualised study area is known (Fig. 13h), and fitness is incluenced by local ecoclines only, the sites can be divided into three subsets, **EL**, **EL**, and **EL**, as explained above for regional ecoclines (ER). The species' performance at the medium local spatial scale is, however, in all but exceptional cases also influenced by condition or impact ecoclines (ES sets in Fig. 13e). The influence from condition or impact ecoclines may be more or less independent of the influence by local ecoclines. Assuming that the species' maximum fitness under favourable local environmental conditions, i.e., positions along local ecoclines near the species' optimum, is known for all grid cells, and that fitness is influenced by condition or impact ecoclines only, the sites can be divided into three subsets, **ES**, **ES**, and **ES**_{α}. Accordingly, based upon the combined effects of local and condition or impact ecoclines, but disregarding eventual effects of interspecific interactions, the following regions in the H-diagram can be recognised:

 $EL_{+} \cap ES_{+}$: sites in which the species has positive fitness and thus may maintain source populations

 $(EL_T \cap ES_U) \cup (EL_T \cap ES_T)$: sites in which the species has low negative fitness but may occur for shorter or longer periods as sink populations

 $(\mathbf{EL}_{T} \cap \mathbf{ES}_{T})^{C}$: sites in which the species has too low negative fitness to establish, even for a shorter time, and hence fails to occur

At medium local spatial scales, the species' performance can be influenced by several subcategories of interspecific interactions. The magnitude of these influences may, but do not necessarily have to, be predictable from positions along major, local and condition or impact, ecoclines. The New Zealand trees example of Leathwick & Austin (2001), referred in the section 'Importance of structuring processes at different spatial and temporal scales', illustrates the case of apparent non-predictability. Furthermore, at the medium local spatial scale, distributions of species with larger individuals are more likely to be influenced by interspecific interactions than distributions of species with smaller individuals. One possible outcome of influence by interspecific interactions, illustrated in Fig. 13e, is enlargement of the region in which viable populations occur (positive fitness) because of positive interactions with another species, IP. The region in the H-diagram in which the species has positive fitness because of this positive interaction is denoted $I(EL_{\odot} \subset ES_{\circ})$. Two sites in which the species maintains viable populations due to the interaction with IP are shown by blue dots in Figs 13e and 13h. If negative interactions with a species IN are in operation, $I(EL_{+} \cap ES_{+})$ is expected to be reduced compared to the situation in which negative interactions are unimportant (this is illustrated for the micro spatial scale in Fig. 13i). Furthermore, the region in which the species has low negative fitness but may occur for shorter or longer periods as sink populations because of interaction with IP, is denoted $I(EL_{T} \cap ES_{T})$. The modifying effects of condition or impact ecoclines and interactions with other species on the target species' overall ecological response to one local ecocline are illustrated in the E-curves in Fig. 13f, while Fig. 13g shows the E-curves for response to another local ecocline for which no such modifying effects are in operation. The species may be present or absent from individual grid cells within the extent of occurrence at local spatial scales for several reasons, of which within-population demographic processes are expected to be the most important (Fig. 12b). However, limited physiological tolerance to background factors and lack of dispersal to all sites within the area of extent may also contribute to absence at this spatial scale (Fig. 12b, Table 2). Fig. 12h shows the D-map for a hypothetical, relatively rare species.

Micro scales. Species with small individuals may also show variation in performance at micro spatial scales, e.g., within one cell of the grid used to address variation at the medium local spatial scale (Fig. 13h) in which the species is present. At micro spatial scales, local ecoclines (EL sets in Fig. 13i) may still be the major determinants of the species' performance (Fig. 12c); several examples of local ecoclines with large variation also at micro scales are given in Table 1. If the species' long-term average maximum fitness in grid cells of an appropriately conceptualised study area is known for all grid cells (Fig. 13l), and fitness is influenced by local ecoclines only, the sites can be divided into three subsets, $EL_{,}$, $EL_{,}$ and EL_{0} , as explained above for the local spatial scale. The performance of the species at micro spatial scales may be influenced by condition or impact ecoclines, but such influences are not taken into account in the example in Fig. 13. Towards micro spatial scales or, for larger-sized species such as trees, towards local spatial scales with grain size approaching the dimension of full-grown individuals, interspecific interactions are likely to influence the species' performance increasingly strongly while at the same time the magnitude of this influence becomes less and less predictable from positions along major ecoclines. Two possible outcomes of influence by interspecific interactions, illustrated in Fig. 13i, are partial enlargement of the region **EL**, in which populations with positive fitness may occur because of positive interactions with a species IP, and partial contraction of this region due to negative interactions with a species IN. An example of complex, interacting influences of the two species IP and IN on the fitness of the target species, is illustrated in Fig. 13i by the regions I(EL) in which fitness is positive and by the region I(EL), which is characterised by low negative fitness so that sink populations may be found. The modifying effects of interactions with other species on the target species' overall ecological response to two major local ecoclines are illustrated by the E-curves (Figs 13j-k). At micro spatial scales, species are absent from grid cells mostly because of space limitation and within-population demographic processes. The exact spatial scale interval in which variation is large, at which space limitation becomes a major structuring process, depends on the size of individuals of the target species. Fig. 13l shows the corresponding D-map for a hypothetical, relatively rare species.

Assessment. The HED framework, illustrated for plants and other low-mobile organisms in Fig. 13, summarises patterns of variation in the performance of species in conceptual ecological and geographical spaces and also illustrates the major processes expected to be responsible for these patterns. The framework can inform several steps in DM studies:

1. In Step 1, problem formulation and specification, the framework can guide formulation of a realistic meta-model of the main processes supposed to influence the distribution of the target species at different scales, and the relationships between these factors.

- 2. In Step 3, collection of explanatory data, the framework can guide decisions about which explanatory variables are important for the modelled target.
- 3. In Step 4, conceptualisation of the study area, the framework can guide decisions about study-area extent and grain.
- 4. In Steps 5,ii and 7, the E-curves provided by the framework can provide background for decisions about how to transform explanatory variables, for choice of modelling method, and how the model should be specified.
- 5. In Step 10, model evaluation, to jugde if modelling results are reasonable from a theoretical point of view.

Emphasising the scale dependency of distributional patterns, the HED framework conceptualises a top-down hierarchical approach to practical distribution modelling, in line with the proposal of Pearson & Dawson (2003), and in line with similar ideas expressed, among others, by Gibson et al. (2004), Pearson et al. (2004), Austin (2007) and Franklin (2009).

Extending the HED framework to modelled targets other than species

The HED framework for species distribution modelling rests on solid, empirically based evidence: on environmental complex-gradients (and ecoclines) that are important on different spatial and temporal scales; on shapes of species' overall response curves to these gradients; and on processes responsible for these patterns. Thus, how far the HED framework can be extended to other natural phenomena depends on the degree to which the gradient analytic perspective applies to them. In this chapter I address the relevance of the GAP and the HED framework to some natural phenomena other than species.

The category of targets, species excepted, which has most often been subjected to DM, is nature types or land-cover types in the widest sense, including typologies for communities and ecosystems. A multitude of land-cover typologies exist, which are based upon different paradigms (e.g., Whittaker 1962, Økland 1990a, van der Maarel 2005). Because natural variation to a large extent is continuous along continuous environmental complex-gradients (McIntosh 1967, Whittaker 1967, Økland & Bendiksen 1985, Økland 1990a, Austin 2005), I use the terms 'type', 'typology' and 'typification' throughout, rather than 'class' and 'classification'.

From the GA perspective, the most important properties of a type system are: (1) how predictable the hypervolume in ecological space occupied by each type is, i.e., how predictable the aggregated performance of the type is from positions along major environmental complexgradients; and (2) how large the hypervolume spanned by each type is. Predictability and hypervolume dimensions depend on the criteria used to define the types, i.e., the principles of typification on which the system is based. Three different principles of typification, that are expected to differ in these respects, can be identified:

Vegetation types defined by dominance of one or a few plant species (dominance types; Whittaker 1962, 1978). Species respond to environmental complex-gradients and dominance types may therefore, in principle, be restricted to specific intervals along major complex-gradients. Dominant species tend to have broad amplitudes along the major environmental complexgradients – typically they are core species according to CURS model terminology (Collins et al. 1993) – and, accordingly, occupy large hypervolumes in ecological space. This is examplified by *Vaccinium myrtillus* along the 'lime richness' ecocline in boreal non-wetland terrestrial forests, which spans more or less the entire gradient (Fig. 14). Dominance by *V. myrtillus* thus does not give very specific information about where along the ecocline the site is situated. Dominance types defined by polythetic criteria, i.e., co-dominance by many species, are likely to occur over



wetland terrestrial forests as an example. The overall ecological response of eight species is shown. Ideal delimitation of the series of five basic types at the ecological system level on well-drained, submesic sites is shown by vertical gray lines. Shaded areas indicate intervals along the Fig. 14. A gradient analytic interpretation of nature-type definitions, using variation along the local ecocline 'lime richness' in boreal nonecocline where types are expected not to be unambiguously separable by floristic criteria. a narrower range of environmental conditions than types defined by oligothetic (few-species) criteria, which are in turn likely to be restricted to a narrower range than types defined by monothetic (one-species) criteria. Predictability of dominance types is determined by: the magnitude of stochastic variation in the dominant(s)' performance, e.g., due to demographic processes; the number of alternative dominants; and the intensity of interspecific interactions with other dominating species.

Vegetation types defined by a characteristic species combination, as typically exemplified by plant communities of the Braun-Blanquet or other phytosociological 'schools', the types of which are defined strictly by the species composition without any opening for taking environmental conditions into account (see Whittaker 1962, Westhoff & van der Maarel 1978, Økland 1990a). As with dominance types, predictability and hypervolume dimensions in ecological space depend on the floristic criteria used to define the types, which vary greatly between type systems (e.g., Whittaker 1962, Økland & Bendiksen 1985). However, being defined by dominating, constant, differential or otherwise characteristic species, plant community types occupy a hypervolume of limited extent in ecological space, which to considerable degrees is predictable from positions along major environmental complex-gradients. The sharpness of the borders of this hypervolume will depend on the strength of the environmental indication by the species that define the type.

Site-types defined by characteristics of the species composition as well as position along major complex-gradients, i.e., defined by position along one or more gradients and, typically, operationalised by use of species as practical criteria for identification (Cajander 1913, 1921, Eneroth 1931, Økland & Bendiksen 1985, Halvorsen et al. 2009). Such site-types by definition occupy restricted intervals along one or more ecoclines. Predictability in ecological space depends on the quality and precision of the criteria for separating types (Fig. 14).

Based upon these considerations, I hypothesise that overall ecological response curves (E-curves in the HED framework) for nature types will be unimodal and increasingly flat-topped (platykurtic), approaching plateau-shaped curves, with increasing emphasis on ecological conditons in the definition of types [i.e., from (1) to (3)]. The dimension of the interval along each important environmental complex-gradient occupied by each type will depend on how broadly the type is circumscribed, which is, in general, predictable from the types' positions in the hierarchy of types. Types defined by vegetation, 'habitats', sites, land cover, or related phenomena, are social contructions [in the sense of Hacking (1999)] and thus cannot be claimed 'natural' [Whittaker (1951), Økland & Bendiksen (1985), Økland (1990a), Halvorsen et al. (2009); also see Austin (2005)]. Accordingly, the concept of structuring processes applies to nature types only indirectly via their impact on the species occurring in the types. In terms of the HED framework, this implies that the H-diagram and the D-map can be used to visualise patterns of nature-type distributions, and the role of environmental complex-gradients in explaining these patterns, in abstract and rasterised geographical spaces. The concepts of maximum fitness, accessible area (D), and impacts by interspecific processes, do, however, not make sense. Fitness should instead be replaced by a relevant measure of predictability, such as probability of presence.

Similar reasoning can be applied to other modelled targets, which I will illustrate by two examples. Bryn et al. (2012) used MaxEnt to model the upper potential climatic forest line (UP-CFL) in Norway by use of environmental explanatory variables. The UPCFL is mainly climatically determined, occupying a very restricted interval along regional gradients (Aas & Faarlund 2000). This corresponds to a narrow-peaked, i.e., leptokurtic, E-curve. For UPCFL, only the regional scale and bioclimatic gradients are relevant. If observations of the empirical forest limit (EFL) had been used as response variable in the modelling, variation at local scales would also have been relevant. The HED framework might then, with adaptations, be useful for conceptualising effects of adverse local environmental conditions on EFL relative to UPCFL.

The second example is the modelling of periglacial phenomena, i.e., cryoturbation, sporadic permafrost and sorted solifluction, by use of a set of environmental explanatory variables by Hjort & Marmion (2009), for a study area in N Finland. Because periglacial phenomena result from processes governed by variation along regional as well as local environmental complex-gradients, periglacial phenomena can be expected to occupy a restricted hypervolume in ecological space. The response to most of the relevant gradients is likely to be unimodal because periglacial phenomena arise as results of recurrent freezing and thawing cycles. This can be implemented as unimodal E-curves in the HED framework. Like for nature types, neither of the concepts of maximum fitness, accessible area (**D**), nor interspecific processes, make sense for the forest limit and periglacial processes, and fitness has to be replaced by a meaningful measure of predictability.

CHOICE OF DATA MODEL

Collection and preparation of data for the modelled target (Steps 2 and 6)

Collection (Step 2 in the 12-step DM process; Fig. 8) and preparation (Step 6) of response variables from raw data for the modelled target have been extensively discussed in the literature and extensive documentation shows that the quality of response data strongly affects modelling results [e.g., see reviews by Franklin (2009) and Peterson et al. (2011)]. Factors that influence response-data quality can be divided into general factors and factors which may cause bias in the model of the overall ecological response obtained in Step 8 in the 12-step process. The former, which will only be briefly commented on here, include: (1) number of presence observations, more is generally better (Hirzel & Guisan 2002, Loiselle et al. 2008, Feeley & Silman 2011); (2) detectability of the modelled target (MacKenzie et al. 2005, Kéry et al. 2010, Olea & Mateo-Tomás 2011); (3) determination errors (cf. Robertson et al. 2010); (4) other aspects of recording quality, i.e., errors in records of presence and/or absence of the target for reasons other than those mentioned in (2) or (3); (5) historical bias (Hortal et al. 2008, Feeley & Silman 2011); and (6) spatial autocorrelation in the response variable (Segurado et al. 2006, Veloz 2009, Chapman 2010, Merckx et al. 2011).

A gradient analytic perspective is useful for understanding how properties of data for the modelled target and response variables derived from these data result in bias in models of the overall ecological response. Basically, bias in models may result when the sample of observations of the response variable is not representative for the modelled target's distribution in the study area. Two kinds of representativity, and associated sampling bias, can be discerned (Økland 1990a, Kadmon et al. 2003, Franklin 2009): (1) representativity in geographical **space**, i.e., that every potential observation unit in the study area has the same probability for being sampled; and (2) representativity in environmental space, i.e., that each interval of unit length along each environmental explanatory variable of interest is equally well covered by the sample. Sampling bias resulting from lack of representativity of the two kinds are termed geographical sampling bias and environmental sampling bias, respectively. Representativity in geographical space is typically achieved by systematic or random sampling, while representativity in environmental variables space can be achieved by stratified sampling, using environmental variables for stratification. Several sampling designs may be applied, e.g., gradsect sampling (Austin & Heyligers 1989) and restricted random sampling by randomisation within selected blocks (Økland 1990a, T. Økland 1996). Representativity in environmental space is considered essential in general-purpose gradient analytic studies, i.e., studies with the main

purpose to extract species compositional gradients and to interpret these gradients environmentally (Økland 1990a).

Neither geographical nor environmental sampling bias need to result in inferior distribution models. Most distribution modelling methods are group discriminative methods (Mateo et al. 2010) by which environmental characteristics of observed presence observations are contrasted with those of **background observations**, a collective term used for uninformed observations, i.e., absences, random grid cells or pseudo-absence observations. Because the response variable is modelled as a function of the supplied explanatory variables in Steps 7 and 8, the decisive factor for bias in models is performance distribution bias, i.e., systematic deviation of aggregated performance of the modelled target along environmental gradients, as estimated by use of a sample, from the true distribution of aggregated performance (cf. Elith et al. 2011). This explains why geographical bias in response data subjected to DM does not reduce the predictive performance of the model unless the geographical bias also entails performance distribution bias (Loiselle et al. 2008). Good coverage of variation along important environmental variables by a sample of species observations made along unpaved roads, and climatic bias in samples of observations made along main roads, explain differences in the quality of distribution models built from the respective types of data [compare McCarthy et al. (2011) and Kadmon et al. (2004)].

Barry & Elith (2006) regard lack of real absence observations as a shortcoming of presenceonly (PO) data, but from a GA perspective it is not the eventual lack of absence observations *as such*, but performance distribution bias in the set of observed presence observations, as contrasted with the set used as background observations, regardless of these being real absences, random grid cells or pseudo-absences, which is the potential source of bias in models. Thus, Elith et al. (2011) maintains that the only basic difference between presence/absence and presence-only data is that the latter does not provide information about the prevalence of the modelled target. Nevertheless, comparative studies of distribution models obtained from different sets of response variables for the same modelled target show that models based upon random or systematic sampling are generally better than models based upon selectively sampled data (Edwards et al. 2006), and that representativity in environmental space affects model performance (Kadmon et al. 2003).

Selectively sampled observations of observed presence, e.g., obtained from museum collection databases, are known to be burdened with geographical and environmental bias as well as performance distribution bias (e.g., see Loiselle et al. 2008, Robertson et al. 2010). Theoretical reasoning therefore suggests that use of target-group background observations will improve distribution models because 'target-group background may be interpreted as a random sample from the (biased) sampling distribution' (Phillips & Dudík 2008: 173). The term 'target-group background observations' is used to denote background observations with similar bias as a set of observed presence observations, chosen to reduce performance distribution bias. A typical example of a relevant target group (Anderson 2003) from which to pick background observations is observed presences recorded for all species in the genus to which a targeted species for DM belongs, obtained from the same museum collections database. Comparative analyses have confirmed that target-group background observations improve distribution models (Phillips & Dudík 2008, Phillips et al. 2009, Mateo et al. 2010), and several studies have demonstrated that the method used for choosing pseudo-absence observations affect DM results (Lütolf et al. 2006, Lobo 2008, Stokland et al. 2011). Use of target-group background observations in DM is further discussed in the chapter on model evaluation.

Performance distribution bias is likely to be more detrimental to DM when the purpose is ecological response modelling (ERM), i.e., to find and understand general patterns in the overall ecological response of the modelled target to the supplied explanatory variables, than

when the purpose is spatial prediction modelling (SPM), i.e., to optimise the fit between model predictions and the true distribution of the modelled target's performance in the study area. Let us assume that the modelling method is good in the sense that it accurately estimates the general pattern of variation in aggregated performance of the modelled target. Performance distribution bias in the response variable will then, inevitably, result in a biased model of the overall ecological response. From an ERM perspective, this is problematic as such, regardless of the predictive performance of the model. From an SPM perspective, this is not problematic if the predictive performance of the biased model is not lower than that of alternative models. Loiselle et al. (2008) found that that the relative predictive performance of DMs could not be predicted from type or amount of sampling bias. This should, however, not be taken as an argument for accepting data for the modelled target that has lower quality than what can possibly be achieved. Care should therefore be taken to improve all steps in the process by which raw data are filtered to obtain the response variable. Thus, Peterson et al. (2011: 67) state 'that occurrence data are not simple documentations of species' presences and absences, but rather the result of complex filtering by very diverse processes. This complexity must be considered early in the design of each study ... as a means of ... avoiding the classic "garbage in, garbage out" situation'.

Collection of explanatory data (Step 3)

The choice of explanatory variables strongly impacts the result of DM, as pointed out by Araújo & Guisan (2006) and demonstrated by Austin et al. (2006), Coudun et al. (2006), Lassueur et al. (2006), Parolo et al. (2008), Syphard & Franklin (2009), Austin & van Niel (2011b) and Synes & Osborne (2011). With some noticeable exceptions, e.g., Austin & van Niel (2011b: 9) who conclude that 'explicit statements justifying the selection of predictors based on ecological principles are needed', questions related to the choice of explanatory variables for DM such as which variables to choose and which categories of variables are relevant, have received much less attention than, for instance, questions related to the quality of data for the response variable and the relative performance of modelling methods (Franklin 2009). Because the explanatory variables serve different roles in ecological response modelling (ERM) and spatial prediction modelling (SPM), all judgements of appropriateness of different explanatory variables need to take modelling (PPM) depends on the specific purpose of the modelling [this will not be further addressed here, but see, e.g., Austin & van Niel (2011a) and Synes & Osborne (2011)].

In order to be relevant for ERM, an explanatory variable has to satisfy three conditions: (1) it represents an ecocline or a proximal structuring process such as an interspecific interaction or a demographic process, that is known or assumed to be responsible for variation in performance of the modelled target; (2) its relationship with an important ecocline or a proximal structuring process is, or is assumed to be, well understood and well-documented and strong; and (3) the response to this explanatory variable is of specific interest to the modeller. To be included in an SPM model, an explanatory variable has to satisfy one condition only: it must account for variation in a sample of rasterised observations of the modelled target that is not accounted for by other variables.

I distinguish three categories of explanatory variables which differ with respect to relevance for each of the ERM and SPM purposes:

1. *Environmental explanatory variables* in the strict sense, i.e., variables used to represent (i.e., serve as proxies for) regional, local and condition or impact ecoclines. Environmen-

tal explanatory variables used in DM are often derived from a primary data source, of which perhaps the most important is digital elevation models (DEMs). DEMs are used to calculate slope and aspect which can, in turn, be used to calculate more complex measures such as radiative input or a proxy for radiative input such as a 'heat index' (Dargie 1984, Parker 1988, Økland & Eilertsen 1993). Furthermore, topographic position derived from DEMs can be used to estimate soil moisture, e.g., by the 'topographic wetness index' (Moore 1991, van Niel et al. 2004). Error is likely to propagate during the process of calculating complex indices from DEMs and other primary data sources, and the quality of the primary data is therefore critically important for explanatory variables derived from these data to be useful for DM (Franklin 1995, van Niel et al. 2004, Lassueur et al. 2006, van Niel & Austin 2007). Airborne laser scanning (ALS) technology (e.g., Lefsky et al. 2002, Anderson et al. 2010, Murphy et al. 2011) may open for increased access to considerably improved, while at the same time costefficient, DEMs in the near future. Thus, for instance, Korpela et al. (2009) were able to construct a surface topography model for a mire with an accuracy of 5-10 cm which comes close to the vertical differences (1-5 cm) at which Sphagnum and liverwort species tend to replace each other along the depth-to-the-water-table gradient (Økland 1986a, 1989b). Recent applications of vertical canopy profile information obtained by ALS also show that laserscanning data may be useful for constructing environmental explanatory variables for DM at medium local to micro spatial domains. For instance, the ability to identify individual trees by ALS (Næsset & Økland 2002, Holmgren & Persson 2004, Forzieri et al. 2009, Hill & Broughton 2009) opens for construction of good proxies for local radiation gradients. This may also open for improved models of variation along the 'water saturation' ecocline in forests, which is associated with the variation from underneath large trees and in dense forest to openings between trees (Økland & Eilertsen 1993, T. Økland 1996, T. Økland et al. 2003; also see Austin & van Niel 2011a).

I include in the concept of 'environmental explanatory variable in the strict sense' all explanatory variables that are used as proxies of regional, local and condition or impact ecoclines. Many of the local and condition or impact ecoclines listed in Table 1 have, to my best knowledge, not yet been represented by explanatory variables in DM, even when the spatial domain addressed by the modelling and the geographical position of the study area suggest that these ecoclines are relevant. The same applies to many other ecoclines described in NiN (Halvorsen et al. 2009) The most likely reasons for not including explanatory variables that represent these ecoclines are lack of recognition of their importance, difficulties in finding appropriate proxies for them, and difficulties in obtaining 'wall-to-wall' coverage for such proxies. Nevertheless, many so far unexploited opportunities are likely to exist, e.g., by using old data in new and creative ways. One example is provided by Marage et al. (2008) who combined Napoleonic cadastral maps and aerial photographs with information about land-use history and current stocking rates to construct management history variables that considerably improved SPMs of the rare herb *Eryngium spinalba* in the French Alps.

For SPM models, the appropriateness of strictly environmental, as well as of other types of explanatory variables, is pragmatically determined by each explanatory variable's ability to explain variation in the performance of the modelled target. For ERM models, however, availability of environmental explanatory variables that appropriately represent the major environmental complex-gradients is crucial. In many, or most, cases, the choice of a particular explanatory variable for ERM can be justified by reference to correlative studies that demonstrate importance of the ecocline in question,

e.g., for the group of organisms to which a targeted species belongs, and/or, in addition, by reference to a mechanism or process known to be important. Furthermore, an environmental explanatory variable that is not a proximal factor may be appropriate for ERM if it expresses variation in the intensity of an important structuring process that is not directly related to position along a major ecocline or if it can serve as a proxy for an important ecocline (e.g., Guisan & Zimmermann 2000, Austin 2007). The use of proxies in ERM needs particular attention. For DM results to express general patterns in species' overall responses to environmental complex-gradients, as required by the ERM purpose, the explanatory variables used in the modelling have to be good proxies for underlying, distribution-limiting factors, in general, and not only within a local area (Austin 2007, Austin & van Niel 2011b). This is most typically exemplified by topographic position, which is locally often strongly correlated with conditioning factors such as 'water saturation' and 'drought severity' (see the chapter 'Regional, local and condition or impact ecoclines'). However, as expressed in Boyko's 'bio-geoecological law' (Boyko 1947) and exemplified by, e.g., Nordhagen (1943), Økland & Bendiksen (1985), Økland (1990d), and T. Økland (1996), species' aggregated performance along such local topographic, e.g., ridge-depression, gradients, varies between regions because regional complex-gradients modify the relationship between the conditioning factors and local topography. Accordingly, modelled relationships with topography need to be interpreted within a broader, regional context, based upon good understanding of the ecological processes involved (Austin & van Niel 2011a).

2. Land-cover explanatory variables, i.e., categorical variables by which each point in the study area is uniquely allocated to one land-cover type. In contrast to environmental explanatory variables in the strict sense, which are relevant for DM because they *di*rectly represent the factors to which species respond, land-cover explanatory variables lack such a direct influence. Land-cover explanatory variables are relevant for SPM if they explain variation in the performance of the modelled target, for ERM if they serve as good proxies for major environmental complex-gradients or in other ways reflect variation in the intensity of an important structuring process. This will be the case if and only if the land-cover types, i.e., the 'levels' of the categorical land-cover variable, can be 'translated' into well-defined intervals along specific, major environmental complex-gradients. The degree to which this will be the case depends on the criteria used to define the land-cover types, as reflected in the principles of typification. The division of nature-type systems into three categories in the chapter 'Extending the HED framework to modelled targets other than species', is also relevant for land-cover variables used as explanatory variables in ERM for the reason that the two properties that characterise these categories are decisive for their value as explanatory variables. These two properties are: predictability in ecological space, and hypervolume dimensions, i.e., the width of the intervals along major environmental complex-gradients spanned by the type.

Vegetation types, defined by dominance of one or a few plant species, constitute the least appropriate category of land-cover variables for use in ERM, typically giving an imprecise environmental signal (e.g., Odland 2009). Dominance types should therefore be used as explanatory variables in DM with great caution. In particular, this applies to ERM purposes. Vegetation types (plant communities) defined by a characteristic species combination typically give a more precise environmental signal. Because maps of vegetation types (vegetation maps) are available for many areas (e.g., Franklin 1995, van der Maarel 2005, Bryn 2006) and provide 'wall-to-wall' coverage, they are potentially attractive as a source of data for DM. The appropriateness of vegetation

type variables derived from vegetation maps for ERM depends on the strength of their environmental signal, i.e., the extent to which these types can be interpreted in terms of well-defined intervals along major complex-gradients which, as with dominance types, depends on the floristic criteria used to define the types. From a theoretical point of view, site-types defined directly by position along major complex-gradients in addition to characteristics of the species composition are more appropriate for DM than vegetation types because the former are expected to be more sharply characterised in environmental terms. Land-cover explanatory variables derived from nature-type maps are appropriate for ERM if a strong environmental signal follows from the definition of types and, in addition, criteria for discriminating between types are clear and well documented, and the site-type map has high cartographic precision. Maps based on site-types that consistently reflect variation along important local or condition or impact ecoclines such as 'lime richness' and that can be used to derive good proxies for important environmental complex gradients, are particularly valuable for ERM, because they can be used to provide variables with 'wall-to-wall' coverage that are hard or impossible to obtain by direct measurement. Geological maps are typically operationalised as proxies for 'lime richness' in this way (e.g., Parviainen et al. 2008, Hemsing & Bryn 2012).

Land-cover explanatory variables have been shown to improve the predictive power of distribution models, e.g., by Tingley & Herman (2009), Platts et al., (2010) and Zafra-Calvo et al. (2010). For instance, in the study of observational data for 2604 vascular plants in Europe, rasterised to the coarse regional spatial scale by use of cells 50×50 km, Thuiller et al. (2004) found that GAM models based upon climatic and land-cover explanatory variables explained more of the deviance than models based upon climatic data only. However, predictions from models with and without land-cover explanatory variables did not differ with respect to precision. This was interpreted by Thuiller et al. (2004) as an indication that climate was the main determinant of distributions at this spatial scale. Contrasting results have been obtained in studies of vascular plants by Parviainen et al. (2008) and Pearson et al. (2004), in which observational data rasterised to coarse local (500×500 m grid cells) and fine regional (1×1 and 10×10^{-1} 10 km grid cells) spatial scales, respectively, were used. In both studies, land-cover explanatory variables markedly improved distribution models for some species while not for others. A noteworthy result of both studies was that models for peatland species were particularly strongly improved by incorporation of land-cover explanatory variables. This result was interpreted as due to the lack of other explanatory variables that 'captured' variation along the paludification gradient which is decisive for the presence or absence of these plants. This indicates that land-cover explanatory variables can contribute in important ways to the performance of SPM models, and potentially also to ERM models, as surrogates for environmental explanatory variables (in the strict sense) that are hard or impossible to measure directly.

'Wall-to-wall' coverage of land-cover information may be obtained by field surveys (traditional vegetation, or land-cover, mapping) or, in principle, more cost-efficiently, by analysis of remote sensing data [RSD; see Franklin (2009) for a comprehensive survey of sensor types and data and examples of explanatory variables that can be derived from them]. The value of explanatory variables derived from RSD depends on their quality (i.e., precision), their interpretability and their relevance, i.e., the degree to which they represent, and in the context of ERM can be interpreted as, proxies for important environmental complex-gradients. These issues are discussed in detail by Bradley & Fleishman (2008) who conclude that land-cover maps derived from RSD are often inappropriate for DM, even if the modelling purpose is pragmatic and applied (SPM). They give three reasons why maps and explanatory variables derived from RSD may perform poorly in DM contexts: (i) they are not sufficiently detailed, (ii) they reflect variation along important environmental gradients too poorly, and (iii) they reflect important mechanisms too vaguely. Data derived from sensors like ALS may escape this criticism in cases where explicit spatial and/or environmental interpretation of the primary data is possible.

3. *Biotic explanatory variables*, i.e., variables representing the performance of other species, including information about species richness, production etc., have very rarely been used in DM. Noticeable exceptions are: Leathwick & Austin (2001), who studied tree species in New Zealand; Heikkinen et al. (2007), who studied four owl species in Finland; Araújo & Luoto (2007), who studied the European distribution of the butterfly species *Parnassius mnemosyne*; Meier et al. (2010), who studied tree species distribution in Switzerland; and Pellissier et al. (2010), who studied N Norwegian vascular plant species.

Biotic explanatory variables are directly relevant for ERM modelling when spatial domains are addressed in which the presence of other species is known or suspected to influence the presence (or absence) of the modelled target, typically a species, directly. For small plants and other small organisms with low mobility, biotic variables are particularly relevant for ERM at fine local and micro spatial scales (e.g., see Fig. 13). It should be noted that the expected response of a species to a biotic variable (performance of another species) is not unimodal, but monotonous. The monotonous relationship follows directly from the nature of interspecific interactions, the effect of which is known to be consistently positive, consistently negative or neutral.

The appropriateness of biotic explanatory variables for SPM depends, pragmatically, on each variable's ability to explain variation in the performance of the target species. Meier et al. (2010) show that biotic explanatory variables can explain a substantial amount of variation in distribution models, and that there is little overlap between the variation explained by biotic and abiotic variables. Biotic explanatory variables are likely to be particularly relevant for SPM in the following two situations: (i) When the presence of one species is known to influence the performance of the target species directly, by negative or positive interactions (Araújo & Luoto 2007). As in ERM and PPM, this is particularly relevant for SPM at fine local and micro spatial scales. (ii) When the presence of one species is a good indicator of sites in which the target species is present (e.g., because the indicator species has more or less the same relationship to the environment as the target species) or absent (e.g., because the indicator species has a more or less complementary relationship to the environment as the target species). Use of the observed presence of another species with similar relationship to the environment as the target species as explantory variable has the potential, from a theoretical point of view, to improve SPM models particularly strongly in cases where the relationship of the 'explanatory species' to the environment is well known and the latter is more common, more throughly searched for, mapped with higher precision, or more easily detected, than the target species.

Biotic variables have been used in DM mostly to account for effects of negative interspecific interactions. However, as highlighted in the HED framework (e.g., see Fig. 13), positive interactions should also be taken into account. An example of positive impacts by other species accounted for in distribution models, is the study by Heikkinen et al. (2007), showing that presence of woodpeckers significantly enhanced performance of four owl species in Finland.

Conceptualisation of the study area: choice of spatial domain (Step 4)

'Choice of spatial scale' is stressed in almost all texts on DM methodology as highly important. Nevertheless, in practice the spatial domain is very often taken to be the one for which relevant rasterised explanatory variables are available. This practice has probably lead to distribution models that are in many respects suboptimal, as discussed among others by Guisan & Zimmermann (2000), Austin (2007), Franklin (2009), Anderson & Raza (2010) and Barve et al. (2011). From a theoretical point of view and regardless if the purpose is ecological response modelling (ERM) or spatial prediction modelling (SPM), the spatial domain or domains to be addressed in a specific DM study should be determined after careful consideration of spatial scales at which the variation of the studied phenomena is large, and which explanatory variables are likely to be important for explaining this variation. The HED framework is likely to prove useful in this conceptualisation process.

ERM purposes are typically specific, such as modelling of the climatic envelope of a species or modelling of a species' response to explanatory variables that serve as proxies for local ecoclines. The appropriate scale domain (or domains) for specific-purpose ERM studies can often be determined directly from knowledge of the spatial scale interval in which variation in the modelled target is large and in which potentially relevant explanatory variables have large variation. The large majority of DM studies addresses regional spatial domains, some address coarse local spatial domains (e.g., Edwards et al. 2005, Marage et al. 2008), while few address the medium local domains (e.g., Guisan et al. 2006a, Lassueur et al. 2006, Parolo et al. 2008, Edvardsen et al. 2011). DM methodology appears not yet to have been applied to the fine local or micro scale domains, although analysis of performance patterns at these spatial scales may potentially fill large gaps in our knowledge about species' responses to specific local ecoclines and the importance of interspecific interactions. One obvious reason why DM methods have not been used to address domains in the fine local scale intervals is the lack of easily available explanatory variables. General-purpose ERM studies require a top-down hierarchical modelling framework that starts with analyses of patterns at regional spatial scales and from there proceeds towards finer (local or micro) scales, guided by a conceptual modelling framework such as the HED framework outlined in Fig. 13.

The SPM purpose is typically associated with applied DM. The choice of spatial domain in SPM should therefore be guided by considerations of optimal choice of grain size from the point of view of the intended use of predictions from the model. However, in almost all practical cases limited resources constrain data availability and data quality and many compromises have to be made. The spatial domain therefore has to be chosen as the best compromise between what seems optimal from the user's point of view, what is possible given available data, and what is optimal given the distributional properties of the modelled target. VanDerWal et al. (2009) and Stokland et al. (2011) show that the goodness-of-fit of SPM models, and the importance attributed to different explanatory variables, depends on the extent of the study (also see Barve et al. 2011).

Insights from a carefully prepared framework of conceptual models like the HED framework may provide valuable guidance in the process of finding good compromises with respect to choice of spatial domain.

Transformation of explanatory variables (Step 5,ii)

As a consequence of the third fundamental insight of the gradient analytic perspective, that species occur within a restricted interval along each major complex-gradient, overall ecological

responses of species, nature types and many other natural phenomena with respect to major complex-gradients follow unimodal or truncated unimodal curves. Accordingly, distribution models have to account for complex, but realistic, response-curve shapes (Guisan & Zimmermann 2000, Guisan et al. 2002, Franklin 2009, Dormann 2011). This task can be accomplished in several ways, of which transformation of explanatory variables is one. Some DM methods, as exemplified by machine learning methods such as random forests (RF) and boosted regression trees (BRT), handle complex, non-linear relationships between response and independent variables, as well as interactions between explanatory variables, implicitly in the modelling process (Elith et al. 2008, Hastie et al. 2009). However, most DM methods are, or are based upon, regression-type approaches by which the relationship between response and independent variables is described by a parameterised mathematical function.

The two main categories of variable formats usually recognised by DM methods, continuous and categorical, are transformed by different procedures. Categorical variables can be transformed simply by reducing the number of factor levels (categories) to the smallest number of ecologically relevant classes (Franklin 2009); see discussion about the use of land-cover explanatory variables in the chapter 'Collection of explanatory data (Step 2)'. This transformation is, however, only occasionally applied in practical DM [but see, e.g., Parviainen et al. (2008) and Edvardsen et al. (2011)].

Continuous variables are treated differently by different methods. Some methods, such as generalised additive models (GAM) and DM methods derived from GAM, perform piecewise linear spline transformations as part of the modelling processes (Wood 2006). The large class of regression-based DM methods, to which generalised linear models (GLM) and maximum entropy models (MaxEnt) belong, are, however, constrained to parameterise a model by optimising the fit to the *supplied* explanatory variables. In the procedure implemented as default in the software for MaxEnt modelling developed by Phillips and colleagues (Phillips et al. 2006, Phillips & Dudík 2008), each continuous variable is automatically transformed into a set of derived predictors of up to six basic types prior to analysis, as part of an automatted transformation, model specification and model selection procedure (Halvorsen in press).

Transformation of explanatory variables into derived variables that facilitate modelling of reasonable systematic relationships between response and explanatory variables in a flexible way, i.e., resulting in unimodal or truncated unimodal curves that may be skewed and/or kurtotic, can be accomplished in two principally different ways: (1) by representing each explanatory variable with a representative set of derived variables, and (2) by representing each explanatory variable with one more complex, derived variable. The term **parametric spline** (e.g., Hastie et al. 2009) is used for the latter case. The (set of) derived variable(s) are subjected to model selection (Step 8,i) followed by model parameterisation (Step 8,iii). A set of derived variables which meets the demands for flexibility of realistic response-curve shapes can be obtained in many ways, e.g., by deriving a set of polynomial functions of the explanatory variable, the degree of complexity of which is determined by the order of the polynomial (Heegaard 1997, Venables & Ripley 2002); by deriving a set of monotonous transformations of the explanatory variable, such as linear, quadratic, and hinge transformations (Phillips et al. 2006, Phillips & Dudík 2008); by using deriving other, non-linear, derived variables such as the zero-skewness transformation (R. Økland et al. 2001, 2003); or by including non-linear transformations such as 'deviation predictors'. 'Deviation predictors' can, for instance, be obtained as the absolute value of the difference between the original value for the explanatory variable and the value at which the estimated aggregated performance peaks. Parametric splines are obtained as the fitted values of a regression model which specifies the relationship between the targeted response variable and the explanatory variable. Several response functions can be used, among others: the twoparameter gaussian function (e.g., Gauch & Chase 1974, Westman 1980); the three-parameter

beta function with fixed species tolerances (Austin et al. 1994, Austin & Nicholls 1997); HOF models with up to four parameters (Huisman et al. 1993, Oksanen 1997, Oksanen & Minchin 2002); and the five-parameter beta function (Oksanen 1997).

The importance of choice of transformation function for the quality of DM models appears not to have been systematically explored, despite the frequent recognition in the literature that this is an important issue (Guisan & Zimmermann 2000; Austin 2007, Franklin 2009). From a gradient analytic perspective, e.g., as implemented in the HED framework, this is most unfortunate because of the core role of Steps 7–8 of the DM process by which overall ecological response curves are fit to explanatory variables. Choosing transformations that balance flexibility with realism is particularly important in ERM, while in SPM this is important as far at it influences the model's predictive performance.

All explanatory variables and variables derived from those by transformation should be linearly transformed onto one standard scale before analysis in order to make relative variable values and model parameters comparable (Økland 1990a, Økland et al. 2001, Dormann 2011). This can be done in several ways, e.g., by standardisation by centering and division with the standard deviation, by which mean and standard deviation of the transformed variable are 0 and 1, respectively, and by **ranging** (Gower 1967), by which the variable is linearly rescaled onto a scale with a minimum value of 0 and a maximum value of 1.

In DM methods of the regression type, choice of transformation is an integrated part of model specification (Step 7,ii).

Collection of presence/absence data for model calibration and evaluation (Step 9)

Model calibration (Step 10) requires, and model evaluation (Step 11) benefits strongly from, access to a representative sample of presence/absence data that is collected independently of the data used to parameterise the model. Reasons for this are extensively discussed in the literature (e.g., see Guisan & Zimmermann 2000, Araújo et al. 2005, Araújo & Guisan 2006, Austin 2007, Peterson et al. 2011). In the present chapter, I will briefly discuss the meaning of independence and representativity in this context, and address some sampling issues.

The term 'independence', applied to two samples of observation units for a modelled target, can be understood in different ways. From a purely statistical point of view, independence means that observation units, of the two samples together, and within each sample, are independent replicates drawn from the same population of potential observation units (Peterson et al. 2011). For a calibration/evaluation sample to be independent of the data used to parameterise the model addressed, neither the observation units of the calibration/evaluation sample itself (Araújo et al. 2005, Dormann et al. 2007, Veloz 2009), nor observation units in the data set used for model parameterisation can be spatially or temporally autocorrelated. Avoidance of spatial autocorrelation can be achieved by separating observation units by a distance larger than the range of the spatial structure of the response variable used in the modelling (Veloz 2009, Stokland & Halvorsen 2011). True statistical independence of biological data sets is, however, almost impossible to achieve because spatially and temporally autocorrelated patterns inevitably result from the demographic processes (Legendre 1993, Nekola & White 1999) which cause individuals and populations to persist, die or get extinct, and give birth to new individuals and populations. Collection of data for model evaluation therefore requires 'care ... taken to assure that independence of samples is sufficient that model evaluation is reliable' (Peterson et al. 2011: 157). This also applies to data sampled for model calibration.

By relaxing demands on the degree of independence needed, in accordance with the suggestion by Peterson et al. (2011) as cited above, our attention is shifted from demands for

strict independence to demands for the sample to be representative for test calibration or testing situation, and for the intended use of the model, as also suggested by Vaughan & Ormerod (2005). Three different kinds of representativity, corresponding to three different schemes for collection of calibration/evaluation data, may, in principle, apply:

- **1.** *Representativity in geographical space*, i.e., that every potential observation unit in the study area has the same probability for being sampled.
- **2.** *Representativity in environmental space*, i.e., that each interval of unit length along each environmental explanatory variable of interest is equally well covered by the sample.
- **3.** *Representativity for the range of model predictions*, i.e., that, within the range of model predictions, each interval of unit width along the scale at which predictions are expressed, is equally well covered by the sample.

I argue that it is the third kind of representativity that is relevant for calibration and evaluation of distribution models. Only by adequate representation of the entire range of sites along the gradient from unsuited to optimal for the modelled target, can the model's full ability to predict the real probability of presence, which is addressed in two different ways by model calibration and model evaluation, be appropriately assessed (Araújo et al. 2005, Edvardsen et al. 2011). Demands for representativity for the range of model predictions can be met by stratified random sampling from the study area itself (e.g., Le Lay et al. 2010, Edvardsen et al. 2011, Stokland & Halvorsen 2011, Auestad et al. 2011) or, if the purpose is to test transferability of model predictions, from by use of a sample from another study area [e.g., see Randin et al. 2006)], using model predictions as stratification criterion. Le Lay et al. (2010) use the term 'model-based field sampling' for this sampling scheme. Other sampling schemes, such as the use of selectively or preferentially sampled data, collected independently of the data used to parameterise the model (e.g., Marage et al. 2008, Newbold et al. 2010, Gogol-Prokurat 2011), come without any guarantee that geographical or environmental sampling bias is lacking or that the biases are different from those of the data used to parameterise the model. Furthermore, such data are unlikely to be representative for the range of modelled predictions. The value of model evaluations based on such pseudo-independent data should be questioned.

STATISTICAL MODEL

Choice of modelling method (Step 7,i)

MaxEnt and BRT are currently among the most popular DM methods (Franklin 2009). Their popularity rests on the combination of relative ease of use due to availability of user-friendly free software and published tutorials (e.g., De'ath 2007, Elith et al. 2008, 2011, Phillips 2011), and good performance in extensive comparative tests of the methods' ability to predict distributions in geographical space; see discussions of criteria for evaluation of DM methods by Elith et al. (2006), Hirzel et al. (2006), Lobo et al. (2008), and Franklin (2009), and references quoted therein. Reports from such tests indicate that more complex methods, i.e., methods that allow more flexible functions to be fit to the data, in general produce models with better predictive performance than simpler methods, and that the former produce models that fit the data too closely (Elith et al. 2006, Tsoar et al. 2007, Jiménez-Valverde et al. 2008, Santika & Hutchinson 2009, Gastón & García-Viñas 2011, Michel et al. 2011, Webber et al. 2011). Results of, and recom-

mendations from, these comparisons, are, however, only valid for the SPM purpose because only SPM models can be judged pragmatically by predictive performance in geographical space.

In fact, completely different sets of optimality criteria apply to ERM and SPM. The ERM purpose calls for a model that in the best possible way summarises the overall ecological response of the modelled target to the gradients(s) of interest, i.e., in ecological space. The expected overall ecological response to important environmental complex-gradients is a unimodal or truncated unimodal curve that may be skewed and/or kurtotic (Fig. 11). The ERM purpose thus calls for fitting of relatively simple, smooth functions like those fitted by DM methods of the regression type, such as generalised linear models (GLM) and generalised additive models (GAM). Austin et al. (2006: 203) list five criteria for judgement of distribution models, which were used to evaluate GLMs on a set of realistic, simulated data for species performance and explanatory variables: '[1] correct selection of explanatory variables; [2] accurate description of species response curves to predictors; [3] correct prediction of species abundance for a given value of the predictors; [4] the ecological rationality of the modelled relationships; and [5] the level of skills necessary to successfully apply a statistical method'. All of these criteria except (5) address performance in the ERM context, and all of the remaining criteria except (1), which typically applies to general-purpose ERM, apply equally to the two sub-categories of ERM. Demands for response models with shapes that accord with expectations from ecological theory, simplicity, and appropriate parameterisation, are also emphasised as important for models with the ERM purpose by other authors, e.g., Austin (2007), Tsoar et al. (2007), and Jiménez-Valverde et al. (2008).

To comply with criteria (2) and (3), ERM models have to be explicitly parameterised, i.e., that the output from Step 8,iii has to be a mathematical function with coefficients that are explicitly estimated. Machine-learning methods like boosted regression trees (BRT), and other ensemble forecasting methods (e.g., BIOMOD), which are not explicitly parameterised, are therefore not appropriate for ERM. MaxEnt, which has been described alternatively as a machine-learning method (Phillips et al. 2008, Phillips & Dudík 2008) and as a statistical learning method (Elith et al. 2011), but which can alternatively be explained by strict application of the maximum likelihood principle (Halvorsen in press), is therefore appropriate both for ERM and SPM.

Which method to choose for a particular DM study thus has to be decided after due consideration of the main purpose of the study – whether it is ERM, SPM, or PPM. In addition, the specific problem formulated should be taken into account when the method is chosen (Franklin 2009, Peterson et al. 2011).

Model specification (Step 7,ii)

The model specification step comprises decisions about the mathematical function that relates the response variable via the derived variables to the explanatory variables (e.g., Guisan & Zimmermann 2000, Franklin 2009). As pointed out in the chapter 'Transformation of explanatory variables', model specification in methods of the regression type is largely performed implicitly in the process of choosing transformation of explanatory variables (Step 5,ii). In machine-learning methods, which provide no explicit parameterisation, no mathematical functional relationship needs to be specified.

One aspect of model specification which is important in DM methods of all kinds, is the treatment of interactions between explanatory variables. In statistical terminology, presence of an interaction between two explanatory variables means that the response to a combination of the two deviates from the expectations from separate models made for each variable.

In models of the regression type, interactions up to a threshold degree of complexity (second, third, fourth order, etc.) are modelled by including new variables for products of the explanatory variables that contribute to the interaction. In BRT, handling of interactions is controlled by the tree complexity parameter, the value of which corresponds to the order of allowed interactions (Elith et al. 2008). Opening for all combinations of high-order interactions in models with many explanatory variables results in extremely complex models. Franklin (2009) therefore recommends that only interaction terms which are meaningful, based upon ecological theory, are included in distribution models. This recommendation accords with the ERM purpose while, from the SPM point of view, it can be argued that distribution models should be judged pragmatically by their predictive performance and that interaction terms are included in models, also the main terms have to be included because interaction terms measure how the response to both variables at the same time deviates from the summed response to each variable, modelled separately (Crawley 2007).

In ecological terminology, the term 'interaction' is typically used in a much wider meaning, to indicate the influence of one explanatory variable or a group of variables on another variable or variable group, in some way (e.g., Austin 2007). Existence of interactions in this broad meaning of the term, can be revealed in many ways other than by including product variables in a model. Interacting effects of explanatory variables on the distribution of modelled targets can, for instance, be quantified by the variation partitioning approach. This is exemplified by Meier et al. (2010), who found that tree distributions in Switzerland were affected both by environmental and biotic explanatory variables, and that the overlap in the variation explained by these two groups of explanatory variables was small. Other examples of DM studies that document effects of interacting species on the distribution of modelled target species, are Austin & Leathwick (2001) for tree species in New Zealand and Heikkinen et al. (2007) for owls in Finland.

Model selection and overfitting of distribution models (Steps 8,i-iii)

The three tasks involved in modelling of the overall response – model selection (Step 8,i), internal model performance assessment (Step 8,ii), and model parameterisation (Step 8,iii) – are often integrated into one process by which parameterised models for many different combinations of explanatory variables are obtained and compared by internal model performance assessment criteria. The outcome of Step 8 is one best model or a set of alternative, good models. A multitude of model selection methods, model comparison criteria, and model performance statistics are available, many of which are tightly coupled with one specific, or a group of, modelling methods (e.g., see Reineking & Schröder 2000, Johnson & Omland 2004, Zuur et al. 2007, Claeskens & Hjort 2008, Hastie et al. 2009). One example is the ratio of explained to residual deviance, weighted by the appropriate degrees of freedom, which is used for internal performance assessment of nested maximum likelihood models by the *F*-ratio test (e.g., Venables & Ripley 2002, Hastie et al. 2009), e.g., in combination manual forward stepwise selection of variables.

A general criterion for a good distribution model is that the model describes the phenomena of interest in an efficient way. The exact meaning of this general statement depends on the main purpose of the DM study. A good ERM model describes the modelled target's overall ecological response to specific explanatory variables (specific-purpose ecological response modelling) as adequately as possible, or identifies the most important explanatory variables and assists understanding of the distribution of the modelled target (general-purpose ecological response modelling). Both sub-categories of the ERM purpose address identification and understanding of generally valid patterns, in ecological space. A good SPM model, on the other hand, accurately predicts the performance of the modelled target in geographical space, e.g., as evaluated on independent evaluation data (Step 11). These criteria for good models, given modelling purpose, can be expressed in terms of internal and external model performance criteria as illustrated in Fig. 15: the best SPM model is the model with lowest prediction error and the best general-purpose ERM model is the model with lowest prediction error that fits overall ecological response curves which accord with expectations from gradient analytic theory. In terms of number of parameters in the model, the best SPM model is expected to be more complex than the best general-purpose ERM model.

The term 'overfitted' is often used in the literature to denote suboptimal models (e.g., Guisan & Zimmermann 2000, Araújo & Guisan 2006, Elith et al. 2006, Phillips et al. 2006, Elith & Leathwick 2009, Elith et al. 2011, Peterson et al. 2011). Few authors do, however, define this term explicitly. Vaughan & Ormerod (2005: 723) define 'overfitting' as the situation by which 'idiosyncracies in the training data set are modelled in addition to the underlying species–environment relationships ... result[ing] in misleadingly good fit to the data'. Peterson et al. (2011: 113) characterise a good model as follows: '... fits well to the known data, ... does not overfit in ways such that its predictive ability is low when presented with independent data'. These quotes pinpoint the combination of unneccessarily many parameters and suboptimal predictive performance in geographical space as typical characteristics of overfitted distribution models. Such models are indicated by 'Type I overfitting' in Fig. 15. Type I overfitted models are more complex than, and have higher prediction error than, the best SPM model.

The best SPM model for a given data set is likely not to be the best model as judged from an ERM point of view. It follows from the definition of the ERM purpose and the fundamental insights of the GA perspective that good ERM models should satisfy the following two criteria [cf. model performance criteria (2) and (4) of Austin et al. (2006), listed above]: (1) the shapes of overall ecological response curves fitted to the data should accord with GA theory, i.e., be unimodal or truncated unimodal, with allowance for variation in skewness and/or kurtosis but not for other complex shapes; and (2) fitted response curves should be as simple as possible in terms of model parameters and included explanatory variables, in accordance with the second insight of the GP perspective stating that few major complex-gradients normally account for most of the variation in species composition that can be explained environmentally. The first criterion applies to both sub-categories of ERM purposes while the second may be irrelevant for some specific ERM purposes. Among models that satisfy criteria (1) and (2), the best generalpurpose ERM model is the one with lowest prediction error on independent data.

According to criterion (2), a simpler model which differs insignificantly from a more complex model in prediction error on independent evaluation data, i.e., with respect to predictive performance in geographical space, is a better general-purpose ERM model. According to criterion (1), an even simpler model is better from the perspective of the ERM purpose if the more complex models fit overall ecological response curves that are unrealistically complex (Jiménez-Valverde et al. 2008). Existence of two criteria for good ERM models, that address different intervals along the model complexity axis in Fig. 15, suggest that the concept of an **overfitted model** should be redefined as 'a distribution model that fits more complex overall response curves than appropriate, given the modelling purpose', and that three types of overfitting should be recognised (cf. J. Dirksen et al., unpubl. results):

- 1. *Type I overfitting*, i.e., that a more complex model has lower predictive performance on independent data than a simpler model.
- 2. *Type II overfitting*, i.e., that a more complex model is similar in predictive performance on independent data than a simpler model.



model complexity (number of parameters)

Fig. 15. Overfitting of distribution models with different purposes as a function of residual variation in response variable and prediction error on independent evaluation data. The best SPM model is the model with lowest prediction error, the best general-purpose ERM model is the model with lowest prediction error that fits overall ecological response curves which accord with gradient analytic theory. Intervals along the model complexity axis which correspond to Type I, II and III overfitting are indicated. The horizontal box with red shading indicates models with prediction error insignificantly different from that of the best SPM model.

3. *Type III overfitting*, i.e., that a more complex model with higher predictive performance on independent data than a simpler model fails to fit realistic overall ecological response curves.

In a study of swamp forests in SE Norway (J. Dirksen et al., unpubl. results), MaxEnt models generated by different model selection methods and different internal model assessment criteria are found to differ strongly with respect to number of parameters, while their predictive performance on independent evaluation data are close to similar. This proves existence of Type II overfitting (J. Dirksen et al., unpubl. results). No indication of Type III overfitting was, however found in that study; the most complex, realistic models were insignificantly inferior to more complex models with respect to predictive performance on independent evaluation data.

Type II and III overfitted distribution models 'explain' more of the variation in the response variable than the best, simpler and realistic models (Fig. 15). The difference in variation explained between overfitted and simpler, realistic models reflects more or less accidental correlations of surplus explanatory variables with, e.g.: effects of interactions between explanatory variables; effects of historical factors; variation along unrecognised condition or impact ecoclines; interspecific interactions; lack of dispersal; or other demographic processes. Type II and III overfitted ERM models are likely to fail to express general relationships of the modelled target

with the environment, by hiding idiosyncratic variation associated with the modelling context (peculariarities of the study area, the time-point the study is carried out, etc.) in a 'black box of explained variation'. Only by retaining variation in the performance of the modelled target in the residuals, can this variation be explicitly addressed by further analyses. This line of reasoning parallels the arguments why constrained ordination is inapproapriate for general-purpose ecological studies: constraining the variation in species composition on supplied explanatory variables removes the potential for generating hypotheses about the causes of variation that is left unexplained in unconstrained ordination (R. Økland 1996).

Model calibration (Step 10)

Model calibration, by which the numerical accuracy of model predictions in terms of probabilities of presence is improved, implies that a monotonous function is fitted to model predictions (Pearce & Ferrier 2000b). Model calibration by use of independent presence/absence data is particularly relevant for distribution models parameterised by use of presence-only data, the output from which are RPPP values that do not allow estimation of the prevalence of the modelled target in the sample (Phillips et al. 2006, Ward et al. 2009). Thus, when the intended use of the PO-parameterised distribution model requires conversion of model predictions to a predicted probability-of-presence (PPP) scale, and/or an estimate for prevalence is required, model calibration by presence/absence data is mandatory (Pearce & Ferrier 2000b, Pearce & Boyce 2006, Elith & Graham 2009, Gastón & Garvia-Viñas 2010, Halvorsen in press). Examples of such applied uses are estimation of population sizes (Edvardsen et al. 2011) and probabilitybased sampling of observation units for monitoring purposes (Halvorsen 2011, Halvorsen & Heegaard 2011). Appropriate calibration also improves the value of model predictions for model-assisted search for new localities of rare species (Edwards et al. 2005, Guisan et al. 2006a, Le Lay et al. 2010, Edvardsen et al. 2011). Several statistical modelling methods, e.g., logistic regression (Cox 1958), can be used for calibrating RPPP values onto a PPP scale (see Pearce & Ferrier 2000b).

The relevance of model calibration depends on modelling purpose. Model calibration generally improves the usefulness of model predictions for applied SPM purposes.

Model evaluation (Step 11)

The purpose of a DM study dictates which evaluation strategy is most appropriate (Araújo & Guisan 2006, Austin 2007, Jiménez-Valverde et al. 2008). Differences between ERM and SPM in this respect are outlined in this section.

It follows from the SPM purpose, which is to provide the best possible spatial predictions for sites in which presence or absence of the modelled target is unknown, that evaluation is a necessary and important step in the SPM process. Distribution models can be evaluated by several methodological strategies, as explained in the chapter 'The distribution modelling process', Step 11 (see Fig. 8). The intended use of an SPM model and, in particular the user's demand for precise spatial predictions from the model (Araújo & Guisan 2006), determines the level of rigour needed in the evaluation process. SPM models constructed with the intention of merely illustrating broad patterns of distribution of the modelled target in the study area require less rigourous evaluation than models built to assist systematic search for new localities of endangered species (Guisan et al. 2006a, Le Lay et al. 2010, Edvardsen et al. 2011) and models that shall form the basis for probability-based sampling of monitoring sites (Auestad

et al. 2011, Halvorsen & Heegaard 2011).

It is only the model's ability to predict performance in geographical space that can be approached by an independent evaluation data set (Araújo & Guisan 2006, Jiménez-Valverde et al. 2008, Braunisch & Suchant 2010, Warren & Seifert 2011): the truth about a modelled target's overall ecological response to all important complex-gradients, in environmental variabler, or ecological, space, can hardly ever be fully unravelled (Austin et al. 2006). Accordingly, ERM models cannot be formally evaluated by use of field data (Austin et al. 2006). Instead, ERM models have to be critically judged for realism by use of theoretical and practical skills (Austin et al. 2006, Austin 2007). Nevertheless, Fig. 15 indicates that assessment of the predictive performance of general-purpose ERM models on independent data is an important element in assessment of the appropriateness of such models. The ability of different modelling *methods and options* (rather than specific models) to extract meaningful structure from realistic data can, and should, be carefully analysed by use of simulated data with realistic properties, built in accordance with GA-based knowledge (Austin et al. 2006).

Independent evaluation data can be used to evaluate transferability of results of projective distribution models (PPM) to geographical areas outside the study area (Wolmarans et al. 2010, Anderson & Gonzalez 2011) while transferability of model predictions in time cannot be evaluated this way (Araújo et al. 2005).

Independently sampled presence/absence data for the modelled target (Step 9) are indispensable for evaluating the predictive performance of SPM-purpose distribution models in geographical space. Evaluation by use of independent data is the only strategy for evaluation of DM models that completely circumvents pitfalls related to sampling bias in sets of raw observations of the targeted phenomenon (Austin 2007, Veloz 2009). Sampling bias is omnipresent in the observed presence data used for training of distribution models, and arise for several reasons (e.g., Araújo & Guisan 2006, Hortal et al. 2008, Loiselle et al. 2008, Robertson et al. 2010, Wolmarans et al. 2010, Elith et al. 2011, McCarthy et al. 2011). A typical example is accessibility-related recording effort, which may result in distribution models in which distance from roads is a significant explanatory variable (Kadmon et al. 2004, Wollan et al. 2008). Importantly, use of the same data set for training and for evaluation, for instance by resubstitution or data-splitting, does not avoid problems related to sampling bias nor to spatial autocorrelation of observations (Araújo et al. 2005, Araújo & Guisan 2006, Segurado et al. 2006, Austin 2007, Raes & ter Steege 2007, Veloz 2009).

Ecological theory is important, both for fully understanding the implications of choice of performance criteria in model evaluation and for appropriate interpretation of evaluation results. This is illustrated by two examples.

The area under curve (AUC) of the receiver operating characteristic (ROC) curve (Hanley & Mc Neil 1982, Fielding & Bell 1997) is currently the most frequently used criterion for evaluation of SPM distribution models (Franklin 2009). One reason for the popularity of AUC is that it can be used with all evaluation strategies. The ROC curve is a graph of the relationship between model sensitivity and model commission error, over all possible RPPP thresholds. Commission error, or 1 – specificity, or the false positive rate, is the probability that presence is predicted in a grid cell from which the target is known to be absent. Sensitivity, the true positive rate, is the probability that presence is predicted in a grid cell in which the target is known to be present. With presence-only data, AUC can be calculated by replacing true commission error with the probability that presence is predicted in a randomly selected grid cell. With presence/absence data, AUC can be interpreted as the probability that the model predicts a higher RPPP value in a random presence grid cell than in a random absence grid cell, while with presence-only data, AUC can be interpreted as the probability that the model predicts a ligher RPPP value in a random presence grid cell than in a random background grid cell (Phillips et al. 2006, 2009). Even though uncritical use of AUC has been rightfully criticised (e.g., Lobo et al. 2008), AUC has retained its position as a good overall indicator of modelling success (e.g., Elith et al. 2006, Wisz et al. 2008).

One result from evaluation of DM models by the AUC criterion that has often been highlighted in DM literature, is that models for rare species tend to be superior to models for common species (e.g., Elith et al. 2006, Jiménez-Valverde et al. 2008, Wollan et al. 2008, Franklin 2009). A species may, however, have low prevalence in a sample, or appear to be rare, for many different reasons (Harper 1981). Observed rarity may, of course, reflect real rarity. This is the case for typical 'satellite' species in the sense of Collins et al. (1993); i.e., species with low fractional amplitude with respect to important environmental complex-gradients – restricted 'distribution in ecological space' - and low aggregated performance. Satellite species typically also have restricted distributions in geographical space, i.e., small extents of occurrence, due to low fractional amplitude with respect to regional ecoclines, i.e., narrow tolerances for climatic factors. Low prevalence then results from the generally positive abundance-occupancy relationship. Observed rarity may be real also for species which combine low prevalence and wide amplitude along important complex-gradients. Such species, which are 'rural' species according to the CURS model (Collins et al. 1993), often also have large extents of occurrence. Low estimated prevalence may also be an artifact of insufficient or biased sampling. AUC does not distinguish between these kinds of rarity, and they are rarely taken explicitly into consideration when DM evaluation results are discussed. This is exemplified by characteristics given to species associated with high AUC in the DM literature, by McPherson & Jetz (2007) as having 'smaller range size' and 'higher habitat specificity', by Tsoar et al. (2007) as having 'more restricted niches', by Jiménez-Valverde et al. (2008) as having 'lower relative occurrence area', by Wollan et al. (2008) as having 'restricted distributions' and by Marmion et al. (2009a) as having 'restricted ranges' and 'low prevalence'. Note that the term 'relative occurrence area' is defined by Lobo et al. (2008) as the ratio between extent of occurrence and the whole extent of the region of study, thus corresponding to the extent of occurrence expressed as a fraction of the entire study area. Steps 7–8 in the 12-step DM process is the key to unravel which aspects of rarity that make models for 'rare' species appear 'better' than models for common species in terms of AUC. The more strongly the model is able to concentrate observed presence grid cells to a restricted interval along an important explanatory variable, the lower will the fractional amplitude of the species be, and the higher will the probability be that the model predicts a higher RPPP value for a random observed presence cell than for a random background cell and, hence, the higher will its AUC be. Thus, low fractional amplitude in multidimensional environmental variables space is the most important determinant of the AUC of DM models (Stokland et al. 2011). Accordingly, the often claimed tendency for models of targets with small extent of occurrence or low prevalence to obtain high AUC values is an indirect effect of the positive, often strongly positive, correlation between rarity in geographical space and restricted tolerance in ecological space (Preston 1948, Brown 1984, Økland 1989a). All other factors equal, models for 'rural' species will not obtain higher AUC values than models for 'core' species, i.e., species with high occupancy and wide amplitude along important complex-gradients, often also with large extent of occurrence (Collins et al. (1993).

The second example is the use of 'target-group background data', as implemented in Maxent software from version 3 (Phillips & Dudík 2008). Target-group background observations are then used instead of all grid cells or a random subsample of all grid cells as background in PO distribution models. In a comparative analysis based upon real data, Phillips & Dudík (2008) found that use of target-group background observations considerably improved the AUC of MaxEnt models. They ascribed this to counteraction of sample bias in museum collection or atlas data, which are known to be biased in specific ways (see Loiselle et al. 2008, Robertson et al. 2010):

'target-group background may be interpreted as a random sample from the (biased) sampling distribution' (Phillips & Dudík 2008: 173). This interpretation is likely to be partly correct, but a full understanding of the behaviour of models (and AUC) with different types of background data requires knowledge of the distribution of background observations along the axes of the environmental variables or ecological space. If observations in the target-group background sample fail to span the entire range of variation along a recorded explanatory variable, the fractional amplitude calculated by use of target-group background. The ranking of these models by AUC will then be shifted in disfavour of target-group background (Stokland et al. 2011). This indicates that target-group background observations may improve distribution models even more strongly than indicated by the results of Phillips & Dudík (2008).

CONCLUSIONS

My main intentions with this essay review are to summarise major insights of the gradient analytic (GA) perspective, to show how this perspective can form a firm foundation for describing and understanding distribution modelling (DM), and to use this GA-based platform to address issues of current interest to distribution modellers. The two main reasons for choosing the GA perspective as a fundament for DM are: (1) that DM is unambiguously placed among gradient analysis techniques by the crucial step 8 in the distribution modelling process, by which the overall ecological response of the targeted phenomenon is modelled as a function of explanatory variables; and (2) that the 'environment-centred' understanding of natural variation implicit in the GA perspective is more appropriate for DM than the 'species-centred' understanding implicit in 'niche theory'. Despite many holes still exist in our knowledge of patterns of natural variation, the basic insights of the GA perspective provide a firm theoretical platform for further development of DM. Important elements of this theoretical platform are: (1) a consistent and explicit terminology; (2) knowledge about how species' performance, in general, varies along environmental complex-gradients, which structuring processes are responsible for species' performance patterns, and the spatial (and temporal) scales at which these patterns can be recognised; and (3) specific knowledge about species' performance patterns in different parts of the world and in particular ecosystems. A new conceptual modelling framework for DM, the HED framework, is proposed. The conceptual modelling framework and insights derived from it can be used in initial phases of a DM study to formulate a meta-model for factors that influence distributions, and in the analytic phase to guide choices of data model, statistical model and interpretation of modelling results. Furthermore, the HED framework can serve as a hierarchical, top-down framework for practical distribution modelling. A tour on the gradient analytic train through the 12-step DM process reveal several issues in need of being scrutinised more carefully, and considerable potentials for improvement of DM practice. The main findings can be summarised in seven challenges for DM:

1. *More knowledge of patterns of natural variation is needed.* Most notably, this applies to descriptive knowledge such as which ecoclines are most important for different organisms in different ecosystems. Basic knowledge of this kind, which can be obtained by gradient analysis, e.g., ordination, of species-in-samples data matrices followed by interpretation of coenoclines using environmental variables-in-samples
data, may bring improvements to several steps in the DM process: choice of explanatory variables (Step 3), choice of grain and extent for the study (Step 4), judgement of the ecological realism of distribution models (Steps 8, 11), and interpretation of modelling results (Step 12). I stress this point as particularly important for three main reasons: (i) because much more knowledge of patterns of natural variation is needed to strengthen DM's theoretical platform; (ii) because research on local or regional patterns, which is descriptive and dependent on 'naturalist' approaches, is currently under strong pressure in a scientific community that honours experimental research on questions of general interest (Lawton 1996, Økland 2007); and (iii) because knowledge of patterns of natural variation is usually not mentioned among challenges for DM.

- 2. A better mechanistic understanding of causes of patterns of natural variation is needed. In particular, this applies to the role of interspecific interactions, positive as well as negative, for species performance patterns. Several studies by DM methods have addressed this question (e.g., Austin & Leathwich 2001, Heikkinen et al. 2007, Meier et al. 2010), the results of which indicate important differences between organism groups in the extent to which interspecific interactions give rise to distributional patterns on spatial scales broader than the fine local scale. Furthermore, these studies demonstrate that, by taking biotic explanatory variables into consideration, DM can give important contributions to basic ecological knowledge. More studies in this direction are encouraged.
- 3. The availability of relevant rasterised explanatory variables needs to be improved. Lack of data sets with 'wall-to-wall' coverage for potentially important explanatory variables rasterised to appropriate grain sizes, is currently one of the most important reasons why the precision of distribution models often fail to match the modeller's ambitions, regardless of modelling purpose. While lack of data is no longer a great problem in modelling of responses to climatic factors at regional and global spatial scales, e.g., due to open access to large data sets such as WorldClim (Hijmans et al. 2005), lack of explanatory variables rasterised to an appropriate grain size remains a major obstacle to modelling of patterns at local and micro spatial scales, i.e., modelling by use of grid cells smaller than 1×1 km as grain. This challenge appears often not to be recognised, as demonstrated by the statement of Franklin's (2009: 77) that 'there is a widely held belief that "GIS data" (digital elevation model) are abundant and ubiquitous'. Important reasons why appropriate explanatory variables are often lacking are: that the costs of obtaining good explanatory variables data tend to increase with decreasing sample extent because the opportunity for re-use, and hence for sharing of costs, decreases; and that many local ecoclines are difficult or expensive to measure. Typical examples of such ecoclines are 'drought severity', 'snow-cover stability' and 'lime richness'. Huge resources can be saved by building open-access archives for layers of explanatory variables, equipped with functionality for interpolation, rasterisation to a widest possible range of grid-cell sizes, and flexibility with respect to output data formats.
- 4. *More studies of patterns at local and micro spatial scales, and multiple-scale studies using DM methods, are needed.* A broadening of the range of spatial scales approached by DM methods is needed. DM studies of patterns at fine spatial scales are likely to complement studies of species composition by ordination methods, fill important gaps in our knowledge of distributional patterns at these spatial scales and the ecological processes that operate on these scales.
- 5. Evaluation by independent data should be established as a standard in DM. Environ-

mental sampling bias is a major quality-reducing factor for distribution models. In spatial prediction modelling, the resulting performance distribution bias should be identified by use of an independently collected sample of presence/absence data that is representative for the range of model predictions. Even though a standard methodology for evaluation of distribution models was established more than a decade ago (e.g., Pearce & Ferrier 2000b), very few distribution models published so far have been subjected to evaluation by these standards [Araújo et al. (2005); but see Edwards et al. (2005), Le Lay et al. (2010), and Edvardsen et al. (2011)].

- 6. Further insights into statistical modelling methods and their options, with particular reference to appropriateness for different types of data and DM purposes, are needed. DM methodology has improved considerably over the last years, e.g., due to several extensive methods comparison studies, starting with Elith et al. (2006). Nevertheless, many important methodological questions still await being addressed. Specifically, this is the case for questions in the interface between data properties and methods and their options. Of particular urgency is demands for careful analysis of interactions between transformation of explantory variables, choice of method for model specification, and criteria for model comparison and internal model performance assessment, in addition to how these interact with modelling method and data properties. Assessement should be made of the extent to which different choices result in overfit models, relative to different modelling purposes.
- 7. *DM methods should be incorporated in studies with a broader scope.* DM methods have proved their usefulness for finding general patterns in distributions and for understanding how explanatory variables influence distributions. Integration of DM approaches into studies with broader perspectives are likely to give new important insights (Guisan & Thuiller 2005). In particular, integration with studies of demography and dispersal are likely to have considerable potentials, e.g., for understanding the roles of source-and-sink dynamics, including migration processes and extinction debt, and interactions between species.

Distribution modelling is established as an important part of the conservation biologist's toolbox and distribution modelling approaches are now recognised as useful for a wide range of applied purposes (Franklin 2009). By addressing the variation in performance of one target phenomenon at a time, such as a species, and by relating this variation to one or several explanatory variables, DM approaches complement multivariate approaches such as ordination methods. Together, DM methods and methods for multivariate gradient analysis equip spatial ecologists with a versatile toolbox with considerable potential for improving our understanding of patterns of natural variation and their causes.

ACKNOWLEDGEMENTS

This study has benefitted strongly from long-term exchange of ideas with, and constructive criticism from, members and affiliates of the geo-ecology research group (formerly 'Identification and modelling of biodiversity') at the Natural History Museum, University of Oslo. In particular, I thank Vegar Bakkestuen for continuous support; Inger Auestad, Trine Bekkby, Lars Erikstad, Knut Anders Hovstad, Eli Rinde and Jogeir N. Stokland and former and present PhD students John W. Dirksen, Anette Edvardsen, Sabrina Mazzoni, Thijs van Son, Bente Støa and Anders K. Wollan for comments on, and suggestions for improvement of, earlier versions of this manuscript. Furthermore, all are thanked for contributions to the empirical distribution modelling studies, published or in preparation, which form the basis for most insights reported in this paper. Thanks are also due to Niklaus Zimmermann for inspiring discussions in an early phase of this study. Special thanks go to Mike Austin and Anders Bryn whose detailed, critical comments on an earlier version of the manuscript considerably improved the final result.

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APPENDIX I: DEFINITIONS

absence — failure of the modelled target to occur in an observation unit, as contrasted with presence

abstract geographical space — a set of grid cells, which corresponds to a specific rasterisation of geographical space, the collective properties of which being addressed without taking geographical co-ordinates into account

abundance — number of individuals of a species or, for other modelled targets, discrete units, or, for clonal organisms, organismal units

aggregated performance — collective term for performance, recorded by some performance measure, aggregated for sets of observations units

allelopathy — the mechanism by which plants release chemicals that affect other plants

amensalism — (0,–) interactions, the outcome of which is neutral for one and negative for the other organism

amplitude response — effect on tolerance limits for a species along a gradient

- area of occupancy the total area of grid cells in which a species is recorded as present
- background observations collective term used for uninformed observations, i.e., absences, random grid cells or pseudo-absence observations
- background stress or disturbance processes that reduce the performance of a species compared to its physiological potential situations, without variation in the magnitude of effects along the complex-gradient
- basic ecocline collective term for regional and local ecoclines

biotic variable — descriptor of potential influences from other organisms

- broad scales spatial scales comparable with those that are addressed by samples with extentgrain ratio of 16 and linear grain > 10^3 , i.e., > 1 km
- calibration model model used for calibration of a distribution model
- calibration plot graph of frequency of presence plotted against model predictions, typically with subsets of observation units in calibration the data set as data points
- categorical variable variable that can take a finite number of positive integer values, each of which indicate affiliation to a class, type, etc.
- coarse local scale spatial scales comparable with those that are addressed by samples with extent-grain ratio of 16 and linear grain of 10^2-10^3 m, i.e., 100-1000 m
- coarse regional scale spatial scales comparable with those that are addressed by samples with extent-grain ratio of 16 and linear grain of $10^{4.5}$ – 10^6 m, i.e., 32–1000 km
- coenocline gradient in species composition
- competition (-,-) interactions, the outcome of which is negative for both organisms complex-gradient (= environmental complex-gradient)
- commensalism (0,+) interactions, the outcome of which is neutral for one and positive for the other organism (= facilitation)
- community organisms which live together at the same time within a restricted area (= biotic component of the ecosystem)
- condition or impact ecocline parallel variation in species composition and important environmental factors, typically with large variation at temporal scales of decades [(6–)10–100 years]
- continuous environmental variables space an environmental variables space in which other observation units than grid cells are shown
- continuous variable variable that can take every value in the real domain

contramensalism — (+,-) interactions, by which no direct dependence exists between the

interacting organisms

cover — vertical projection of biomass

data-splitting — dividing one data set into subsets

data resubstitution — collective term for bootstrapping, jackknifing and crossvalidation

demographic processes — processes, often with a strong stochastic element, that cause variation in a species' performance not possible to explain as the response to environmental

complex-gradients or as the outcome of interactions with other organisms

density — abundance per unit area

- derived (explanatory) variable variables derived from explanatory variables by transformation
- destabilising processes mechanisms which limit biomass by causing its partial or total destruction (= 'disturbance' sensu Grime)

discrete environmental variables space — an environmental variables space in which characteristics of grid cells are shown

- dispersal into new sites transportation and successful establishment of propagules in sites previously unoccupied by the species in question
- distal factor environmental factor that do not, as such, impact species' performance, but which serves as a surrogate or proxy, for more proximal factors
- distribution the physical arrangement of objects of that belong to a specific type category
- distribution modelling research with the purpose of modelling the distribution of observable objects of a specific type
- disturbance (sensu stricto) sudden and unpredictable events leading to biomass destruction

ecocline — the parallel, more or less gradual, co-variation of species composition, i.e., a coenocline, and a major complex-gradient

- ecological response modelling distribution modelling with the main purpose of modelling the relationship between a target, typically the performance of a species, and a set of explanatory variables, to find and understand general patterns in the overall ecological response of the modelled target to the supplied explanatory variables
- ecological space the conceptual space with the major complex-gradients as axes
- environment all external factors that may potentially influence organisms
- environmental sampling bias sampling bias due to lack of representativity in environmental variables space
- environmental complex-gradient a set of more or less strongly correlated environmental variables (= complex-gradient)
- environmental gradient the more or less gradual variation in any environmental 'factor'
- environmental sampling bias sampling bias due to lack of representativity in environmental variables space
- environmental variable descriptor of environmental variation in the widest sense, i.e., an external factor that may potentially influence organisms
- environmental variables space the conceptual geometric space with selected, measurable, environmental variables as axes
- explanatory variable a variable that may potentially account for some variation in a response variable
- extent of occurrence the area which lies within the outermost geographic limits to the occurrence of a species
- extent-grain ratio the linear dimension of the extent divided by the linear dimension of the grain
- extinction debt expected future extinction of species due to events in the past

- fine local scale spatial scales comparable with those that are addressed by samples with extent-grain ratio of 16 and linear grain of 10^{0} – 10^{1} m, i.e., 1–10 m
- fine regional scale spatial scales comparable with those that are addressed by samples with extent-grain ratio of 16 and linear grain of 10^3 – $10^{4.5}$ m, i.e., 1–32 km
- fine scales spatial scales comparable with those that are addressed by samples with extentgrain ratio of 16 and linear grain < 10³ m, i.e., < 1 km
- fitness the average number of descendants in the next generation per individual in the current generation
- fluctuations more or less predictable events leading to biomass destruction
- fractional amplitude tolerance, expressed as the ratio of the species' amplitude along a gradient and the length of the entire gradient, expressed in relevant units
- fractional area the fraction, by area, of an observation unit that is occupied by a modelled target such as a nature type
- frequency of observed presence the fraction of observed presences in a PO data set
- frequency of presence the fraction, or percentage, of observations units in a set, in which the modelled target is present
- general-purpose ecological response modelling to describe and understand distributional variation at relevant scales, without regard to a specific set of explanatory variables
- general-purpose ecological study to summarise the main structure in a species-by-sample data matrix, to relate structure in species composition to external factors, and to generate hypotheses about the processes and mechanisms responsible for these relationships
- geographical sampling bias sampling bias due to lack of representativity in geographical space
- geographical space the conceptual geometric space with geographical co-ordinates x, y and eventually also z, as its dimensions
- global scale spatial scale comparable with that addressed by samples with extent-grain ratio of 16 and linear grain of > 10⁶ m, i.e., > 1000 km
- gradient the more or less gradual variation of a property of the environment, or of a specific type category of natural phenomena
- gradient analytic perspective explanations of natural variation based upon knowledge about environmental gradients and species' responses to these gradients
- gradient analysis interpretation of community composition in terms of species' responses to environmental gradients in the broadest sense
- gradient-dependent stress or disturbance processes that reduce the performance of a species compared to its physiological potential situations, with variation in the magnitude of effects along the complex-gradient
- grain = spatial grain
- grid cell one out of a set of contiguous quadrats of equal size into which the geographical space, or a subspace thereof, is divided
- group discriminative method method that contrast environmental characteristics of presence or observed presence data points with properties of absence, random or pseudo-absence points
- importance value index obtained by combining two or more quantitative performance measures
- independent variable a variable actually used to parameterise a model; independent variables may include raw explanatory variables themselves and/or variables (derived variables) derived from raw explanatory variables by transformation (= predictor, predictor variable)
- internal model performance assessment calculation of model performance statistics directly

by the same data that are used to parameterise the model (= 'verification')

interspecific interactions — interactions between individuals of different species that bring about change in the performance of one or both species relative to their physiological potential

- limited physiological tolerance extrinsic processes which reduce the performance of a species compared to its physiological potential
- local ecocline parallel variation in species composition and important environmental factors (edaphic, moisture-related etc.), typically with large variation at spatial scales of 1 km or finer; under the assumption of no change in type or magnitude of human influence, or other condition or impact ecoclines, patterns will remain more or less unchanged for centuries or millennia
- local scales spatial scales comparable with those that are addressed by samples with extent-grain ratio of 16 and linear grain of 10^{0} – 10^{3} m, i.e., 1–1 000 m
- magnitude response effect on the value for aggregated performance at each point along the gradient within the tolerance limits of the species
- major complex-gradient the few, usually one, two or three, complex-gradients that account for most of the variation in species composition that can be explained environmentally mean abundance — the average of abundance values for a set of observation units
- medium local scale spatial scales comparable with those that are addressed by samples with extent-grain ratio of 16 and linear grain of $10^{1}-10^{2}$ m, i.e., 10-100 m
- micro scale spatial scales comparable with those that are addressed by samples with extentgrain ratio of 16 and linear grain < 10^{0} m, i.e., < 1 m
- migration massive and/or long-term dispersal into new sites which brings about changes in a species' extent of occurrence
- model a description in words, by diagrams, or in mathematical or statistical terms of how one phenomenon (in statistical terms, represented by the response variable) is related to one or more other phenomena (represented by one or more explanatory variables)
- model calibration assessment of the numerical accuracy of model predictions
- model evaluation assessment of model performance by use of data not directly used to parameterise the model (= external model performance assessment, = 'validation' sensu some authors)
- model parameterisation estimation of model parameters (= model estimation, = training of the model, = model 'calibration' sensu some authors)
- model selection application of procedures that assist choice among alternative models
- model specification specification of a mathematical function that expresses how the response variable is related to the independent variables

modelled target — a specific type of observable objects, subjected to (distribution) modelling mutualism — (+,+) interactions to the benefit of both organisms

- observation unit (de)limited areas or volumes in a field site or in the laboratory for, or within which, information about a phenomenon is collected (= raw observation units)
- observed presence occurrence of the modelled target in an observation unit, as contrasted with observation units in which nothing is known about eventual presence or absence of the target
- optimal distribution model distribution model which summarises all variation in the distribution of the modelled target and thus perfectly predicts its distribution
- optimum the gradient position at which the response curve peaks
- overall ecological response variation in a species' aggregated performance with respect to any variable that may be used as axis in the discrete or continuous ecological variables spaces or in ecological space

overfitted model — a distribution model that fits more complex overall response curves than appropriate, given the modelling purpose

parametric spline — one derived predictor variable which is used to represent an explanatory variable to which the response variable may have a complex, non-linear relationship

parasitism — symbiotic (+,-) relationships by which one organism (the parasite) is dependent on another (the host) for nutrient supply and the outcome for the host is negative but not lethal

performance — collective term for the quality (presence or absence) and, eventually also, the quantity, of a natural phenomenon within one observation unit

performance distribution bias — systematic deviation of aggregated performance of the modelled target along environmental gradients, as estimated by use of a sample, from the true distribution of aggregated performance

performance measure — variable used to record performance

- predicted probability of presence predictions from a distribution model, expressing the probability (on a 0-1 scale) that the modelled target is present
- prediction modelling collective term for ecological response modelling and spatial prediction modelling
- presence occurrence of the modelled target in an observation unit, as contrasted with absence
- presence/absence data sample of observation units in which presence or absence of a modelled target is recorded
- presence-only data samples of observation units in which presence is recorded for some observation units while nothing is known about eventual presence or absence in the remaining, uninformed background, observation units
- prevalence the modelled target's frequency of presence in a study area (= occupancy)
- profile technique methods that make predictions from properties of presence data points alone
- projective distribution modelling distribution modelling with the main purpose to transfer model predictions to a spatiotemporal setting different from the one at which the data used for modelling were collected
- proximal factor environmental factor which brings about variation in species' performance
- ranging linear rescaling of a variable onto a scale with minimum value = 0 and maximum value = 1
- rasterisation the process of dividing geographical space, or a subset of this space, into grid cells
- rasterised geographical space geographical space, or a subset thereof, divided into grid cells
- regional ecocline parallel variation in species composition and macroclimatic factors, typically with large variation at spatial scales of 1 km or broader; under the assumption of no change in type or magnitude of human influence, or other condition or impact ecoclines, patterns will remain more or less unchanged for centuries or millennia
- regional scales spatial scales comparable with those that are addressed by samples with extent-grain ratio of 16 and linear grain of 10^3 – 10^6 m, i.e., 1–1 000 km

regular hexadecadal grid — grid with 256 grid cells in a 16 ×16 pattern

- relative predicted probability of presence predictions from a distribution model, expressed on an arbitrary scale
- representativity for the range of model predictions that, within the range of model predictions, each interval of unit width along the scale at which predictions are expressed, is
equally well covered by the sample

representativity in environmental variables space — that each interval of unit length along each environmental explanatory variable of interest is equally well covered by the sample

- representativity in geographical space that every potential observation unit in the study area has the same probability for being sampled
- resilience rate by which initial values of a relevant variable is restored when former perturbation of environmental conditions is reversed

resistance — the magnitude of change in a species' performance in response to a certain amount of perturbation of environmental conditions

- response curve model for a modelled target's overall ecological response with respect to a gradient
- response variable a variable used to characterise a modelled phenomenon (= training data, dependent variable)
- reversibility the tendency for a species' performance to return to the initial magnitude when a former perturbation of environmental conditions is reversed
- sample set of observation units collected to represent a phenomenon under study
- sampling methods and procedures used to acquire information about the phenomenon under study
- shrinkage method model selection method by which the model coefficients are shrunk by imposing a penalty on their magnitude
- space limitation stochastic effects brought about by limitations on the number of individuals, of the same or different species, that can co-occur in an observation unit of a given, small, size
- spatial domain the range, along the scale of metric units, that can be addressed by analysis of a given sample
- spatial extent the size, in geographical space, of the area within which observation units that make up a sample are collected
- spatial grain the size, in geographical space, of one observation unit (= grain)
- spatial interpolation use of models to estimate unknown variable values from observations in georeferenced points
- spatial prediction modelling distribution modelling with the main purpose of optimising the fit between model predictions and the true distribution of the modelled target's performance in the study area in the time interval data were collected
- spatial scale linear grain sizes in samples with extent-grain ratio of 16, typically exemplified by regular hexadecadal grids
- spatial scale interval in which variation is large the range of spatial scales, within which, by analysis of samples with extent-grain ratio of 16, the variation in a variable of interest is distinctly larger than in samples with smaller or larger grain sizes
- species response curve model for a species' overall ecological response with respect to a gradient
- specific-purpose ecological response modelling to describe and understand distributional variation at relevant scales, with regard to a specific set of explanatory variables
- stability the tendency for initial values of a relevant variable to be restored when former perturbation of environmental conditions is reversed
- stress external constraints which limit the rate of dry matter production
- structuring process ecological process which influences species' overall ecological responses to important environmental complex-gradients
- subplot frequency fraction, or percentage, of subplots into which an observation unit is divided, in which a species is present

- subset selection method model selection method by which a discrete subset of predictors is selected and the rest discarded
- targeted response variable a variable used in (distribution) modelling to characterise the modelled target
- target-group background observations background observations with similar bias as observed presence observations, chosen to reduce performance distribution bias
- temporal extent the length of the time interval represented in a sample of observation units
- temporal grain the length of the time interval during which data from one observation unit are collected
- threshold response the situation by which a small change in an environmental factor triggers a large but predictable response
- tolerance the range along a gradient in which the modelled target occurs
- transformation the mathematical operation by which one of several independent variables are derived from a raw explanatory variable
- Type I overfitting that a more complex model has lower predictive performance on independent data than a simpler model
- Type II overfitting that a more complex model is similar in predictive performance on independent data than a simpler model
- Type III overfitting that a more complex model with slightly higher predictive performance on independent data than a simpler model fails to fit realistic overall ecological response curves
- uninformed background observation unit observation unit in which nothing is known about eventual presence or absence of a target
- units subjected to analysis units derived from a set of (raw) observation units, subjected to data analysis
- variation component the variation associated with each unique source of variation in a variation partitioning analysis
- within-population demographic processes processes which determine the fate of individuals, which give rise to occurrence patterns at spatial scales finer than the normal patch size of populations of the species in question

APPENDIX II: INDEX

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