



Using dynamic vegetation models to simulate plant range shifts

R. S. Snell, A. Huth, J. E. M. S. Nabel, G. Bocedi, J. M. J. Travis, D. Gravel, H. Bugmann, A. G. Gutiérrez, T. Hickler, S. I. Higgins, B. Reineking, M. Scherstjanoi, N. Zurbriggen and H. Lischke

R. S. Snell (*rebecca.snell@usys.ethz.ch*), H. Bugmann and A. G. Gutiérrez, *Forest Ecology, Inst. of Terrestrial Ecosystems, Dept of Environmental Systems Science, ETH Zürich, CH-8092 Zürich, Switzerland. AGG also at: Inst. de Conservación Biodiversidad y Territorio, Facultad de Ciencias Forestales y Recursos Naturales, Univ. Austral de Chile, Casilla 567, Valdivia, Chile.* – A. Huth, *Dept of Ecological Modeling, Helmholtz Centre for Environmental Research – UFZ, DE-04319 Leipzig, Germany.* – J. E. M. S. Nabel, M. Scherstjanoi, N. Zurbriggen and H. Lischke, *Dynamic Macroecology, Landscape Dynamics, Swiss Federal Inst. for Forest, Snow and Landscape Research WSL, Zürcherstr. 111, CH-8903 Birmensdorf, Switzerland. JEMSN also at: Dept of Environmental Systems Science, Swiss Federal Inst. of Technology ETH, Universitätstrasse 16, CH-8092 Zürich, Switzerland.* – G. Bocedi and J. M. J. Travis, *Inst. of Biological and Environmental Sciences, Univ. of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen, AB242TZ, UK.* – D. Gravel, *Dépt de biologie, chimie et géographie, Univ. du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC G5L 3A1, Canada.* – T. Hickler, *Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, DE-60325 Frankfurt am Main, Germany, and Goethe Univ., Dept of Physical Geography, Altenhöferallee 1, DE-60438 Frankfurt am Main, Germany, and Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, DE-60325 Frankfurt am Main, Germany.* – S. I. Higgins, *Botany Dept, Univ. of Otago, PO Box 56, Dunedin 9054, New Zealand.* – B. Reineking, *Irstea, UR EMGR Ecosystèmes Montagnards, 2 rue de la Papeterie-BP 76, FR-38402 St-Martin-d'Hères, France, and Biogeographical Modelling, Bayreuth Center of Ecology and Environmental Research BayCEER, Univ. of Bayreuth, Universitätsstr. 30, DE-95447 Bayreuth, Germany.*

Dynamic vegetation models (DVMs) follow a process-based approach to simulate plant population demography, and have been used to address questions about disturbances, plant succession, community composition, and provisioning of ecosystem services under climate change scenarios. Despite their potential, they have seldom been used for studying species range dynamics explicitly. In this perspective paper, we make the case that DVMs should be used to this end and can improve our understanding of the factors that influence species range expansions and contractions. We review the benefits of using process-based, dynamic models, emphasizing how DVMs can be applied specifically to questions about species range dynamics. Subsequently, we provide a critical evaluation of some of the limitations and trade-offs associated with DVMs, and we use those to guide our discussions about future model development. This includes a discussion on which processes are lacking, specifically a mechanistic representation of dispersal, inclusion of the seedling stage, trait variability, and a dynamic representation of reproduction. We also discuss upscaling techniques that offer promising solutions for being able to run these models efficiently over large spatial extents. Our aim is to provide directions for future research efforts and to illustrate the value of the DVM approach.

Understanding and predicting the regional and global distribution of plants is fundamental due to their role in ecosystem functioning (Lavorel and Garnier 2002), carbon storage and release (McGuire et al. 2001), and feedbacks to the global climate system (Sitch et al. 2008). There is still an open discussion about how the current distribution of plants will be impacted by climate change. Global vegetation models already consider shifts in global biome distributions; these models are however based on the simplified assumption that

plants will be able to track rapid climate change (Sitch et al. 2008). This would require some plant species to move over 1 km yr⁻¹ (Loarie et al. 2009), which is particularly unlikely for plants with long generation times, low reproductive rates, or limited dispersal abilities.

This is not to say plants will not migrate at all; range shifts have already been recorded for some plant species in response to on-going climate change (Walther et al. 2005, Jump et al. 2012). However not all plants are shifting their ranges in the way we might have expected: range contractions (Zhu et al. 2012), shifts in the opposite direction (Crimmins et al. 2011), or significant time lags (Bertrand et al. 2011) are just some examples. Range dynamics are transient in space and time, and a variety of factors influence if, when and how species will shift their ranges. Predicting future range shifts

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

requires a better understanding of the processes that influence current distributions, range expansions and contractions.

Species distribution models (SDM) use correlative statistics to relate environmental variables to observed species presence or absence (Guisan and Thuiller 2005). These relationships are then used to project how a species potential habitat niche might shift under different environmental conditions. Although SDMs are the most commonly used tools for evaluating current and future species ranges (Dormann et al. 2012), their limitations and assumptions are also widely acknowledged (Hampe 2004, Heikkinen et al. 2006, Thuiller et al. 2008). SDMs do not explicitly represent the processes that determine the boundaries of the species distribution such as dispersal, demography and biotic interactions (Thuiller et al. 2013). SDMs also assume that species distributions are in equilibrium with the environment, even though range shifts will almost always involve scenarios where species are in disequilibrium with the current climate (Svenning and Sandel 2013). These assumptions cause uncertainty in their ability to predict future range shifts. Therefore, a process-based approach is necessary for understanding the transition phase and how the boundaries of ranges are determined.

Within the SDM field of research, the solution has been to include some processes into existing SDMs (i.e. the hybrid or fitted process-based models), such as dispersal (Engler et al. 2012) and demography (papers in this issue; Dullinger et al. 2012). In this perspective paper, we would like to promote an alternative way forward; improving and using dynamic, process-based, vegetation models to advance our understanding and ability to simulate how processes and interactions influence plant species ranges and their shifts. We aim to do so by: 1) emphasizing why a process-based approach would be beneficial for simulations of species range shifts, 2) evaluating key processes to include and/or improve so as to better simulate range dynamics, and 3) discussing the limitations and methodological challenges associated with using DVMs. We highlight different upscaling approaches using examples, and address the issues of parameterization and model validation. Although DVMs come with their own restrictions, they provide an alternative to SDMs and thus enrich the toolbox for understanding climate change impacts on vegetation.

Dynamic vegetation models (DVMs)

We define a dynamic vegetation model (DVM) as a model that includes processes based on ecological and physiological knowledge of the factors influencing individual plant demography. In particular, the following three points are constitutive for a DVM. First, DVMs simulate more than one species or plant functional type at the same time. Therefore, a fundamental property of DVMs is their explicit treatment of interspecific competition. Second, DVMs simulate the dynamic changes through time in the occurrence, abundance, and productivity of plant species (or functional types). These changes reflect how individual plant performance is influenced by environmental conditions, biotic interactions (mostly resource competition, but some models also include herbivory), and disturbances. Third, plant population dynamics and demographic rates are not prescribed but are instead emergent properties of these models. DVMs simulate

the processes and interactions shaping plant demography; including reproduction, growth, recruitment and mortality.

Using a dynamic model with multiple interacting processes has several advantages for studying plant range shifts. First, species presence or absence at a particular site is a direct consequence of interactions with lower-level processes and higher-level constraints such as the physiological response to the environment, dispersal limitations, biotic interactions, and even historical contingencies if management is taken into account (Schumacher and Bugmann 2006). Including multiple processes and their interactions is important to capture non-linear and non-additive relationships (Wu and David 2002). Second, a process-based approach is flexible to the development of novel interactions under new environmental conditions. For example, species respond to climate independently of each other (i.e. species migrate, not communities; Huntley 1991) which could lead to non-analog communities with unknown behavior in the future (Williams and Jackson 2007). Third, the dynamic nature of DVMs allows us to address questions about when and how range shifts will occur. DVMs can account for long-term, transient ecological processes like succession (Hickler et al. 2012, Bodin et al. 2013), as well as lags caused by dispersal limitation (Normand et al. 2011) and biotic interactions (Svenning et al. 2014). Finally, it is likely that different processes are important at the leading versus trailing edge of a migrating species (Thuiller et al. 2008). For long lived organisms such as trees, consideration of longevity, plasticity and tolerance can be particularly important for understanding local extinction rates at trailing edges, which in turn influence the advancement of other species.

Despite their potential, only a few studies have used DVMs to study range shifts explicitly. Scheller and Mladenoff (2008) used LANDIS-II to illustrate that the future northward migration of tree species in northern Wisconsin may strongly be limited by interspecific competition and landscape fragmentation. TreeMig simulated species range shifts along transects through Siberia and the Alps under future climate change (Epstein et al. 2007, Nabel et al. 2013) and for parts of Switzerland under Holocene conditions (Lischke et al. 2006). LPJ-GUESS simulated vegetation range shifts for Sweden (Koca et al. 2006) and Europe (Hickler et al. 2012), however these simulations assumed unlimited seed dispersal.

While increasing complexity can be an advantage, it may be an important reason why DVMs are not used as frequently to study range shifts. Complex models are difficult to parameterize and approach the limits of current computational resources. The addition of processes and parameters makes it hard to evaluate error propagation, to understand the different sources of uncertainty, and their relative importance. Including processes also requires a good understanding of the underlying mechanisms, which is not always available. Finally, DVMs were not necessarily designed to study range dynamics explicitly and thus may be limited in their extent or comprehensiveness, or lacking important processes such as seed dispersal, which can have strong consequences for simulating range dynamics. We address some of these limitations below.

We use a sample of DVMs covering all four categories (Box 1, Table 1) to illustrate the variation in the models available, and point to the gaps and processes that are

Dynamic global vegetation models (DGVMs) simulate biogeochemical cycles, vegetation distribution, structure and the ecological processes and disturbances that determine the balance between different plant types, such as establishment, competition, growth and mortality (Cramer et al. 2001). DGVMs include feedbacks between the atmosphere and land surface, and are often coupled with General Circulation Models to simulate the global climate. DGVMs typically do not simulate individual species, but group similar species into plant functional types (PFTs). DGVMs were designed to predict global or continental distributions of biomes, carbon pools and fluxes.

Hybrid DGVMs combine the generalized ecophysiological process representations of DGVMs with the detailed patch-scale population dynamics of forest gap models (Sato et al. 2007, Scheiter and Higgins 2009). This structure allows these models to simulate vertical structure and competition for light within a grid cell, as well as more realistic representations of mortality, gap formation and succession. Hybrid models are often applied over smaller areas at a finer resolution compared to DGVMs, which means the PFTs can be parameterized to better represent regional vegetation or individual species (Hickler et al. 2012).

Forest gap models simulate forest dynamics at the stand scale (typically, several hectares) by considering tree population dynamics on multiple patches. They include individual-based calculations of tree growth, competition for light, space and water, regeneration, and mortality as functions of the abiotic environment (climate, soil). The death of a large tree creates a gap in the canopy, which causes increased growth and recruitment in understory trees and results in forest succession (Bugmann 2001). Forest structure is derived by averaging the properties simulated at several patches, usually representing spatial scales > 10 ha. Spatially explicit forest gap models include additional spatial interactions and processes such as seed dispersal, spread of disturbances or competition from neighboring grid cells (e.g. FORMIND, Köhler and Huth 2007; reviewed by Bugmann 2001).

Forest landscape models often apply upscaled versions of forest gap models over a grid-based landscape (typically, several 100 to 10 000 ha) by selecting a range of methods and processes to upscale. TreeMig, for example, uses a height structured description of tree populations and includes seed production and dispersal (Lischke et al. 2006). LandClim is an example of a spatially explicit, stochastic landscape model; it simulates processes at the patch scale (i.e. growth and mortality) on annual time steps, whereas landscape-scale processes (i.e. disturbances, harvesting, and seed dispersal) are simulated in decadal time steps (Schumacher and Bugmann 2006).

typically present or missing from DVMs. We refer to Bugmann (2001), Lischke (2001), Scheller and Mladenoff (2007), and Quillet et al. (2010) for a more comprehensive review of DVMs.

Important elements for simulating range dynamics

All DVMs include formulations of the main ecological processes determining plant population dynamics, specifically

reproduction, establishment, growth and mortality (Table 2). Each of these processes is influenced by the environment, plant physiology, competition, community structure, and subject to trait variability and selection (Fig. 1). The representation of these processes however differs greatly among models. Some of these processes, such as reproduction and establishment, are currently included as very simple formulations. Additionally important processes, such as seed dispersal and trait variability, are only included in a few DVMs (Table 2). We have chosen to focus on these four processes since we believe they could be

Table 1. Additional details about the models used as examples in the text. An 'x' means the processes is included (in parentheses, if only in a rather limited way), and a blank means the process is not included. Cell sizes and spatial extent refer to applications so far, which are mostly flexible and depend on the availability of environmental input data. Subscripts: ¹Sitch et al. (2003), ²Scheiter and Higgins (2009), ³Snell (2014), ⁴Scherstjanoi et al. (2013), ⁵Lischke et al. (2006), ⁶Schumacher and Bugmann (2006), ⁷Köhler and Huth (1998).

	Dynamic vegetation model							
	DGVM		Hybrid DGVM			Forest landscape model		Forest gap model
	LPJ-DGVM ¹	aDGVM ²	LPJ-GUESS ¹	LPJ-DISP ³	LPJ-Gappard ⁴	TreeMig ⁵	LandClim ⁶	FORMIND ⁷
Reproduction	x	x	x	x	x	x	x	x
Dispersal				x		x	x	x
Establishment	x	x	x	x	x	x	x	x
Reaching maturation (determined by)		age		age		tree height	age	stem diameter
Trait variability	(x)	x	(x)					
Grid cell resolution	~55–300 km	1 ha stand on a 37 km grid	30 m–200 km	18 km	1 km	25 m–1 km	25 m	20 m
Extent	global	Africa	forest stand to global	eastern North America	Switzerland 70 000 km ²	Switzerland 70 000 km ²	500 km ²	500 km ²
Temporal scale	day to year	day to year	day to year	day to year	day to year	year	year to decade	day to year
Number of species or PFTs	9 PFTs	4 PFTs but variability within those types	16 species and PFTs	10 species and PFTs	15 species	30 species	30 alpine species, 4 New Zealand species	up to 400 species (grouped in 5–15 PFTs)

Table 2. General descriptions of how each process is typically represented in different model types (Box 1). For every model type, there will be exceptions however the aim of this table is to identify the common trends.

Processes	Dynamic vegetation model type			
	DGVM	Hybrid DGVM	Forest landscape model	Forest gap model
Reproduction	Percentage of carbon allocated to seeds.		Parameter based on size and/or species.	Parameter based on size and/or species.
Dispersal	Perfect dispersal. ⁺	Perfect dispersal for most, otherwise a fixed species (or PFT) dispersal kernel.	Fixed species (or PFT) dispersal kernel.	Fixed species (or PFT) dispersal kernel.*
Establishment	Climatically suitable PFTs establish uniformly as small trees.	Climatically suitable PFTs establish as small trees, abundance depending on environmental conditions at forest floor and (in some cases) in proportion to adult density.	Landclim – parameter based on species and landcover type, influenced by climate, soil, and light. TreeMig – filters for germination and seedling survival, young tree growth and survival with species specific parameters.	Species specific parameters for actual evapotranspiration, light and degree-day sum determine the species which could establish. Establishment is then a stochastic process from that pool, limited by a maximum number of small trees per area.
Individual tree growth	Plant physiology approach: carbon uptake based on photosynthesis, respiration, and allometric scaling (dynamic partitioning for aDGVM).		Species specific growth rate, influenced by light, growing degree days and drought.	Species specific growth rate, influenced by light, growing degree days and drought. Some gap models take a plant physiology approach and simulate growth as an emergent outcome (e.g. FORMIND, similar to DGVMs).
Competition		Competition for light, water, nutrients and space**		
Disturbances	Fire	Small gaps created by single tree death and large gaps by stand-replacing disturbances Fire, herbivory	Fire, wind, herbivory, management	Fire, wind*, landslides*, management

⁺ Perfect dispersal is the assumption that seeds can arrive at any suitable location regardless of absolute distance or barriers.

*Only in spatially explicit forest gap models. **For every DVM type, there are some models which include nutrient competition and some which do not.

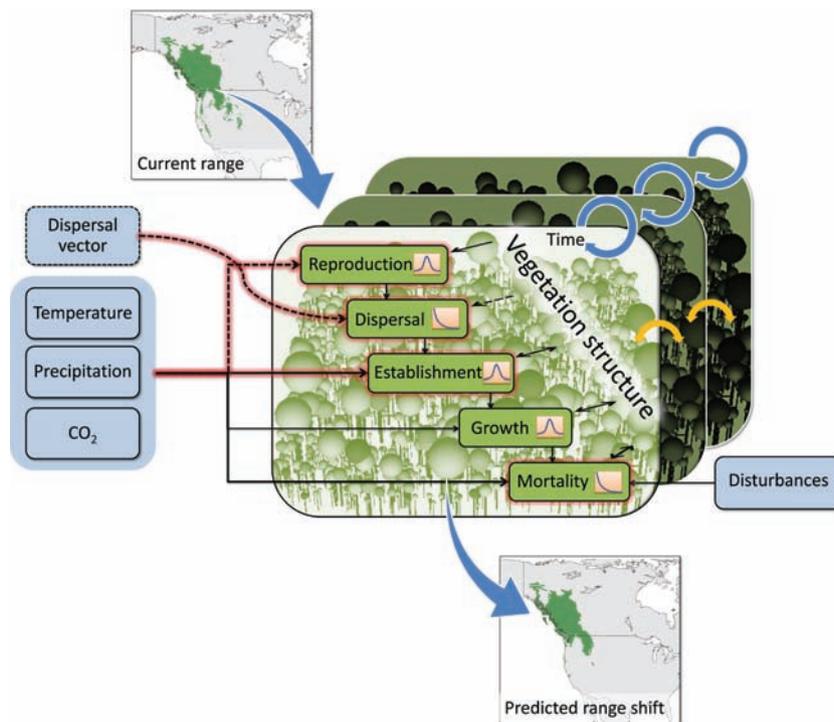


Figure 1. The interaction between processes in dynamic vegetation models (DVMs) and how they could be used for studying species range shifts. Each grid cell within the species range (represented by the large box) interacts with the neighbouring cells (yellow arrows). For each grid cell, a variety of processes are simulated (represented by the small green boxes). Blue boxes represent input, and the transfer of information is shown with arrows. Solid lines show the processes/links which are typically included in the DVMs, and dotted lines indicate the processes/links which should be added. Highlighted in red, are the processes which are discussed in more detail in the text. The frequency distributions inside each box indicate trait variability. The image of forest structure is from FORMIND (Köhler and Huth 1998), the upper map uses distribution data from Little (1971) and was generated in R (<<http://CRAN.R-project.org/package=maps>>).

better represented in DVMs, and would be particularly beneficial for the future application of DVMs to simulate species' range dynamics.

Reproduction

Plant reproductive effort is known to vary as a function of age and size (Thomas 2011) and environmental conditions (Ladeau and Clark 2006, Bykova et al. 2012). The onset of reproduction, or maturation age, can also be influenced by abiotic factors (Sakai et al. 2003). As variations in plant reproduction affect migration rates (Clark et al. 2001) and species distributions (Bykova et al. 2012), it is important to include these relationships in DVMs.

All DVMs include some representation of reproduction, but the implementation varies strongly between models (Table 2). In general, PFT or species-specific parameters describe seed or propagule production and the onset of reproduction (Table 1, 2). For example in TreeMig and FORMIND, the onset and amount of seed production is determined by tree height and species (Lischke et al. 2006, Köhler and Huth 2007). Alternatively, in LPJ-GUESS and aDGVM propagule production is, at least partly, a function of assimilated carbon or net primary productivity. In both cases, larger or more productive plants produce more seeds than smaller plants. As growth is determined by environmental conditions, reproduction is only indirectly influenced by external factors. It would be relatively simple to replace the existing reproduction parameters with functions that more directly relate seed production to plant characteristics such as age, and environmental factors such as temperature and precipitation, provided the required empirical data are available. For example, a dynamic carbon allocation approach has already been adopted in aDGVM (Scheiter and Higgins 2009) for partitioning among roots, stems and leaves depending upon environmental conditions, and could be adapted to include reproduction.

Using dynamic calculations for reproductive rates would allow DVMs to simulate some additional effects of global change on plant range dynamics. When grown under elevated CO₂, trees may reach reproductive maturity at smaller sizes, younger ages and allocate more to reproduction (Ladeau and Clark 2006). If future climate change and increased CO₂ modify life history strategies, we may expect to see faster migration rates (i.e. younger maturation age and higher fecundity) although potentially at the cost of shorter life spans (Sakai et al. 2003, Bugmann and Bigler 2011).

Interannual variability in reproduction may have important consequences for the dynamics of range expansions (Mustin et al. 2013). A direct link between reproduction and climate would also allow DVMs to simulate masting in a more mechanistic way (as opposed to a simple mast frequency based on average occurrence intervals). In nature, the occurrence of a masting event is related to large scale climatic cues, such as high summer temperatures during ENSO events (Koenig and Knops 2005). Increasing temperature is expected to result in more frequent mast events (Schauber et al. 2002) whereas

decreasing precipitation will likely reduce mast frequency (Perez-Ramos et al. 2010). If reproductive effort was directly linked to plant performance under varying climate, DVMs could be used to investigate hypotheses about the influence of climate change on mast frequency and resulting effects on species range shifts.

Dispersal

The dispersal characteristics of a plant species are a key determinant of how likely it is to track climate change (Bullock et al. 2012) and any predictive model of transient range dynamics at large scales should include this process. DVMs have typically assumed that the colonization of new sites is not limited by dispersal; seeds of all species (or functional types) arrive every year in every simulated grid cell if the environmental conditions allow establishment. This assumption is justifiable when projecting potential equilibrium vegetation under alternative climate scenarios, or when simulating successional dynamics at a local scale where dispersal limitation is unlikely. The few DVMs that explicitly include seed dispersal use a fixed species/PFT-specific dispersal kernel (Table 2). However, the distribution of the distances travelled by seeds can be sensitive to wind conditions (Stephenson et al. 2007) or to the behavior and composition of animal dispersal agents (Morales et al. 2013). Importantly, this variability can have a non-linear effect on population spread rates (Bullock et al. 2012). There is an urgent need to integrate emerging approaches for modeling both wind and animal dispersal of seeds into DVMs to better simulate transient range dynamics.

Mechanistic models are now available for simulating wind dispersal (Kuparinen 2006, Nathan et al. 2011). For local scale simulations, fine scale resolution models that explicitly simulate air flow and turbulence (Thompson and Katul 2013) might be useful for capturing seed dispersal and range dynamics along altitudinal gradients. For larger spatial extents, models such as WALD (Katul et al. 2005) could provide new possibilities. WALD requires minimal parameters that are relatively straightforward to collect (e.g. seed release height and seed terminal velocity), is computationally efficient and retains links to key mechanisms involved in seed transport by wind. WALD has also been shown to perform well in capturing rare, long-distance dispersal events (Katul et al. 2005) that are most important for range shifts (Clark et al. 2001).

Significant progress has recently been made in modeling seed dispersal by animals (Nathan et al. 2008, Bullock et al. 2011). At a relatively small spatial extent, the realized dispersal kernel could emerge from the DVM based on simulated interactions between seed properties, animal characteristics (e.g. gut retention time, fur adhesion time), distribution and the spatial structure of the environment. The explicit consideration of animal seed dispersal could significantly alter migration rates if there is a spatial mismatch between the plant and the disperser. The coupling with DVMs could be achieved using a hierarchical approach, where dispersal kernels would be generated using a mechanistic model for the specific landscape characteristics of the local grid cell.

One important consideration will be the thematic resolution of plants (i.e. species or PFTs) and knowledge about their seed dispersal vectors. Simulating the range dynamics at a species level would require a model to describe the specific vector that is known to be the most important dispersal agent for each species, as well as simultaneously requiring a distribution model for the specific dispersing agents. However, for DVMs that use a PFT resolution, it may be more appropriate to use 'seed dispersal types' (Vittoz and Engler 2007), where each dispersal type uses a more generic dispersal pattern (e.g. movement rules or landscape-dependent kernel).

It will be relatively straightforward, albeit computationally expensive, to incorporate such mechanistic dispersal modules. The advantage is that DVMs will readily incorporate the effect of climate (Bullock et al. 2012, Travis et al. 2013) and landscape contingencies (Carlo et al. 2013) on seed dispersal, rather than simply assuming a fixed distribution kernel.

Establishment

Plant establishment in new areas is a crucial step for range expansion (Germino et al. 2002, Körner 2012). Seedlings are small (commonly < 15 cm high), and thus respond to environmental variability at a much smaller scale, exhibit different environmental sensitivities and react faster to environmental stress than older trees (Barbeito et al. 2012). Factors specifically important for seedling success are microclimate and microtopography (Scherrer and Körner 2010), facilitation and competition by ground vegetation (Germino et al. 2002, Venn et al. 2009), herbivory (Myster 2009), and nutrients (Zurbriggen et al. 2013). Due to the large number of seedlings and the large degree of stochasticity in this stage, DVMs usually simulate establishment as the transition of a young tree above a threshold size, such as minimum tree diameter in FORMIND (e.g. stem diameter of 10 cm; Köhler and Huth 2007) or minimum tree height in TreeMig (e.g. height above 1.37 m; Lischke et al. 2006). This implies that the seedling stage is not explicitly included, and most DVMs would require an additional size or age class to distinguish seedlings from older trees (Wehrli et al. 2007, Zurbriggen et al. 2013). As seedlings may have different environmental constraints, the transition from the seedling to later stages should be represented more explicitly in DVMs.

For example, a refined submodel for regeneration that included herbivory and shading was found to improve simulated species composition and successional dynamics in a forest gap model (Wehrli et al. 2007). Thus, submodels that focus on the establishment phase and simulate seedlings as individuals (Peringer and Rosenthal 2011) could be used as part of a stochastic, multi-scale approach. Seedlings would be simulated at a fine scale and adult trees at coarser spatial and temporal resolutions. Alternatively, it may be more efficient to use these complex individual-based models to upscale the processes and their influencing factors (see upscaling section below). Although the establishment phase is a crucial step in range shifts, the large variability in this stage can make it difficult to establish clear relationships between environmental factors and establishment success

(Meiners et al. 2000). More experimental studies and novel parameterization techniques will improve our ability to model plant establishment.

Trait variability

Individual plants can show large variability in traits, both within and between populations. Theoretical evidence suggests that ignoring intra-specific variability may cause substantial errors in projections of species range dynamics (Atkins and Travis 2010, Bocedi et al. 2013). Local adaptation, phenotypic plasticity and blocking effects by maladapted individuals (Borges 2009) could influence the rate of species range expansions, contractions and local extinctions. Traditionally, DVMs have not explicitly treated variability, plasticity or heritability of traits: species (or PFTs) have one set of parameters that is applied to every individual. However, some traits in these models vary in response to climatic conditions, such as the leaf to fine root ratio, leaf nitrogen content and leaf area to sapwood cross-sectional area ratio (Sitch et al. 2003, Hickler et al. 2006), and the aDGVM2 model even allows each individual to have a potentially unique set of traits (Scheiter et al. 2013). Due to the likely importance of trait variability for range dynamics, we propose several approaches that could be used to incorporate intra-specific (or intra-PFT) variability in DVMs.

The first approach is the simplest, and would require minimal or no modifications of the existing DVMs. Each species (or PFT) would be composed of a finite set of environment types, each of which is locally adapted to different environmental conditions. For example, rather than simulating broadleaf evergreen trees as a single PFT where each individual or cohort has the exact same parameters, broadleaf evergreen trees would be simulated as ten PFTs. Each simulated individual would be assigned randomly to one of these ten types that, for example, would range from cool- to warm-adapted, with temperature-adapted base respiration rates (Lavigne and Ryan 1997). Heritability could be coarsely captured by having the offspring retain the identical environmental type as their parent. This assumption could be relaxed to accommodate a situation where heritability is less than 100% by allowing an individual's phenotype to deviate to one of the neighbouring environmental types with a given probability.

A second method would take a quantitative genetics approach. This method assumes that many alleles contribute to variability in local adaptation, but does not explicitly simulate alleles or loci. Each individual or cohort would hold a single quantitative trait value determining the conditions to which it is optimally adapted. Continuous variability in local adaptation to one or more environmental conditions would be allowed, such as a temperature optima and drought tolerance. In the simplest case, offspring would have the same 'environmental condition values' as their parent with some degree of randomness (e.g. values would be drawn from a normal distribution with a mean equal to that of its parent).

A third approach takes advantage of the individual-based structure of some DVMs and allows each individual

to adopt a potentially unique combination of trait values. For example, plants in aDGVM2 are defined by traits that specify the influence of the environment on rates of plant growth, respiration, carbon assimilation and allocation (Scheiter et al. 2013). Individuals with a poor combination of traits die, and those with a better combination survive and reproduce. Tradeoffs between traits prevent the emergence of an individual adapted to all conditions. Inheritance of traits is managed by a genetic optimization algorithm which allows mutation and recombination to define the combination of traits in seeds, while at the same time restricting gene flow to within suites of individuals. The assemblages of plant communities that emerge are adapted to a site's biotic and abiotic conditions (Scheiter et al. 2013).

A fourth method – the most complex, although potentially the most biologically realistic – takes an allelic modeling approach (Schiffers et al. 2013). In this case, a finite number of loci contribute to the degree of local adaptation to particular conditions. A sophisticated genetic architecture (e.g. linkage, epistasis, pleiotropy) underpinning the traits can be incorporated. This fourth option would allow DVMs to generate reliable estimates for the rate of local adaptation. Unfortunately, the information needed to parameterize models to include this degree of ecological genetic realism is not yet available.

In general, parameterizing models that incorporate local adaptation will be a major challenge. However, we anticipate that considerable progress could be made over the next decade using the first three methods. For example, for the first two methods, data from reciprocal transplant or warming experiments can provide the information needed to define population dependent plasticity of physiological traits (Gunderson et al. 2000, Ishizuka and Goto 2012), while species distribution maps or experiments can indicate the range of climatic tolerances for each species. There is also potential for inverse modeling approaches (Hartig et al. 2012) to infer the characteristics of local adaptation. One further challenge when incorporating local adaptation will be in determining the starting conditions for our scenarios. Thus careful thought will be required about the assumptions we make regarding initialization (e.g. in determining the nature of a spin-up).

Important processes that require more information

Above we discussed four processes that we believe need to be improved in DVMs to better simulate species' range dynamics. However, other limiting processes and factors may be of high importance for simulating changes in species' ranges. Tree mortality, for example, is a key process particularly for populations at the trailing edge of species distributions (Jump et al. 2009). Although progress has been made over the past 15 yr in the statistical modeling of tree mortality (Wyckoff and Clark 2002, Bigler and Bugmann 2004, Wunder et al. 2008), the existing models do not lend themselves for integration into DVMs because their structure and parameter values appear to vary in both time and space (Macalady and Bugmann 2014). In addition, the mechanisms underlying global change-induced tree mortality remain hotly debated (cf. McDowell et al. 2013).

Thus, more empirical and theoretical work needs to be done before mortality processes can be represented in DVMs in a meaningful way.

Another example is how rising atmospheric CO₂ levels could affect competition among plants by promoting changes in growth (Dawes et al. 2011) or water-use efficiency in trailing edges (Peñuelas et al. 2008), with strong consequences for range dynamics. In fields such as this, more synthesis work is required that must be based on a solid theoretical basis (Bugmann and Bigler 2011), as additional short-term experiments are unlikely to provide conclusive answers.

Further examples include global warming impacts on seed development, germination and establishment (Milbau et al. 2009), understanding frost tolerance of different plant tissues (Charrier et al. 2013), how changes in growing season length, growing degree-days and chilling temperature will affect plant phenology (Zhao et al. 2013), and the importance of soil processes (Lenka and Lal 2012). Overall, models are a reflection of what we know, and they never will be better than the underlying data and our knowledge about ecological processes. Developing a solid theoretical understanding of the processes briefly reviewed above will allow us to incorporate them into DVMs and improve our ability to predict species range dynamics.

Methodological challenges and how to cope with them

While it is possible to improve existing processes and add more, this can lead to increasingly complex models that are difficult to parameterize. Furthermore, a common requirement for simulating species range shifts is to increase simulated spatial extents, which also increases the computational requirements. As the computational demand can be reduced only partly with technical methods (e.g. parallelization, optimizing the code), we need to consider scaling solutions (Lischke et al. 2007). These are more than a methodological technique, however. They also help to understand how local scale processes effectively influence larger scale community organization.

For our purposes, scaling refers to all methods that change the spatial, temporal or thematic resolution of a model (thematic resolution refers to the description of state variables). Upscaling refers to the derivation of models that operate at coarser resolution (Fig. 2), often with simplified model formulations while retaining the essential information and dynamics of the original model. Upscaling approaches are complicated by the nonlinearity of processes, interactions, feedbacks and heterogeneity, and range from pure or approximated analytical derivations of aggregated model formulae to heuristic assumptions, or the creation of an entirely new model (reviewed by Lischke et al. 2007). In most situations, analytical derivations are not feasible for vegetation models due to the complexity of resource competition. Therefore upscaling is often conducted heuristically, with subsequent tests of the upscaled model against simulations using the original model (Acevedo et al. 1995).

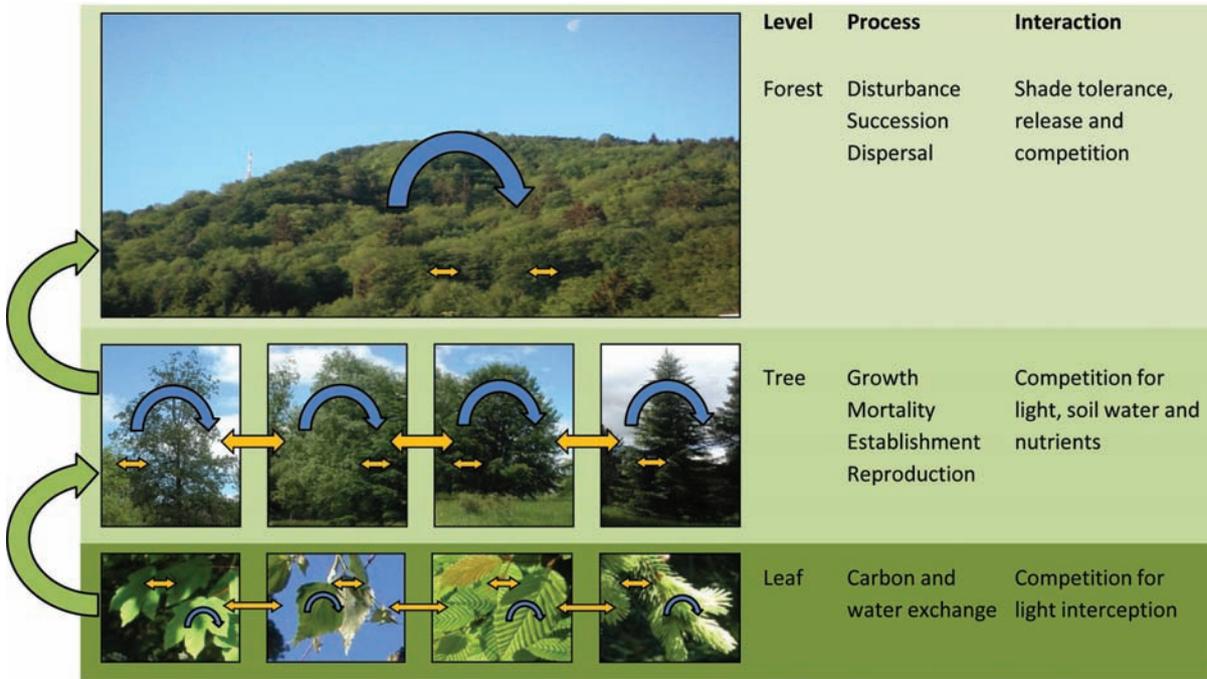


Figure 2. Principle of model upscaling. The rows illustrate the different thematic and spatial scales in a forest. Entities (e.g. leaves or trees) differ among each other and in their spatial position, creating heterogeneity. Blue arrows indicate the dynamics within a level, i.e. temporal changes influenced by the same and other entities. These relationships can lead to feedbacks and are often nonlinear. Yellow arrows show interactions between entities. Higher levels can feed back ('constrain') to lower levels. Green arrows indicate the model upscaling. Upscaling means to derive formulations for the upper level variables, processes and interactions given the lower scale interactions, processes and variables. For example, the formulation of the upper level variables can be the average or sum of the lower level state variables. Photos are courtesy of H. Lischke.

Sophisticated upscaling approaches have the potential for extending the applicability of DVMs but have only started to be applied in this field. Below we discuss some approaches to DVM upscaling, within the scope of improving predictions of range dynamics. Broadly, we divide the approaches into those that decrease spatial resolution versus those that maintain spatial resolution but change thematic or temporal resolution. We end the section by discussing ways to improve model parameterization and evaluate simulation results.

Approach 1: decreasing spatial resolution

There is a strong trade-off between the spatial resolution of DVMs and the spatial extent of the study region (Table 1). DVMs that use a fine grid cell resolution typically operate over a smaller spatial extent (e.g. resolution of 20 m, spatial extent of 500 km²), whereas those that simulate larger areas also have coarser grid cell resolution (e.g. 50 km, spatial extent global). However increasing grid cell resolution is a non-trivial task. DVMs that use coarser resolutions typically simulate a small patch of land (< 1 ha) every 50 km, and assume this small area is representative of the entire grid cell. One of the most important issues is how to handle the loss of information in larger cells, namely within cell heterogeneity of processes and variables, and the impact of their spatial location within the cell on spreading rates.

Within-cell heterogeneity

As cells become coarser, we lose information about fine scale landscape heterogeneity. Naive upscaling of the landscape, such as applying the same model to drivers averaged over coarser cells, can lead to strong systematic biases and impact simulated migration rates by reducing overall dispersal mortality (arrival in unsuitable habitat) and inflating spread rates (Bocedi et al. 2012). If the frequency distribution of a driver (e.g. temperature) within a grid cell is known, the entire model can be run for discrete classes of the driver and then averaged with the frequency distributions (Löffler and Lischke 2001). When there is heterogeneity of the state variables of the model, such as heterogeneity created by population shifts, more sophisticated upscaling methods may be required (e.g. scale transition theory; Melbourne and Chesson 2006).

Within-cell spread

When grid cell resolution is large (> 10 km), as is the case for most DGVMs (Cramer et al. 2001), the fact that the location of individuals within a grid cell is unknown may become problematic. If we assume them to be located in the centre of the cell, seeds are unlikely to disperse outside the grid cell. If we assume them to be homogeneously spread over the cell (e.g. as in TreeMig and LPJ-GUESS), new individuals that arrive would immediately travel the distance across the entire grid cell. Such discretization errors have made it almost impossible, thus far, to represent seed dispersal in coarse-scale model applications in a mechanistic

way. Two approaches have recently been applied in DVMs to represent within cell spread.

Using within-cell patch architecture – each grid cell in LPJ-GUESS contains a number of replicated patches (the size of a patch is usually 1000 m², Fig. 3A), and each patch contains multiple cohorts for each PFT. This within-cell patch architecture was used to simulate dispersal through a grid cell (Snell 2014). New PFTs arrive in a grid cell (cell to cell movement was determined by seed dispersal kernels), and establish in just one patch. Since patches do not have defined locations within the cell, a random spatial distribution of patches was assumed (Fig. 3A) and the plant was considered to have crossed the cell when a certain proportion of patches had been occupied. The rate of this within-cell filling is a classic issue for epidemiology when describing the spread of disease in a population (Berger 1981), and is often solved using a logistic growth function. Following this approach, LPJ-DISP uses a logistic curve to calculate the number of patches who had the potential to receive seeds from a neighbouring patch given a certain percentage of patch occupancy in the grid cell (Fig. 3B). Establishment success within each patch was still dependent on seed production, available space and competition for light. Using this approach, LPJ-DISP was able to realistically simulate plant migration across a test landscape (Fig. 3C; Snell 2014).

Using a meta-modelling approach – DVMs with fine resolution in time and space can be used to simulate plant migration over a small spatial extent using a wide range of initial conditions. Simulation results on the time to cross the grid cell can then be synthesized using statistical functions of migration rates given those initial conditions and local environment. TreeMig has already been used for this purpose; simulated migration rates were related to number of species, drought stress and degree day (Meier et al. 2012) and then used in a species distribution model. Note that a statistical model obtained this way would be restricted by the range of input variables, so caution should be taken when attempting extrapolation to new situations. Although this method requires a considerable amount of computing effort to generate the data, it is a promising upscaling approach.

Approach 2: Simplify state variables and reduce temporal resolution

Maintaining a fine spatial resolution implies that some processes or state variables need to be simplified so as to reduce computational expenses and allow for an increase of the simulated spatial extent. We suggest three potential avenues for doing so.

'One for many' approach

In DVMs, it is common to stratify state variables into more or less homogenous groups, and to simulate only representative units. This strategy is already employed in forest gap models with the cohort approach, where growth is calculated for one individual of the cohort and all individuals in the same cohort are identical (Bugmann 2001). Using PFTs instead of species is another common method

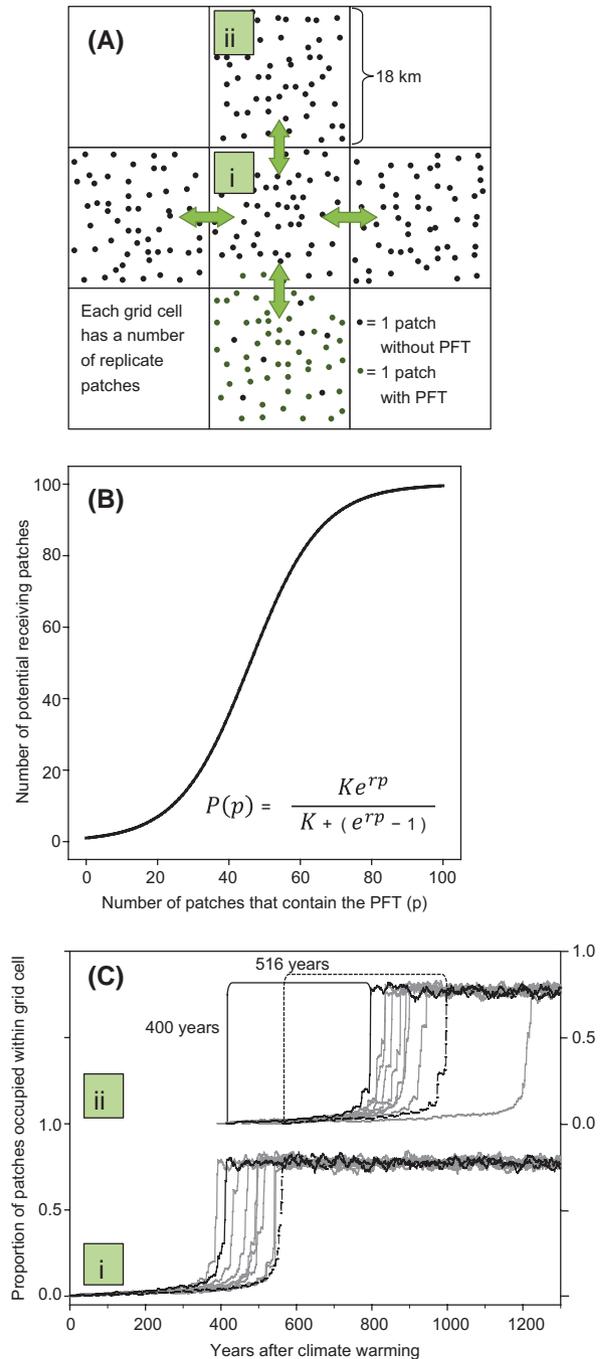


Figure 3. Simulating dispersal within large grid cells in LPJ-DISP (Snell 2014). (A) A sample 3×3 'landscape' of grid cells, each grid cell has a number of replicate patches within. (B) Within cell spread rate (or filling) is determined by logistic curve. It is used to calculate the probability of dispersal between patches, where P is the population of available patches for receiving seeds (i.e. have at least one neighbouring patch that contains the PFT) when there are p patches that contain reproducing adults for that PFT. The carrying capacity, K , is the total number of patches in one grid cell, and r is the spread rate. (C) A sample of 10 simulations, the same 2 grid cells are shown (these would be located in position i and ii in (A)). Each line represents one simulation, the black lines show two of the 10 simulations. In the solid black scenario, it takes 400 yr to cross the one cell (migration rate 45 m yr^{-1}). In the dashed black scenario, it takes 516 yr to cross the same cell (migration rate 35 m yr^{-1}). The average migration rate is 41 m yr^{-1} . The difference between the simulations is caused by stochastic processes and disturbances.

used to simplify thematic resolution (Köhler et al. 2000, Sato et al. 2007). The same idea can be applied to landscapes by simulating only representative cells. Grid cells with similar environmental drivers and species compositions often entail repetitive calculations in grid-based DVMs. To reduce this redundancy, a dynamic two-layer classification (D2C) concept was proposed (Nabel and Lischke 2013). With the D2C concept, the majority of modelled processes are simulated in specific representative cells that constitute a new coarser layer. Only those processes that can lead to cell-specific changes, such as seed dispersal and establishment, are simulated on the original grid. The main challenges of this concept are the organizational overhead required for the assignment and tracking of representative cells. The main benefit is the conservation of detailed small-scale dynamics for simulations with a larger extent.

Simplifying vegetation heterogeneity and stochasticity

Many vegetation models rely on stochastic descriptions of demographic processes and disturbances to create spatial and temporal variability in ecosystems. However, stochastic processes require many replicates to estimate the mean and variance, and ensure adequate scaling properties (Melbourne and Chesson 2006). Several approaches have been developed to avoid these replicates while retaining information about their variability.

Aggregation of vegetation heterogeneity by using distributions – in forest gap models, vertical forest structure is described by cohorts of different heights and stand heterogeneity is maintained by simulating multiple patches at different development stages. Patch-to-patch variability of these properties is essential for shade-intolerant species to persist (Gravel et al. 2010). In TreeMig, the vertical structure was simplified by using height-structured population dynamics. The variability between patches within a grid cell was also simplified, by assuming that all trees within each height class are randomly distributed over the stand. This results in dynamically changing probability distributions of light conditions within the stand, which in turn influence the process rates, and the dynamics (Lischke et al. 1998). This aggregation of individuals strongly reduced the simulation time to just 5% of the original time, which opened the way for a spatially explicit implementation. Such upscaling methods may however introduce errors, such as unrealistically fast height growth and accelerated spread.

Upscaling stochastic disturbances – forest gap models are strongly driven by stochastic stand-replacing disturbances, which require many replicates and increases simulation time. To reduce the simulation effort for disturbances, the GAPPARD upscaling method was developed (Scherstjanoi et al. 2013). GAPPARD uses the output of a single patch simulation with no disturbances from bare ground to determine the succession of patch states after a disturbance. Then, together with the probability distribution of the times since disturbance (on the basis of the disturbance frequency), the expectation value of the disturbed forest's state is calculated at each point in time. To account for temporal changes in model forcing (e.g. as a result of climate change), GAPPARD performs a series of non-disturbed simulations under different environmental conditions and interpolates between the results. Applying

GAPPARD to LPJ-GUESS allowed the model to simulate future climate change impacts at a 1 km resolution for all of Switzerland forests (Scherstjanoi 2013), in 10% of the time compared to LPJ-GUESS with 100 replicate patches yielding similar results. In its current form, GAPPARD is not suitable for simulating dispersal but it could be used for detecting regions of interest in a computationally efficient way before detailed range shift simulations.

Aggregation of temporal resolution

Increasing the length of the (discrete) time step can help speed up models. The effect of temporally variable drivers can be aggregated by long-term expected values for process rates based on the distribution of the variables (Lischke et al. 1997). However, when the timing of the drivers interacts with the model states, such as phenology, a multi-scale approach is preferable. Multi-scale temporal simulations calculate different processes at different time scales, and are already used in most DVMs (Table 1). For example, LPJ-GUESS and FORMIND calculate photosynthesis and water balance on a daily time step, but calculate growth and reproduction on an annual time scale. For simulating range dynamics, each of the processes reviewed above (i.e. reproduction, dispersal, establishment, and trait variability) could be a candidate for temporal upscaling, but more research would be needed. For example, the expensive simulation of wind dispersal (hourly or daily time steps) could be replaced by an upscaled description of migration (annual time steps). A detailed upscaling study would be needed to test if the dynamics at the fine temporal resolution could be adequately captured within a longer time step. It is also important to note that the relevance of temporal aggregation increases with the length of the study period. Paleo-applications, which simulate vegetation shifts after the last glacial maximum (Henne et al. 2011) are particularly good candidates for temporal upscaling, as time scales are long and uncertainty about the interannual variability in climatic reconstructions large (Simonis et al. 2012).

The link to reality: parameterization and validation

DVMs are built from knowledge of the underlying ecological and physiological processes. However, the models are only as good as the data used to feed them. Data are required for model parameterization, external data sets describing environmental conditions, and independent observational data on vegetation to evaluate the simulation results.

The traditional way to parameterize DVMs uses results from field measurements and from the literature to evaluate parameter values for a species or vegetation type. However, parameters based on a specific site or for particular regions can lead to weak model performance if applied outside the area for which they were initially intended (Badeck et al. 2001) because factors not explicitly covered by the model may be masked by parameter values. In addition, within-species plasticity or differences between populations can be similar to or larger than differences between species (Lavigne and Ryan 1997). Such variations need to be accounted for as they could impact simulated migration rates (Nabel et al. 2012).

If we want to use DVMs to simulate species range dynamics, new approaches should be incorporated in parameter calibration to better reflect parameter values across the whole species range. Bayesian methods for model fitting (Purves et al. 2008, Hartig et al. 2012) provide a framework to estimate parameter values or probability distributions of parameter values. They allow the inclusion of field data of different types in the estimation process (van Oijen et al. 2005, Hartig et al. 2012) which increases the quantity of data that can be used for such purposes. In addition to Bayesian methods, further approaches of inverse modelling are available to identify parameter values for which no information or not enough direct information is available. For example, demographic rate parameters in forest gap models can be tuned so that the simulated mature forest corresponds in its biomass, tree density and species composition to real forests (Groeneveld et al. 2009).

Model parameterization will also benefit from the establishment and expansion of large vegetation databases. One example is the TRY database that includes information on life history and physiological attributes of plants (Kattge et al. 2011). Forest inventories are also becoming more available on internet platforms (e.g. USDA forest inventory, French NFF, Smithsonian Inst., Swiss NFI) offering new possibilities to estimate important plant attributes (Purves et al. 2008) and testing model predictions (Hurtt et al. 2010). These databases can also be used to re-evaluate the parameters currently being used in DVMs.

A different approach to parameterization is that adopted by aDGM2 (Scheiter et al. 2013). Here the model focuses on parameterizing general biophysical processes, such as how transpiration rate is influenced by leaf size and each plant has a trait that evolves within the model that defines its leaf size. Ultimately this approach reduces the dimensionality of the parameterization process, since the parameterization process does not define the traits of individuals, but defines the biophysical laws that influence the performance of these trait-states.

Evaluating simulation results is an on-going challenge for modellers, but necessary to determine how well the processes and species have been represented. The first step of a model evaluation is to compare observed vegetation distribution to simulated distribution using modern climate. A combination of plot-based forest inventories, species distribution maps, potential natural vegetation maps, and remotely sensed data could be used to do so. Human impacts on the landscape and disequilibria between climate and distributions (Normand et al. 2011) present a special challenge. Either human impact processes will have to be added to the model (Heiri et al. 2009) or human impact removed from the observational data.

The second step is to evaluate potential range shifts simulated by DVMs. This step is more difficult because the involved processes are slow and operate over large temporal and spatial scales. Independent observational data should ideally represent several time-steps. Pollen-reconstructed landscapes are one option (Williams et al. 2004), as are phenomenological observations of recent altitudinal (Jump et al. 2012) or latitudinal (Walther et al. 2005) shifts of species. Data requirements have always been a challenge for modelling efforts, but recent developments in

parameterization methods and the increasing availability of larger databases will help alleviate some of these limitations.

Future directions

The ability to predict current and future distributions requires an understanding of the processes that influence species range dynamics. Dynamic vegetation models already include many processes that are important for simulating species range dynamics and they provide a tool for improving our understanding of range dynamics even without making any modifications. Most of this paper addresses the processes that are lacking and other limitations when using DVMs. It is difficult to quantify beforehand, the degree to which overcoming these limitations would impact the simulated range shifts within the context of a given research question; this could only be tested by sensitivity analyses and comparing simulations between the extended and original model.

As they currently are, DVMs can offer predictions of range shifts under future climate change that include the effect of demography, competition and disturbances. This should be a vast improvement over null models which assume no impact from biotic interactions. As DVMs simulate changes in vegetation type and structure, they can also be used to describe changes in habitat characteristics that may influence range expansions for other species, such as animals (see Linder et al. 2012 for an overview). DVMs can also generate relationships that can be used by other models. For example, DVMs could record population changes such as establishment, time to transition into new height classes, and mortality. We could use such model output to generate relationships between the environment and population demographic parameters (r , d , and K ; Svenning et al. 2014). DVMs could also be used to estimate the competition matrix for the community of forest tree species, which are used by some SDMs to represent biotic interaction (Kissling et al. 2012).

It would also be very useful to see more studies which simulate a species range shift using both SDMs and process based models (Keenan et al. 2011), or studies which use DVMs to perform a stepwise inclusion of the processes discussed here. These comparisons could be used to analyze the relative influences of different ecological processes and interactions on range dynamics, and could provide a method to evaluate the benefit of increasing model complexity. Such analyses will help to identify knowledge gaps and to direct future empirical and modeling work. DVMs have great potential to contribute to the study of vegetation range dynamics, and we hope to see more of this in the future.

Acknowledgements – This paper arose from two workshops entitled ‘Advancing concepts and models of species range dynamics: understanding and disentangling processes across scales’ for which funding was provided by the Danish Council for Independent Research – Natural Sciences (grant no. 10-085056 to S. Normand). JEMSN and MS have been supported by grants of the Swiss National Science Foundation (SNF 315200-122434) and the COST section of the Swiss State Secretariat for Education, Research and Innovation (SBF C07.0123). AGG was funded by grants

Marie Curie IEF (FORECOFUN-SSA PIEF-GA-2010-274798) and CONICYT-PAI-82130046. We extend a special thanks to Signe Normand for her very helpful comments on an earlier version of this manuscript.

References

- Acevedo, M. F. et al. 1995. Transition and gap models of forest dynamics. – *Ecol. Appl.* 5: 1040–1055.
- Atkins, K. E. and Travis, J. M. J. 2010. Local adaptation and the evolution of species' ranges under climate change. – *J. Theor. Biol.* 266: 449–457.
- Badeck, F. W. et al. 2001. Tree species composition in European pristine forests: comparison of stand data to model predictions. – *Clim. Change* 51: 307–347.
- Barbeito, I. et al. 2012. Factors driving mortality and growth at treeline: a 30-year experiment of 92 000 conifers. – *Ecology* 93: 389–401.
- Berger, R. D. 1981. Comparison of the Gompertz and logistic equations to describe plant-disease progress. – *Phytopathology* 71: 716–719.
- Bertrand, R. et al. 2011. Changes in plant community composition lag behind climate warming in lowland forests. – *Nature* 479: 517–520.
- Bigler, C. and Bugmann, H. 2004. Predicting the time of tree death using dendrochronological data. – *Ecol. Appl.* 14: 902–914.
- Bocedi, G. et al. 2012. Projecting species' range expansion dynamics: sources of systematic biases when scaling up patterns and processes. – *Methods Ecol. Evol.* 3: 1008–1018.
- Bocedi, G. et al. 2013. Effects of local adaptation and inter-specific interactions on species' responses to climate change. – *Ann. N. Y. Acad. Sci.* in press.
- Bodin, J. et al. 2013. Shifts of forest species along an elevational gradient in southeast France: climate change or stand maturation? – *J. Veg. Sci.* 24: 269–283.
- Borges, R. M. 2009. Phenotypic plasticity and longevity in plants and animals: cause and effect? – *J. Biosci.* 34: 605–611.
- Bugmann, H. 2001. A review of forest gap models. – *Clim. Change* 51: 259–305.
- Bugmann, H. and Bigler, C. 2011. Will the CO₂ fertilization effect in forests be offset by reduced tree longevity? – *Oecologia* 165: 533–544.
- Bullock, J. M. et al. 2011. Process-based functions for seed retention on animals: a test of improved descriptions of dispersal using multiple data sets. – *Oikos* 120: 1201–1208.
- Bullock, J. M. et al. 2012. Modelling spread of British wind-dispersed plants under future wind speeds in a changing climate. – *J. Ecol.* 100: 104–115.
- Bykova, O. et al. 2012. Temperature dependence of the reproduction niche and its relevance for plant species distributions. – *J. Biogeogr.* 39: 2191–2200.
- Carlo, T. A. et al. 2013. Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes. – *Ecology* 94: 301–307.
- Charrier, G. et al. 2013. Evaluation of the impact of frost resistances on potential altitudinal limit of trees. – *Tree Physiol.* 33: 891–902.
- Clark, J. S. et al. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. – *Am. Nat.* 157: 537–554.
- Cramer, W. et al. 2001. Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. – *Global Change Biol.* 7: 357–373.
- Crimmins, S. M. et al. 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. – *Science* 331: 324–327.
- Dawes, M. A. et al. 2011. Species-specific tree growth responses to 9 years of CO₂ enrichment at the alpine treeline. – *J. Ecol.* 99: 383–394.
- Dormann, C. F. et al. 2012. Correlation and process in species distribution models: bridging a dichotomy. – *J. Biogeogr.* 39: 2119–2131.
- Dullinger, S. et al. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. – *Nat. Clim. Change* 2: 619–622.
- Engler, R. et al. 2012. The MIGCLIM R package – seamless integration of dispersal constraints into projections of species distribution models. – *Ecography* 35: 872–878.
- Epstein, H. E. et al. 2007. Simulating future changes in Arctic and subarctic vegetation. – *Comput. Sci. Eng.* 9: 12–23.
- Germino, M. J. et al. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. – *Plant Ecol.* 162: 157–168.
- Gravel, D. et al. 2010. Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees. – *Oikos* 119: 475–484.
- Groeneveld, J. et al. 2009. The impact of fragmentation and density regulation on forest succession in the Atlantic rain forest. – *Ecol. Model.* 220: 2450–2459.
- Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. – *Ecol. Lett.* 8: 993–1009.
- Gunderson, C. A. et al. 2000. Acclimation of photosynthesis and respiration to simulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. – *Tree Physiol.* 20: 87–96.
- Hampe, A. 2004. Bioclimatic envelope models: what they detect and what they hide. – *Global Ecol. Biogeogr.* 13: 469–471.
- Hartig, F. et al. 2012. Connecting dynamic vegetation models to data – an inverse perspective. – *J. Biogeogr.* 39: 2240–2252.
- Heikkinen, R. K. et al. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. – *Prog. Phys. Geogr.* 30: 751–777.
- Heiri, C. et al. 2009. Forty years of natural dynamics in Swiss beech forests: structure, composition, and the influence of former management. – *Ecol. Appl.* 19: 1920–1934.
- Henne, P. D. et al. 2011. Did soil development limit spruce (*Picea abies*) expansion in the central Alps during the Holocene: Testing a palaeobotanical hypothesis with a dynamic landscape model. – *J. Biogeogr.* 38: 933–949.
- Hickler, T. et al. 2006. Implementing plant hydraulic architecture within the LPJ dynamic global vegetation model. – *Global Ecol. Biogeogr.* 15: 567–577.
- Hickler, T. et al. 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. – *Global Ecol. Biogeogr.* 21: 50–63.
- Huntley, B. 1991. How plants respond to climate change – migration rates, individualism and the consequences for plant-communities. – *Ann. Bot.* 67: 15–22.
- Hurt, G. C. et al. 2010. Linking models and data on vegetation structure. – *J. Geophys. Res.* 115: G00E10.
- Ishizuka, W. and Goto, S. 2012. Modeling intraspecific adaptation of *Abies sachalinensis* to local altitude and responses to global warming, based on a 36-year reciprocal transplant experiment. – *Evol. Appl.* 5: 229–244.
- Jump, A. S. et al. 2009. The altitude-for-latitude disparity in the range retractions of woody species. – *Trends Ecol. Evol.* 24: 694–701.
- Jump, A. S. et al. 2012. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. – *Ecography* 35: 204–210.

- Kattge, J. et al. 2011. TRY – a global database of plant traits. – *Global Change Biol.* 17: 2905–2935.
- Katul, G. G. et al. 2005. Mechanistic analytical models for long-distance seed dispersal by wind. – *Am. Nat.* 166: 368–381.
- Keenan, T. et al. 2011. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO2 matters! – *Global Change Biol.* 17: 565–579.
- Kissling, W. D. et al. 2012. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. – *J. Biogeogr.* 39: 2163–2178.
- Koca, D. et al. 2006. Modelling regional climate change effects on potential natural ecosystems in Sweden. – *Clim. Change* 78: 381–406.
- Koenig, W. D. and Knops, J. M. H. 2005. The mystery of masting in trees. – *Am. Sci.* 93: 340–347.
- Köhler, P. and Huth, A. 1998. The effects of tree species grouping in tropical rainforest modelling: simulations with the individual-based model FORMIND. – *Ecol. Model.* 109: 301–321.
- Köhler, P. and Huth, A. 2007. Impacts of recruitment limitation and canopy disturbance on tropical tree species richness. – *Ecol. Model.* 203: 511–517.
- Köhler, P. et al. 2000. Concepts for the aggregation of tropical tree species into functional types and the application to Sabah's lowland rain forests. – *J. Trop. Ecol.* 16: 591–602.
- Körner, C. 2012. Alpine treelines. Functional ecology of the global high elevation tree limits. – Springer.
- Kuparinen, A. 2006. Mechanistic models for wind dispersal. – *Trends Plant Sci.* 11: 296–301.
- Ladeau, S. L. and Clark, J. S. 2006. Elevated CO2 and tree fecundity: the role of tree size, interannual variability, and population heterogeneity. – *Global Change Biol.* 12: 822–833.
- Lavigne, M. B. and Ryan, M. G. 1997. Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. – *Tree Physiol.* 17: 543–551.
- Lavelle, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. – *Funct. Ecol.* 16: 545–556.
- Lenka, N. K. and Lal, R. 2012. Soil-related constraints to the carbon dioxide fertilization effect. – *Crit. Rev. Plant Sci.* 31: 342–357.
- Linder, H. P. et al. 2012. Biotic modifiers, environmental modulation and species distribution models. – *J. Biogeogr.* 39: 2179–2190.
- Lischke, H. 2001. New developments in forest modeling: convergence between applied and theoretical approaches. – *Nat. Resour. Model.* 14: 71–102.
- Lischke, H. et al. 1997. Calculating temperature dependence over long time periods: derivation of methods. – *Ecol. Model.* 98: 105–122.
- Lischke, H. et al. 1998. Aggregation of individual trees and patches in forest succession models – capturing variability with height structured random dispersions. – *Theor. Popul. Biol.* 54: 213–226.
- Lischke, H. et al. 2006. TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. – *Ecol. Model.* 199: 409–420.
- Lischke, H. et al. 2007. Model up-scaling in landscape research. – In: Kienast, F. et al. (eds), *A changing world: challenges for landscape research*. Kluwer, pp. 259–282.
- Little, E. L. Jr 1971. Atlas of United States trees, Volume 1, conifers and important hardwoods. – U. S. Dept of Agriculture Miscellaneous Publication 1146.
- Loarie, S. R. et al. 2009. The velocity of climate change. – *Nature* 462: 1052–1055.
- Löffler, T. J. and Lischke, H. 2001. Incorporation and influence of variability in an aggregated forest model. – *Nat. Resour. Model.* 14: 103–137.
- Macalady, A. K. and Bugmann, H. 2014. Growth-mortality relationships in *Pinus edulis* reveal shifting mortality thresholds and climate sensitivity across warmer and cooler droughts. – *PLoS One* in press.
- McDowell, N. G. et al. 2013. Improving our knowledge of drought-induced forest mortality through experiments, observations, and modeling. – *New Phytol.* 200: 289–293.
- McGuire, A. D. et al. 2001. Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO2, climate and land use effects with four process-based ecosystem models. – *Global Biogeochem. Cycle* 15: 183–206.
- Meier, E. S. et al. 2012. Climate, competition and connectivity affect future migration and ranges of European trees. – *Global Ecol. Biogeogr.* 21: 164–178.
- Meiners, S. J. et al. 2000. Tree seedling establishment under insect herbivory: edge effects and interannual variation. – *Plant Ecol.* 151: 161–170.
- Melbourne, B. A. and Chesson, P. 2006. The scale transition: scaling up population dynamics with field data. – *Ecology* 87: 1478–1488.
- Milbau, A. et al. 2009. Effects of a warmer climate on seed germination in the subarctic. – *Ann. Bot.* 104: 287–296.
- Morales, J. M. et al. 2013. Frugivore behavioural details matter for seed dispersal: a multi-species model for cantabrian thrushes and trees. – *PLoS One* 8: e65216
- Mustin, K. et al. 2013. Red noise increases extinction risk during climate change. – *Divers. Distrib.* doi: 10.1111/ddi.12038
- Myster, R. W. 2009. Tree seedling survivorship, growth, and allocation in the Cross Timbers ecotone of Oklahoma, USA. – *Plant Ecol.* 205: 193–199.
- Nabel, J. E. M. S. and Lischke, H. 2013. Upscaling of spatially explicit and linked time and space discrete models studying vegetation dynamics under climate change. – In: Page, B. et al. (eds), *27th International Conference on Informatics for Environmental Protection*. Shaker, pp. 842–850.
- Nabel, J. E. M. S. et al. 2012. Impact of species parameter uncertainty in simulations of tree species migration with a spatially linked dynamic model. – In: Seppelt, R. et al. (eds), *International Congress on Environmental Modelling and Software: Managing Resources of a Limited Planet, Sixth Biennial Meeting International Environmental Modelling and Software Society (iEMSs)*.
- Nabel, J. E. M. S. et al. 2013. Interannual climate variability and population density thresholds can have a substantial impact on simulated tree species' migration. – *Ecol. Model.* 257: 88–100.
- Nathan, R. et al. 2008. Mechanisms of long-distance seed dispersal. – *Trends Ecol. Evol.* 23: 638–647.
- Nathan, R. et al. 2011. Mechanistic models of seed dispersal by wind. – *Theor. Ecol.* 4: 113–132.
- Normand, S. et al. 2011. Postglacial migration supplements climate in determining plant species ranges in Europe. – *Proc. R. Soc. B* 278: 3644–3653.
- Peñuelas, J. et al. 2008. Twentieth century changes of tree-ring delta C-13 at the southern range-edge of *Fagus sylvatica*: increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. – *Global Change Biol.* 14: 1076–1088.
- Perez-Ramos, I. M. et al. 2010. Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. – *Ecology* 91: 3057–3068.
- Peringer, A. and Rosenthal, G. 2011. Establishment patterns in a secondary tree line ecotone. – *Ecol. Model.* 222: 3120–3131.

- Purves, D. W. et al. 2008. Predicting and understanding forest dynamics using a simple tractable model. – *Proc. Natl Acad. Sci. USA* 105: 17018–17022.
- Quillet, A. et al. 2010. Toward dynamic global vegetation models for simulating vegetation–climate interactions and feedbacks: recent developments, limitations, and future challenges. – *Environ. Rev.* 18: 333–353.
- Sakai, A. et al. 2003. Altitudinal variation in lifetime growth trajectory and reproductive schedule of a sub-alpine conifer, *Abies mariesii*. – *Évol. Ecol. Res.* 5: 671–689.
- Sato, H. et al. 2007. SEIB-DGVM: a new dynamic global vegetation model using a spatially explicit individual-based approach. – *Ecol. Model.* 200: 279–307.
- Schauber, E. M. et al. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. – *Ecology* 83: 1214–1225.
- Scheiter, S. and Higgins, S. I. 2009. Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. – *Global Change Biol.* 15: 2224–2246.
- Scheiter, S. et al. 2013. Next-generation dynamic global vegetation models: learning from community ecology. – *New Phytol.* 198: 957–969.
- Scheller, R. M. and Mladenoff, D. J. 2007. An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. – *Landscape Ecol.* 22: 491–505.
- Scheller, R. M. and Mladenoff, D. J. 2008. Simulated effects of climate change, fragmentation, and inter-specific competition on tree species migration in northern Wisconsin, USA. – *Clim. Res.* 36: 191–202.
- Scherrer, D. and Körner, C. 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. – *Global Change Biol.* 16: 2602–2613.
- Scherstjanoi, M. 2013. Towards an efficient plant physiology-based modeling of spatial forest dynamics. – PhD thesis, École Polytechnique Fédérale de Lausanne.
- Scherstjanoi, M. et al. 2013. GAPPARD: a computationally efficient method of approximating gap-scale disturbance in vegetation models. – *Geosci. Model Dev.* 6: 1517–1542.
- Schiffers, K. et al. 2013. Limited evolutionary rescue of locally adapted populations facing climate change. – *Phil. Trans. R. B* 368: 20120083.
- Schumacher, S. and Bugmann, H. 2006. The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. – *Global Change Biol.* 12: 1435–1450.
- Simonis, D. et al. 2012. Reconstruction of late Glacial and Early Holocene near surface temperature anomalies in Europe and their statistical interpretation. – *Quat. Int.* 274: 233–250.
- Sitch, S. et al. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. – *Global Change Biol.* 9: 161–185.
- Sitch, S. et al. 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate–carbon cycle feedbacks using five dynamic global vegetation models (DGVMs). – *Global Change Biol.* 14: 2015–2039.
- Snell, R. S. 2014. Simulating long distance seed dispersal in a dynamic vegetation model. – *Global Ecol. Biogeogr.* 23: 89–98.
- Stephenson, C. M. et al. 2007. Testing mechanistic models of seed dispersal for the invasive *Rhododendron ponticum* (L.). – *Perspect. Plant Ecol. Evol. Syst.* 9: 15–28.
- Svenning, J. C. and Sandel, B. 2013. Disequilibrium vegetation dynamics under future climate change. – *Am. J. Bot.* 100: 1266–1286.
- Svenning, J. C. et al. 2014. The influence of interspecific interactions on species range expansion rates. – *Ecography* 37: 1198–1209.
- Thomas, S. C. 2011. Age-related changes in tree growth and functional biology: the role of reproduction. – In: Meinzer, F. C. et al. (eds), *Size- and age-related changes in tree structure and function*. Springer, pp. 33–64.
- Thompson, S. E. and Katul, G. G. 2013. Implications of nonrandom seed abscission and global stilling for migration of wind-dispersed plant species. – *Global Change Biol.* 19: 1720–1735.
- Thuiller, W. et al. 2008. Predicting global change impacts on plant species' distributions: future challenges. – *Perspect. Plant Ecol. Evol. Syst.* 9: 137–152.
- Thuiller, W. et al. 2013. A road map for integrating eco-evolutionary processes into biodiversity models. – *Ecol. Lett.* 16: 94–105.
- Travis, J. M. J. et al. 2013. Dispersal and species' responses to climate change. – *Oikos* 122: 1532–1540.
- van Oijen, M. et al. 2005. Bayesian calibration of process-based forest models: bridging the gap between models and data. – *Tree Physiol.* 25: 915–927.
- Venn, S. E. et al. 2009. Do facilitative interactions with neighboring plants assist the growth of seedlings at high altitudes in alpine Australia? – *Arct. Antarct. Alp. Res.* 41: 381–387.
- Vittoz, P. and Engler, R. 2007. Seed dispersal distances: a typology based on dispersal modes and plant traits. – *Bot. Helv.* 117: 109–124.
- Walther, G. R. et al. 2005. An ecological 'footprint' of climate change. – *Proc. R. Soc. B* 272: 1427–1432.
- Wehrli, A. et al. 2007. Improving the establishment submodel of a forest patch model to assess the long-term protective effect of mountain forests. – *Eur. J. For. Res.* 126: 131–145.
- Williams, J. W. and Jackson, S. T. 2007. Novel climates, no-analog communities, and ecological surprises. – *Front. Ecol. Environ.* 5: 475–482.
- Williams, J. W. et al. 2004. Late-quaternary vegetation dynamics in North America: scaling from taxa to biomes. – *Ecol. Monogr.* 74: 309–334.
- Wu, J. G. and David, J. L. 2002. A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. – *Ecol. Model.* 153: 7–26.
- Wunder, J. et al. 2008. Growth-mortality relationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged European forests. – *Oikos* 117: 815–828.
- Wyckoff, P. H. and Clark, J. S. 2002. The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. – *J. Ecol.* 90: 604–615.
- Zhao, M. F. et al. 2013. Plant phenological modeling and its application in global climate change research: overview and future challenges. – *Environ. Rev.* 21: 1–14.
- Zhu, K. et al. 2012. Failure to migrate: lack of tree range expansion in response to climate change. – *Global Change Biol.* 18: 1042–1052.
- Zurbriggen, N. et al. 2013. Performance of germinating tree seedlings below and above treeline in the Swiss Alps. – *Plant Ecol.* 214: 385–396.