Methods

Next-generation dynamic global vegetation models: learning from community ecology

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Summary

• Dynamic global vegetation models (DGVMs) are powerful tools to project past, current and future vegetation patterns and associated biogeochemical cycles. However, most models are limited by how they define vegetation and by their simplistic representation of competition.

• We discuss how concepts from community assembly theory and coexistence theory can help to improve vegetation models. We further present a trait- and individual-based vegetation model (aDGVM2) that allows individual plants to adopt a unique combination of trait values. These traits define how individual plants grow and compete. A genetic optimization algorithm is used to simulate trait inheritance and reproductive isolation between individuals. These model properties allow the assembly of plant communities that are adapted to a site's biotic and abiotic conditions.

• The aDGVM2 simulates how environmental conditions influence the trait spectra of plant communities; that fire selects for traits that enhance fire protection and reduces trait diversity; and the emergence of life-history strategies that are suggestive of colonization–competition trade-offs.

• The aDGVM2 deals with functional diversity and competition fundamentally differently from current DGVMs. This approach may yield novel insights as to how vegetation may respond to climate change and we believe it could foster collaborations between functional plant biologists and vegetation modellers.

Introduction

A grand challenge in plant ecology is to understand how climate and vegetation interact to define the past, current and future distribution of vegetation. In principle, this challenge could be addressed by modelling the rate at which individual plants grow, reproduce and die and how these rates are influenced by the plant's traits and the abiotic and biotic environment. A variety of conceptual constructs and associated research programmes have been developed and used to address this challenge. One of these research programmes is the DGVM (Prentice *et al.*, 2007) programme, while another is community ecology (Keddy, 1992; Weiher & Keddy, 1995a,b; Chesson, 2000; Shipley *et al.*, 2006).

Dynamic global vegetation models use ecophysiological principles to model the distribution of plant functional types (Prentice *et al.*, 2007). DGVMs are motivated by two quite different goals. First, these are models for articulating and developing our understanding of the factors that influence past, current and future distribution of vegetation at regional to global scales (Prentice *et al.*, 2007). Secondly, DGVMs have been developed to serve as a component of earth system models, that is, they provide a dynamic representation of the land-surface energy budget and an accounting system for components of global carbon (C) and water budgets (Bonan, 2008).

Dynamic global vegetation models have been used successfully to address a range of questions in applied and theoretical ecology. For example, DGVMs showed that large areas of the world would be forested in the absence of fire (Bond *et al.*, 2005) and that the absence of angiosperms would dramatically reduce the area covered by evergreen forests, because high transpiration rates of angiosperms promote local precipitation, which in turn maintains rainforests (Boyce & Lee, 2010). As DGVMs only require climate and soil data to run simulations, they allow us to simulate past and future vegetation. For example, Scheiter *et al.* (2012) explored the role of fire for C_4 grass expansion in the late Miocene, Prentice *et al.* (2011) investigated how vegetation cover and C stocks changed after the last ice age, and Kuemmerle *et al.* (2012) modelled the potential habitat of the European bison during the Holocene. A large number of studies have used DGVMs to explore the impacts of climate change on the C cycle and

biome patterns (Cramer *et al.*, 2001), and models have recently been extended to investigate how land use influences the C cycle (Bondeau *et al.*, 2007). DGVMs have been linked with general circulation models (GCMs) to create fully coupled biosphere-atmosphere models. Such fully coupled models are important tools for the analysis of both the impacts of climate on vegetation and how these changes in vegetation cover influence climate via changes in albedo, leaf area index (LAI) and water fluxes (Raddatz *et al.*, 2007; Brovkin *et al.*, 2009).

Despite the fact that DGVMs have allowed vegetation ecologists and earth system scientists to address a range of important questions, the applicability of DGVMs is limited by two major weaknesses. The first relates to how these models use plant functional types (PFTs) to represent vegetation. DGVMs typically use a small set of plant attributes to define a limited number of static plant functional types. The second common weakness is that DGVMs poorly represent competition (Fisher *et al.*, 2010; Quillet *et al.*, 2010), essentially because competition is modelled at the PFT level and not at the individual plant level (Clark *et al.*, 2010, 2011a). Both weaknesses cast doubt on the ability of DGVMs to model how changes in climate might force switches in vegetation structure.

Several of the deficiencies of the DGVM approach are, in turn, the explicit focus of community ecology (Keddy, 1992; Weiher & Keddy, 1995a,b) and coexistence theory (Chesson, 2000). Community assembly models aim to understand how properties of plants, often referred to as functional traits, influence the assembly of plant communities at a site. The community assembly programme involves two intimately linked activities (Weiher & Keddy, 1995b). First, a minimum set of traits is identified that can be used to predict the composition of an ecological community at a site (Keddy, 1992). Secondly, the series of environmental filters that act on these traits to determine the community assembly process is identified. For example, van der Valk (1981) found that life span, propagule longevity and propagule establishment were traits that determined how flooding (the environmental filter) determines which species may establish in a wetland. A weakness of this approach is that it generally describes observed vegetation patterns by using statistical models (regression models, statistical mechanics models or Bayesian multilevel models) rather than process-based, mechanistic models (Webb *et al.*, 2010; Götzenberger *et al.*, 2012).

Coexistence theory aims to explain community structure using heuristic models and empirical analyses (Warner & Chesson, 1985; Tilman, 1988; Chesson, 2000; Clark *et al.*, 2010). Such models describe the mechanisms that allow coexistence of species by focusing on niche differentiation, tradeoffs between plant traits and storage effects. However, coexistence theory still struggles to explain the paradox of high diversity (Hutchinson, 1961), an issue that Clark, in a series of studies, suggests can be resolved by considering individual-level variation and tradeoffs in a high-dimensional trait space (Clark *et al.*, 2004, 2010).

The aim of this paper is to review deficiencies in the DGVM programme and to provide a viewpoint on how DGVMs need to be improved to address these deficiencies. We articulate this viewpoint by first describing a conceptual scheme of how next-generation DGVMs could be structured. We then describe our implementation of such a DGVM and provide examples of model behaviour that highlight how this new model differs from the current generation of DGVMs. We conclude by discussing how this approach could foster more intimate collaboration between dynamic global vegetation modellers and the broader community of ecologists and evolutionary biologists.

Description

Deficiencies of DGVM modelling

Hidden calibration of plant functional types (PFTs) Dynamic global vegetation models simulate the behaviour of PFTs. These provide a means to use a finite set of parameters to aggregate traits of individual plants with similar ecological behaviour (Díaz & Cabido, 1997; Lavorel *et al.*, 1997; Kattge *et al.*, 2011). These parameters seek to aggregate several sources of variability in these traits, including between individual variation, between population variation as a result of local adaptation, between species variability as well as variability as a result of the statistical uncertainty associated with measuring and estimating these parameters. In practice, many of these sources of variability are not quantified in DGVMs and most models define PFTs using point estimates of parameters that describe plant traits (Prentice *et al.*, 2007). Such an aggregation implies a loss of information and obscures aspects of plant behaviour and variation in behaviour that is known to influence the likelihood of coexistence (Clark *et al.*, 2011a). An additional concern is that the parameter value used in a model to describe a trait is often not a maximum-likelihood estimate of the parameter, but rather a permissible value, and modellers tend to choose (whether consciously or subconsciously) a permissible value that enhances model performance. Hence, trait values are often hidden model-tuning parameters and simulation results may well be biased by this hidden calibration process. Furthermore, trait values are generally selected such that models perform well for ambient environmental conditions simply because most benchmarking data sets are derived from ambient conditions. However, this assumes that trait values used to parameterize PFTs were valid under past environmental conditions and will still be valid under future conditions (Clark & Gelfand, 2006).

To illustrate some of these parameterization issues, we ran the aDGVM (Scheiter & Higgins, 2009) where each individual tree had the same point estimates for traits; and values of four selected traits were drawn from normal distributions with means defined by the point estimates and standard deviations covering a feasible range of values (Fig. 1). As one would expect, there is more variability between the output of replicate simulations when using variable traits, but, more significantly, there is a systematic bias where variable-trait simulations project higher mean biomasses than fixed-trait simulations (Fig. 1). The latter effect arises because, by selecting a range of trait combinations, one increases the chance that trait combinations that allow individuals to grow larger and produce more biomass are simulated. Fisher *et al.* (2010) used a similar approach to explore model uncertainties in the JULES-ED model. They conducted a sensitivity analysis
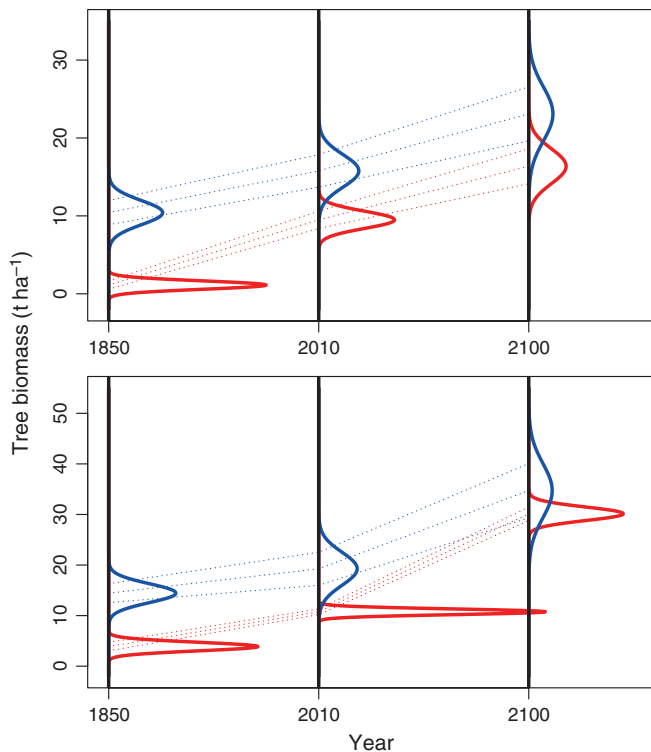
Fig. 1 Sensitivity analysis of tree biomass to fixed traits or randomly selected traits in the aDGVM (Scheiter & Higgins, 2009) for two savanna study sites in the Kruger National park, South Africa (Skukuza, upper panel; Pretoriuskop, lower panel). 'Fixed traits', shown in red, indicates that the four traits, specific leaf area (SLA), light extinction in canopy, canopy radius to tree height ratio and carbon allocation to stem biomass, are constant and equal for all trees, whereas 'variable traits', shown in blue, indicate that trait values were selected randomly for each tree. Mean and standard deviations are 10 ± 3.2 for SLA, 0.37 ± 0.13 for light extinction in canopy and 0.37 ± 0.13 for canopy radius to tree height ratio. Carbon allocation to stem biomass was increased or decreased by a random number between 0 and 0.3, and therefore C allocation to root biomass was decreased or increased by the same amount. The mean values were used for the 'fixed trait' simulations. Density distributions were generated by 100 replicate simulations.

where five model parameters related to demography and competition were selected by using a Latin Hypercube exploration of the trait space. This study showed that simulated biomass for different parameter combinations was highly variable under ambient conditions and that variability in biomass projections increased further in forward projections. While the practice of using permissible parameter estimates for defining PFTs in DGVMs might have been understandable in the past, we now have excellent databases (e.g. the TRY database, Kattge *et al.*, 2011) that allow us to generate more objective estimates of trait values and methods to inversely parameterize DGVMs by using these trait databases as prior information (Hartig *et al.*, 2012).

A special case of hidden calibration of DGVMs relates to bioclimatic limits (Haxeltine & Prentice, 1996). Many DGVMs use bioclimatic limits to constrain the range of environmental conditions where modelled PFTs can grow (e.g. BIOME3 (Haxeltine & Prentice, 1996) or LPJ (Sitch *et al.*, 2003)). Bioclimatic limits are based on empirically observed limits of PFTs; however, these

empirical rules have no formal physiological basis. For example, Sitch *et al.* (2003) assumes that the minimum coldest-month temperature for survival of the tropical herbaceous PFT (C_4 photosynthesis) and the maximum coldest-month temperature for establishment of temperate herbaceous PFT (C_3 photosynthesis) occur at 15.5°C. However, these threshold temperatures are influenced by the CO_2 concentration (Ehleringer *et al.*, 1997). Similarly, a cold-tolerance limit might be a result of a failure of vegetative growth or the failure of a reproductive process (Bykova *et al.*, 2012). The lack of explicit physiological justifications for the bioclimatic limits in many DGVMs means that bioclimatic limits are, in effect, calibration parameters that force PFTs to grow in the 'correct' climate region. Ideally these bioclimatic limits should be explicitly linked to physiological processes or removed from DGVMs.

Depauperate functional diversity A second problem associated with the parameterization of functional types relates to the question of how many species, or what degree of functional diversity, do we need to sustain ecosystem function, both in real ecosystems (Hooper *et al.*, 2005, 2012) and in modelled ecosystems. An illustrative example of this issue is the Amazon dieback phenomenon. Cox *et al.* (2004) projected a collapse of the Amazon rainforests under future climate conditions as a result of anticipated decreases in precipitation. These simulations project a widespread loss of the 'broadleaved evergreen tree' PFT and its replacement by C_4 grasses and bare soil (Cox *et al.*, 2004). These changes imply a transition from the forest biome to savanna and grassland biomes. Repeating Cox *et al.* (2004)'s simulation experiments with different DGVMs showed that the magnitude of dieback is sensitive to the model used (Huntingford *et al.*, 2008; Sitch *et al.*, 2008; Galbraith *et al.*, 2010), suggesting that the simulated collapse might be an artefact of the fact that rainforests are typically represented by a single PFT (e.g. 'broadleaved evergreen tree') in DGVMs. More specifically, Galbraith *et al.* (2010) found that much of this variability can be attributed to differences in temperature sensitivity in different models and Poulter *et al.* (2010) highlights the importance of parameters describing vegetation dynamics such as establishment rates or rooting depth. In reality, one might expect that phenotypic plasticity, local adaptation and shifts in the tree community structure, for instance shifts to more drought-tolerant forest tree types, may buffer the impacts of decreasing precipitation and thereby avoid a catastrophic dieback of the Amazon rainforest. Such compositional shifts have been reported for tropical forests in Ghana, where long-term drought increased the abundance of drought-tolerant deciduous trees and these changes were associated with increases in the total biomass stocks (Fauset *et al.*, 2012). Analogously, increasing functional diversity in DGVMs by increasing the number of PFTs and increasing trait diversity by allowing trait values of vegetation to be dynamic may avoid a modelled collapse of the Amazon.

Competition Competition does influence a variety of ecological processes that have consequences for community assembly and the distribution of biomes. For example, Clark *et al.* (2011b), in an analysis of temperate forest species, showed that the effects of

competition on growth rates and mortality risk exceed the effects of climate, while Bond & Midgley (2012) argued that the atmospheric CO_2 concentration determines the outcome of grass and tree competition in subtropical regions, and thereby the continental-scale distribution of savanna, forest and grassland biomes (Higgins & Scheiter, 2012). DGVMs differ considerably in how they represent competition between functional types. One approach, often used to simulate competition for space, is to assume that the best performing PFT is able to occupy open space and ultimately dominate the vegetation stand. Such models often use net primary productivity (NPP) as a measure of performance (e.g. BIOME3, Haxeltine & Prentice, 1996) and the outcome is typically that one PFT dominates. When modelling competition more explicitly, there are two broad approaches that have been adopted in DGVMs. One approach is to use Lotka–Volterra type differential equation models, where competition coefficients are used to describe competition between functional types. This approach has been adopted, for instance, by TRIFFID (Cox, 2001) and CTEM (Arora & Boer, 2006). The disadvantage of this approach is that the number of competition parameters increases as a square of the number of PFTs. Moreover, such competition coefficients do not describe the mechanism of competition but rather the aggregated outcome of competitive interactions. This makes them a poor choice for projecting how competitive hierarchies might change in novel ecological settings, for instance under conditions of elevated CO_2. Additionally, such competition coefficients are difficult to measure directly in field experiments, and inverse model parameterization techniques are required (Freckleton & Watkinson, 2000; Higgins et al., 2010).

An alternative is to model the impact of each individual plant or each PFT on the resource pool, which, in turn, influences the growth of other individual plants or PFTs. For example, many DGVMs use a bucket model for soil hydrology (e.g. the aDGVM (Scheiter & Higgins, 2009); LPJ (Sitch et al., 2003); LPJ-GUESS (Smith et al., 2001)). In such models, each PFT extracts water from the bucket based on the PFT's rooting depth, transpirational demand, drought tolerance and soil water availability. The water extracted by each PFT influences the water available to other PFTs and thereby ensures that only PFTs adapted to the local site conditions persist. In such models, the focus is therefore on modelling the ecosystem engineering and ecosystem modulating impacts of plants on their environment, which feeds back to influence the performance of competitors (Jones et al., 1994; Linder et al., 2012). A further advantage of modelling competition via the resource pool is that, in contrast to Lotka–Volterra models, the number of parameters increases linearly with the number of PFTs. Competition models of this kind are also consistent with the aims of earth system models, which are in part interested in the engineering and modulating effects of vegetation on the climate system (e.g. Boyce & Lee, 2010) and how these effects feed back and influence the conditions that determine vegetation distribution (Cox et al., 2000; Brovkin et al., 2009). Modelling competition as an engineering feedback additionally provides a natural way to model priority effects, for instance the successional shifts in temperate forest (Hickler et al., 2012) or that forests are fire-excluding

ecosystems that prevent the invasion of C_4 grasslands and savannas (Higgins & Scheiter, 2012; Scheiter et al., 2012).

Phylogenetic biome conservatism A poorly understood, but potentially far-reaching, limitation of current DGVMs is that they assume that convergent evolution is pervasive. Specifically, DGVMs assume that the same climate in different phylogenetic contexts will yield the same evolutionary responses, and that these evolutionary responses are manifest in the traits that define the PFTs. This convergence assumption is now being questioned by several lines of evidence. For instance, savannas are convergent in structure, yet how climate and fire interact differs between continents, with the consequence that each continent's savannas are expected to respond qualitatively differently to climate change (C. Lehmann et al., unpublished). A similar example comes from grasslands, where Buis et al. (2009) showed that compositional differences in the forb communities of South Africa and North America ensured that forb above-ground NPP responded differently to environmental drivers in these two regions. Interestingly, in this study, the above-ground NPP of the grasses did respond similarly to environmental drivers. More directly, Banin et al. (2012) showed that the architectures of the world's tropical forests differ from one another not only as a result of bioclimatic factors, but also as a result of a continent effect, which in this study was used as a proxy for evolutionary history.

Such phylogenetic niche conservatism has been demonstrated at local and regional scales (Losos et al., 2003; Ackerly et al., 2006; Silvertown et al., 2006). A more recent study of > 11 000 plant species from across the southern hemisphere suggests that phylogenetic biome conservatism is widespread. This study found that only 3.6% of speciation events involved daughter species being associated with a new biome, suggesting that many lineages have a limited capacity to adapt to new biomes. These findings imply that the assembly of biomes is highly constrained by the phylogenetic history (Crisp et al., 2009). A counter-example suggests that conservatism is not pervasive. Simon et al. (2009) found that most of the fire-adapted lineages of the Cerrado have sister lineages in fire-free forests ecosystems, suggesting that the assembly of the Cerrado biome involved the convergent evolution of fire-adapted trees from several different tropical forest tree lineages rather than dispersal of fire-adapted lineages. Crisp et al. (2009)'s synthesis and the contradictory results of Simon et al. (2009) suggest that we still have a lot to learn about the situations in which phylogenetic conservatism constrains evolutionary convergence. The message for DGVMs is, however, clear. Phylogenetic history potentially constrains how ecosystems respond to environmental forcing and we should not expect, for example, each of the world's tropical forests to respond in the same way to environmental forcing (Banin et al., 2012).
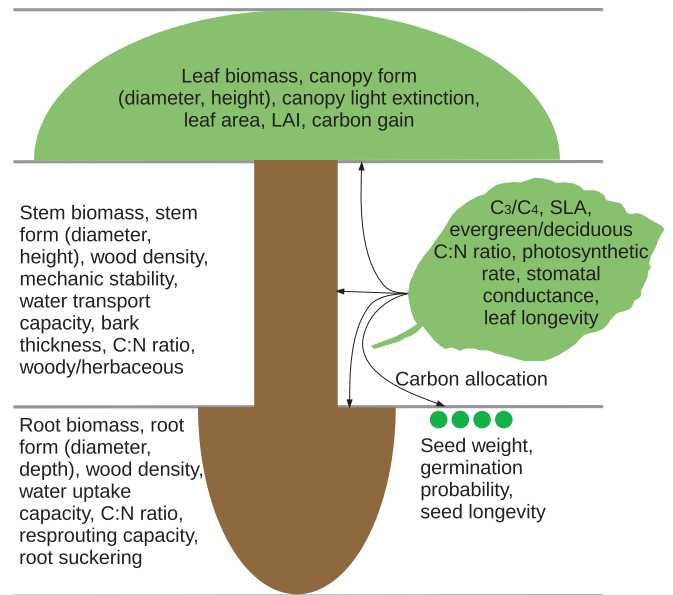
Next-generation DGVMs

We argue that the next generation of DGVMs should implement ideas derived from coexistence theory (Chesson, 2000) and community assembly theory (Keddy, 1992; Webb et al., 2010) into the process-based paradigm of dynamic global vegetation

modelling. Yet, we wish to emphasize that while we can learn a lot from community ecology and coexistence theory, we should also appreciate that these disciplines do not have the same aims as dynamic global vegetation modelling. Community ecology primarily seeks to understand which traits determine fitness in which environmental settings. Much of this understanding can be gained using statistical methods (Shipley, 2010; Swenson & Weiser, 2010; Webb *et al.*, 2010). Coexistence theory generally uses heuristic models to understand which processes and environmental settings promote coexistence (Chesson, 2000). DGVMs, on the other hand, seek to represent and understand the interplay between climate and vegetation. In the paragraphs that follow, we describe a conceptual scheme for a next-generation DGVM that is illustrated in Fig. 2.

We propose that the key challenge for DGVMs is to move away from the fixed-PFT paradigm towards a more flexible trait-based approach, which allows communities to be assembled based on how plants with different trait combinations perform under a given set of environmental conditions. The primary object in such a model is the individual. An individual-based approach (DeAngelis & Mooij, 2005) allows a simulation run to consider many individual plants, each of which can potentially have a unique set of trait values (see Fig. 3 for traits of an

Fig. 3 Traits and state variables of a single plant in a next-generation dynamic global vegetation model (DGVM). Arrows represent allocation of carbon produced by leaves to different biomass compartments of the plant. LAI, leaf area index; SLA, specific leaf area.
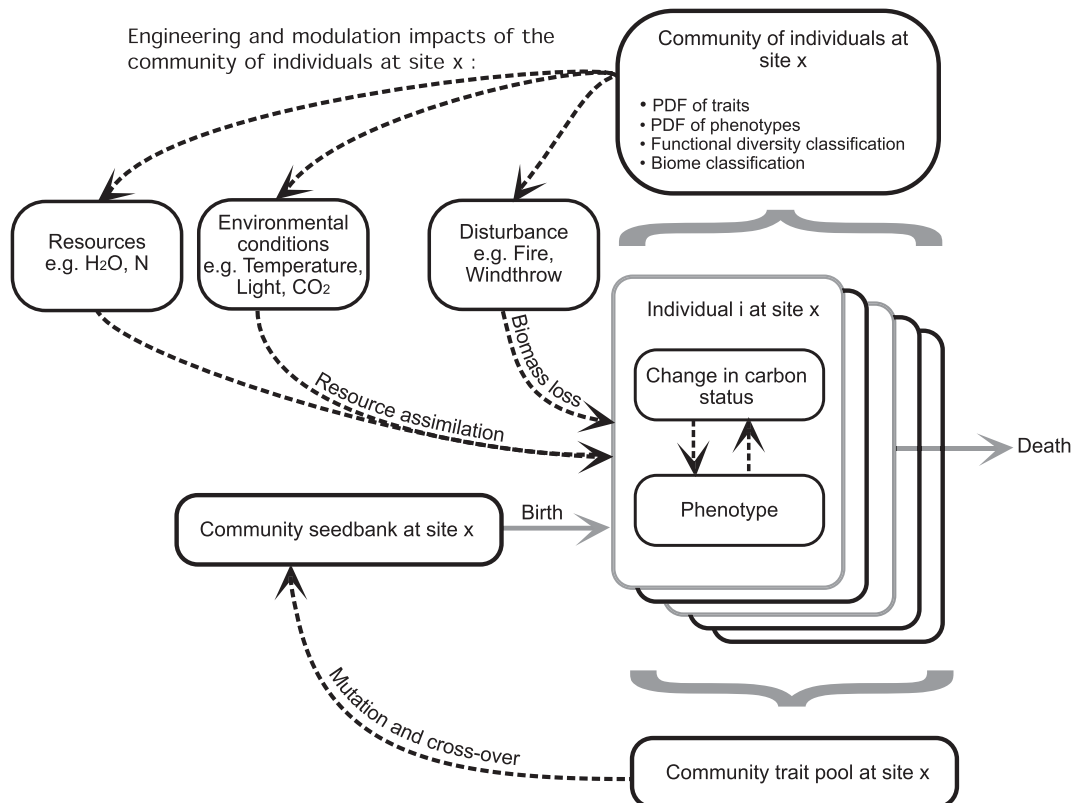
Fig. 2 Conceptual modelling framework for a next-generation dynamic global vegetation model (DGVM) as outlined in the section 'Next-generation DGVMs'. Individuals are characterized by their traits that influence their carbon (C) status and phenotype. All individuals at a site form the community, which influences resources, environmental conditions and disturbances via engineering and modulating impacts. These conditions interact to influence growth of the individuals. Individuals, through reproduction, can add their traits to the community trait pool. Crossover and mutation of the community trait pool yield the community seed bank. PDF, probability density function.

individual plant that one could simulate in DGVMs). In this model structure, the traits describe how the rates of resource assimilation, growth, C allocation and respiration are influenced by the environment; these rates in turn determine the C balance and the state variables that define the phenotype of each individual plant (Fig. 2). Individuals with inappropriate trait values and poor C balance die, whereas individuals with sufficient C gain and trait values that allow seed production, reproduce. This model structure allows for variance in how individual plants respond to variable environmental conditions, which has been shown to promote species coexistence (Clark *et al.*, 2004, 2010).

Reproduction is a key element in next-generation DGVMs, as it transfers traits from one generation to the next (inheritance), allows transfer of traits between reproductive individuals (crossover) and allows novel trait values to enter through mutation. There are many ways that these processes can be modelled. A realistic modelling of these evolutionary processes (e.g. how dispersal, pollination processes or reproductive biology influences gene flow) is not warranted; rather we require an effective algorithm that rapidly generates and selects for individual trait combinations that are adapted to the abiotic and biotic environment at a site. A pragmatic approach, which we follow, is to use a genetic optimization algorithm to manage the transfer of traits between generations. Genetic optimization algorithms are general-purpose optimization routines that use the concepts of recombination and mutation to efficiently find quasi-optimal

solutions to optimization problems (e.g. differential evolution, Storn & Price, 1997). In the context of DGVMs, the vectors that describe trait values of each reproducing individual are added to the community trait pool. Traits are mutated and recombined to produce a community seed bank of seeds that can potentially germinate (Fig. 4). Trait filtering occurs through the reproduction and mortality functions; trait combinations that do not produce offspring do not contribute their traits to the next generation, whereas those that produce many seeds dominate the community trait pool.

What emerges from trait filtering is a community of individuals at a site. The information on this community can be summarized in various ways: as a probability density function (PDF) of traits or a PDF of phenotypes – the phenotype can be used to classify individuals as belonging to a specific functional type, or the phenotypes at a site can be used to assign a site to a biome type (Fig. 2). The properties of individuals can additionally be used to calculate changes in resource availability (e.g. soil water, light environment) and environmental conditions (e.g. surface temperature). Hence, competitive effects are simulated by modelling the engineering and modulating effects of plants on their environment, which feeds back to influence plant growth (Fig. 2).

The community of individuals at a site additionally determines disturbance regimes (Fig. 2). While DGVMs have in recent years made great strides in improving the representation of fire
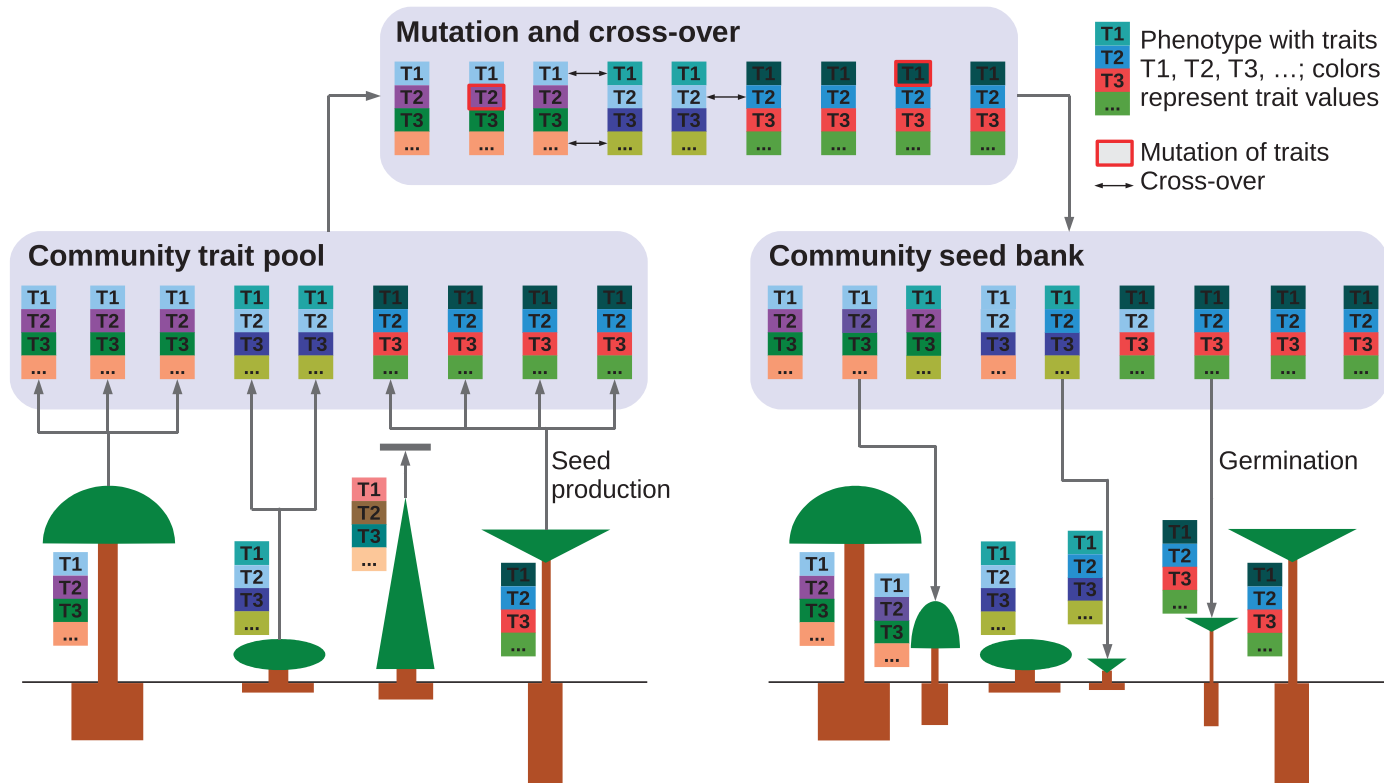
Fig. 4 Seed bank model in a next-generation dynamic global vegetation model (DGVM). Each plant is characterized by a unique trait combination. Reproducing individuals add their seeds to the community trait pool. In the community trait pool, mutation and crossover of seeds generate new trait combinations, which constitute the community seed bank. Randomly selected seeds can germinate, which means that they are added to the plant community as seedlings.

disturbance (Thonicke *et al.*, 2010), the individual-based approach we propose emphasizes the possibility to link traits and phenotypes to fuel properties and to the response of individual plants to fire (Pausas *et al.*, 2004; Pausas & Verdu, 2008). One example of this link is the invasion of Norway spruce in northern Europe in the late-Holocene where it has been shown that the associated changes in the community structure had more impacts on fire regimes than climatic changes (Ohlson *et al.*, 2011). Analogously, individual-level variance in the plant phenotype defines the value of vegetation to herbivores and how vegetation structure will respond to herbivory (Scheiter & Higgins, 2012).

The promiscuous nature of the way that such a genetic algorithm (Fig. 4) simulates reproduction has two major side-effects. First, the trait 'evolution' simulated by such a model cannot be compared with the trait evolution studied by evolutionary biologists. This is because the genetic algorithm will rapidly find optimal solutions to the 'evolutionary' problems posed by the modelled environment. However, reproduction could be constrained to individuals with similar traits or individuals with the same 'species label'. This would restrict gene flow and thereby simulate reproductive isolation. The second side-effect is that the rampant and unconstrained evolution of trait combinations is likely to produce Darwinian demons (Law, 1979), individuals that simultaneously maximize all functions that contribute to fitness. Darwinian demons do not exist in the real world because allocation of resources, for instance, to reproduction ensures that fewer resources are available for other functions such as growth and survival. Identifying such tradeoffs is one of the major activities of life-history theory and of the growing literature on functional plant traits (Reich *et al.*, 1997; Enquist, 2002; Wright *et al.*, 2004; Shipley *et al.*, 2006; Westoby & Wright, 2006; Chave *et al.*, 2009). Process-based vegetation models that explicitly consider tradeoffs between traits are, however, rare (Kleidon & Mooney, 2000; Marks & Lechowicz, 2006; Reu *et al.*, 2011; Pavlick *et al.*, 2012).

The major task for the developer of the kind of DGVM we are proposing is to conceptualize and parameterize life-history tradeoffs. We envisage that there are three major types of tradeoff that need to be considered. The first are mass conservation tradeoffs – the amount of a resource allocated to candidate functions must sum to one. The consequences of these tradeoffs manifest themselves naturally as part of the model's dynamic. For example, allocating more C to bark might protect a tree from fire damage, but this might compromise its ability to grow tall and compete for light (Gignoux *et al.*, 1997). The second kind of tradeoffs are engineering tradeoffs – certain plant structures or architectures are not mechanically feasible. For example, a minimum stem diameter is required to ensure the mechanical stability of a stem of a given height (Niklas, 1994). Similarly, a critical sapwood area is needed to supply foliage with water (Shinozaki *et al.*, 1964). These first two kinds of tradeoffs can be addressed, respectively, by having a sound accounting system in the model and by using established principles of engineering. The third kind of tradeoffs are more diffuse to define and difficult to deal with. We will refer to them as empirical tradeoffs. Empirical tradeoffs are a result of processes not explicitly simulated by the model. For

example, Shipley *et al.* (2006) argued that the tradeoff between leaf photosynthetic rates and leaf longevity is a consequence of cell anatomy. Yet, DGVMs do not explicitly model cell anatomy, meaning that this tradeoff cannot emerge as a result of the model's internal dynamics. We are forced to parameterize this tradeoff using empirically defined functions. We might use the empirical functions identified by Wright *et al.* (2004) to describe the tradeoff between photosynthetic rate and leaf longevity and refrain from attempting to model the mechanisms proposed by Shipley *et al.* (2006). The problem of which processes to model empirically and which to model mechanistically is, of course, a pervasive one in any kind of modelling endeavour.

The aDGVM2: a trait-based dynamic vegetation model

We now turn to the question of whether we can implement a model of the kind narrated in the previous section. In this section, we describe how we modify an existing DGVM (the aDGVM, Scheiter & Higgins, 2009) to realize aspects of the conceptual scheme illustrated in Fig. 2. The aDGVM2 is individual-based, which means that it simulates growth, reproduction and mortality of each individual plant and it keeps track of state variables such as biomass, height and LAI of each individual plant. In addition, each plant is characterized by an individual and potentially unique set of traits describing plant type (grass or tree), leaf characteristics, leaf phenology, C allocation to different plant compartments, allometry of plant architecture, re-sprouting response to fire, reproduction and mortality (Fig. 3). Each plant is tagged with a 'species label'. These 'species' differ in the trait values used for the model initialization. Growth, reproduction and mortality of plants are influenced by both the plant-specific trait combination and the environmental conditions.

Plant traits are linked by tradeoffs to constrain overall plant performance. Mass conservation tradeoffs regulate allocation to roots, stems, leaves, bark, storage and reproduction. Engineering tradeoffs regulate plant architecture (Niklas & Spatz, 2010), while empirical functions define, for example, tradeoffs between specific leaf area (SLA) and leaf longevity (Reich *et al.*, 1997) or between SLA and the capacity of a plant to extract water from the soil. The aDGVM2 simulates soil water competition and light competition via impacts of each individual plant on the resource base. Water uptake of single plants is defined by the fraction of root biomass in different soil layers, the moisture content of these soil layers and by the plant's capacity to extract water from the soil. The light available to a target plant is influenced by the height of neighbouring plants. Light availability and water availability influence the photosynthetic rate and thereby, via C status, the reproduction and mortality rates of each individual plant. Nutrient competition was not considered in this model version, even though it is important (Tilman, 1988).

Reproduction follows the scheme described in Fig. 4. Specifically, individual plants that allocate enough C to reproduction can produce seeds. Seeds of the same species label can exchange trait values, thereby allowing recombination of the community trait pool. Mutation adds new trait values to the community trait pool. Randomly selected seeds are drawn from the resulting

community trait pool and are added to the plant population as seedlings. By simulating inheritance, mutation and crossover, the model generates a large variety of different trait combinations and iteratively, via mortality and reproduction, assembles a plant community that is adapted to and influences the environmental conditions, resource availability and the disturbance regime at a study site.

Results

The following paragraphs describe simulation runs that illustrate major features of the aDGVM2. The environmental space in all simulation experiments is defined to be close to a savanna–forest boundary (9°N and 10°E, 1000 mm mean annual precipitation (MAP)). A first simulation run is designed to illustrate how the assembled communities are influenced by rainfall and CO_2. Simulations are conducted for ambient and elevated CO_2 concentrations (380 and 700 ppm). Additionally, we scale precipitation to generate a rainfall gradient (400, 1000 and 1500 mm). Simulations are conducted with and without reproductive isolation, that is, with and without the restriction of trait exchange to individuals of the same 'species'. A principal component analysis (PCA) shows that at the end of a 2000 yr simulation run, the communities in different scenarios occupy different regions of the trait space (Fig. 5) and are clearly arranged along the rainfall and the CO_2 axes. These simulation runs additionally highlight the importance of simulating reproductive isolation. When reproductive isolation is not simulated the aDGVM2 simulates essentially one strategy per simulation scenario, that is simulated individuals are clustered in the trait space (Fig. 5a). By contrast, when reproductive isolation is simulated and reproduction is restricted to individuals of the same 'species', coexisting strategies emerge and the individuals belonging to different 'species' occupy distinct regions of the trait space (e.g. several clusters emerge for simulation scenarios depicted in green and yellow in Fig. 5b).

A second simulation run illustrates how trait values and plant communities at a site develop over time. The simulation starts by allowing fires to occur. After *c.* 1000 iterations, the assembled community is relatively stable and mean trait values reach a plateau (Fig. 6a). In the second simulation phase (iteration 2001 –4000), fire suppression is introduced. Following the release from fire-induced selection pressure, C allocation to roots increases, which improves water uptake potential, and wood density increases, which reduces the risk of mortality as a result of mechanical instability (Fig. 6a). Therefore, C allocation to bark, which protects trees against fire, decreases. Fig. 6a shows the mean trait value of all individuals in a simulation, whereas Fig. 6(b) shows the frequency of different trait values. Hence, increases in mean wood density (Fig. 6a) can be attributed to increasing abundances of 'species' with high wood density (Fig. 6b). When the system is exposed to fire, the community trait diversity (measured as the total distance between all trait combinations) is, after an initial transient phase, low (Fig. 6c). When fire is suppressed, trait diversity increases. This shift in trait diversity in response to fire agrees with Pausas & Verdu (2008),
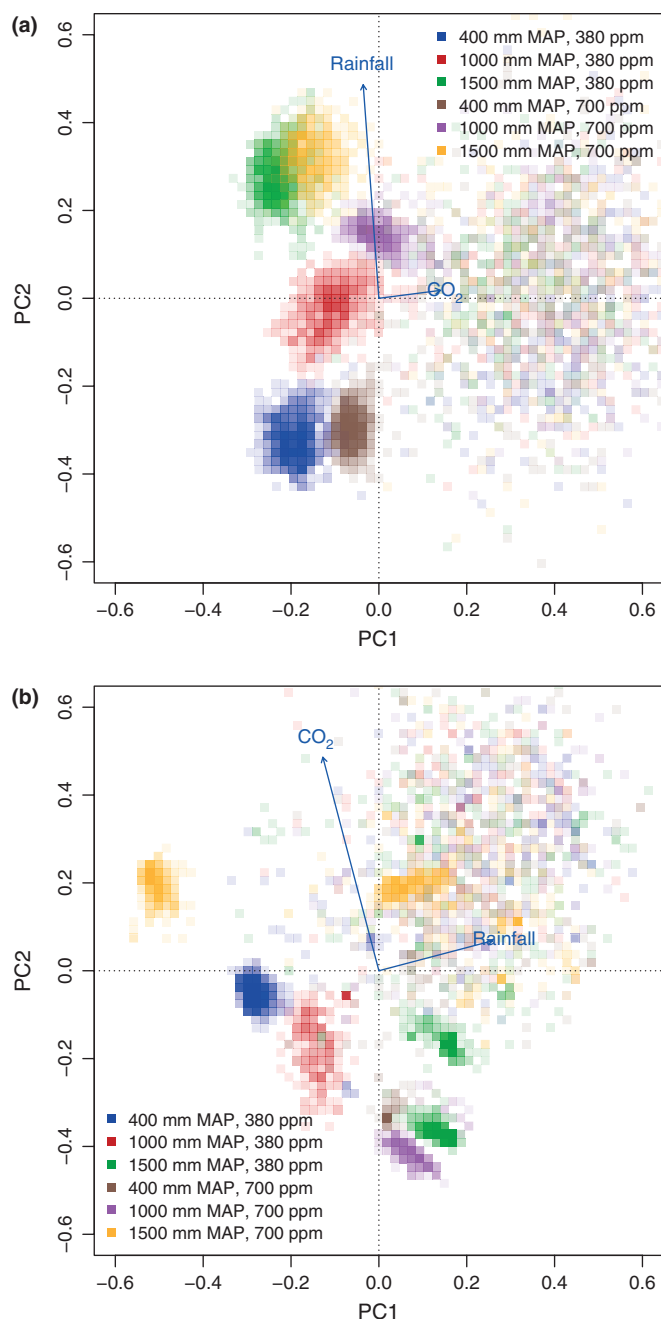
Fig. 5 Principal component analysis (PCA) showing that simulated communities respond to the environmental conditions. Simulations were conducted for a rainfall gradient and for ambient and elevated CO_2 concentrations. Simulations were conducted without reproductive isolation between individuals (trait exchange between all 'species'; a) and with reproductive isolation (trait exchange restricted to individuals of the same 'species'; b). Saturation of different colours represents the number of plants within a region of the trait space. We ordinated a trait by site table. MAP, mean annual precipitation, ppm, parts per million.

who found that trait dispersion was lower in Mediterranean shrubland communities subject to higher fire frequencies.

The distributions of simulated trait values are often multimodal (Fig. 6b), suggesting that the aDGVM2 simulates different life-history strategies that can persist and coexist under the given environmental conditions. In the example simulation (the

same as in Fig. 6), four dominant strategies persist (Fig. 7). These coexisting strategies are consistent with colonization–competition tradeoff models of species coexistence theory. The strategy plotted in blue is the better colonizer as it starts growing early in the growing season (Fig. 7a), has shallow roots (Fig. 7b), is fast-

growing (low wood density, Fig. 7c), allocates a high proportion of the C gain to reproduction (Fig. 7d) and produces smaller seeds (Fig. 7e). By contrast, the strategy plotted in yellow is the better competitor because it has deeper roots (Fig. 7b), higher wood density (Fig. 7c) and produces heavier seeds (Fig. 7e). Accordingly, the tallest trees in the simulated population stem from the yellow strategy (Fig. 7f).

Discussion

In this paper we review limitations of dynamic global vegetation models and argue that many of these limitations could be addressed by integrating concepts from community assembly (Keddy, 1992; Weiher & Keddy, 1995a,b) and plant coexistence theory (Chesson, 2000). More specifically, we propose an approach that models individuals, each of which can potentially have a unique suite of trait values, and uses environmental forcing to drive community assembly through trait filtering and selection.

The approach we outline has several advantages. First, it redefines the process of model parameterization and calibration and thereby avoids hidden model calibration. The trait values that individual plants adopt are not parameterized but emerge from the model dynamics. Environmental conditions and resources influence the fitness of individual plants, thereby filtering which trait combinations dominate and coexist. This is particularly important when environmental conditions change. When using this approach, the model parameterization process switches emphasis from defining trait values to defining functions that describe tradeoffs between traits. This approach reduces the dimensionality of the parameterization process, while increasing the functional diversity the model represents. For example, in a conventional approach, maximum plant height can be defined as a PFT-specific constant. Should one wish to simulate 100 functional types, one would require 100 maximum height estimates. In the new approach, the parameterization process is no longer estimating the maximum height of each PFT, but rather defining the mechanical limits to plant height. One only needs the few parameters that define how height scales with other components of plant architecture, such as stem diameter and wood density (Niklas, 1994; Niklas & Spatz, 2010). However, trait filtering only yields useful results if appropriate filters act on the phenotypes. This filtering process includes not just the abiotic forcing variables but also how vegetation at a site influences resource
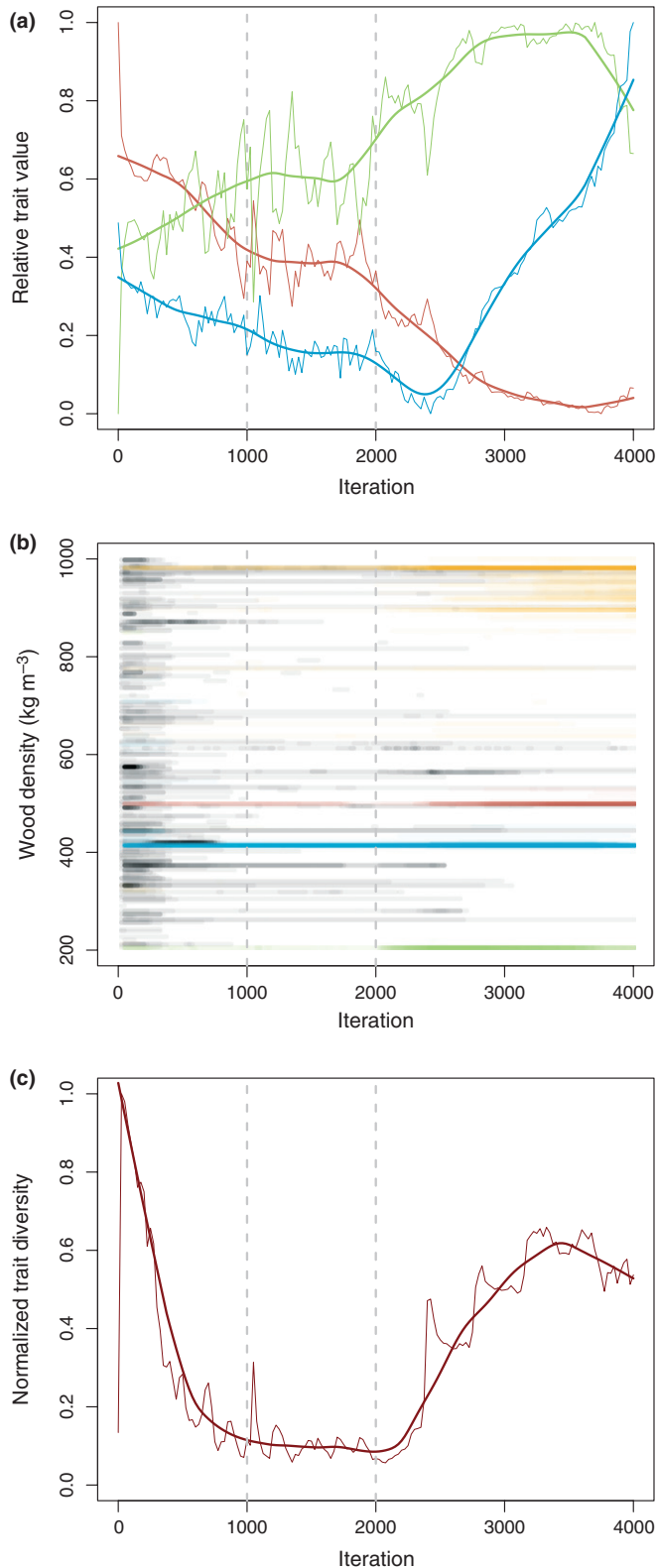
Fig. 6 Trait evolution and trait diversity simulated by the aDGVM2. (a) This shows how mean trait values of all simulated trees evolve. We selected three traits for this plot (carbon (C) allocation to bark, red; C allocation to roots, green; wood density, blue). (b) This shows in detail how wood density of trees evolves. The aDGVM2 simulates, in the specific simulation run, four dominant coexisting strategies, represented by different colours. The grey colour represents strategies that are only present in low abundances, and saturation of colours indicates the number of individuals with different trait values. (c) The evolution of community trait diversity (calculated as the Euclidean distance between the normalized trait values of all trees). The first simulation period (iteration 0–2000) was conducted in presence of fire, after which fire was suppressed.
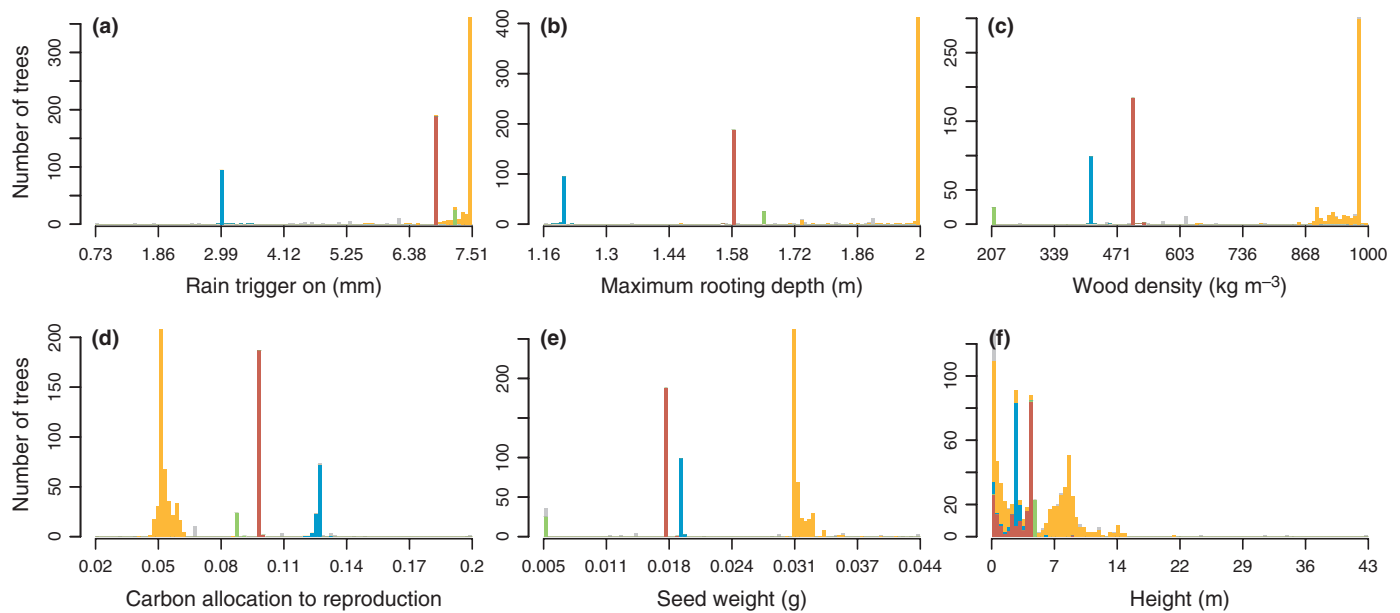
Fig. 7 Histograms of selected plant traits after a 4000 yr simulation. The aDGVM2 simulates, in the specific simulation run (the same as in Fig. 6), four different coexisting strategies, represented by different colours. Grey bars represent other strategies that are only present in low abundances. The 'rain trigger on' trait in (a) describes the value of a running average of precipitation where trees move from the dormant to the metabolic state.

availability, environmental conditions and disturbance regimes. Hence, the success of the approach is largely dependent on the ability to model resource competition and the engineering and modulating effects that plants have on their environments. There is a substantial literature on mechanisms that promote the coexistence of plants (Chesson, 2000) and on modern statistical methods to test which coexistence mechanisms are involved in a specific community (Angert *et al.*, 2009; Clark *et al.*, 2010). Yet few of these mechanisms are explicitly included in DGVMs. The aDGVM2 considers competition for soil water and light at the individual level and allows for the emergence and coexistence of several life-history strategies. However, we readily concede that more sophisticated concepts are warranted. In particular, how to represent in the model structure (Fig. 2) the way in which individuals and species partition environmental variation (Angert *et al.*, 2009; Clark *et al.*, 2010) remains to be explored.

An individual- and trait-based approach allows the number of PFTs in the model to equal the number of modelled individuals (Pavlick *et al.*, 2012). The consequences of increasing functional diversity are potentially far-reaching. For example, it has been proposed that productivity can be higher in highly plastic communities with large phenotypic and niche diversity than in communities where many individuals adopt an optimal trait combination (Norberg *et al.*, 2001). Further, several studies have shown that ecosystem services are a function of both species diversity and functional diversity (Hooper *et al.*, 2012).

Having a model that potentially has thousands of functional types also means that how we represent and interpret model output differs. For example, the classification of simulation output into PFTs or biome types is now a *post hoc* analysis which can be tailored to the aims of the study or to the benchmarking products available. This classification means that modellers can use available trait data (Kattge *et al.*, 2011) more effectively

because the model generates similar trait data. Developing such classification schemes serves to identify the traits required to differentiate between PFTs, both in models and in reality.

The aDGVM2 does, however, pose some computational issues. Being individual-based, it has, in principle, higher computational demands than PFT- and cohort-based models. However, in the context of the computational demands of a full earth system model, the demands are not prohibitive. For example, global simulations with the fully coupled earth system model MPI-ESM1 at a standard resolution used for the Coupled Models Intercomparison Project Phase 5 (CMIP5) simulations take *c.* 360 CPU h per simulation year (R. Schnur, pers. comm.). Running the aDGVM2 at the same resolution (6222 land grid points) would take < 2 CPU h per simulation year. The speed at which the modelled plant community converges to a climatically defined state will, however, depend on the number of modelled individuals, the mutation rate and the algorithm used for trait recombination. Experimentation will be needed to find the right compromise between rapid convergence of the assembled community and computational efficiency.

Dynamic global vegetation models assume that convergent evolution is pervasive – that is, they assume that functional diversity is defined by a series of labile traits that, given the same selective pressures, will converge to the same ecological optimum. This assumption is highly questionable (Buis *et al.*, 2009; Crisp *et al.*, 2009; Banin *et al.*, 2012) and the consequences of making this assumption are still poorly understood. As a starting point for investigating this issue with DGVMs, one should conduct carefully designed sensitivity analyses that explore how the community assembly process is influenced by different ways of initializing, parameterizing and constraining functional diversity and by different parameters to describe mutation and crossover.

In conclusion, we believe this paper has illustrated that it is possible to construct a DGVM that deals with functional diversity in a fundamentally different way, one that is consistent with theories of plant community assembly and with theories of plant coexistence. We anticipate that pursuing such next-generation DGVMs will provide opportunities for fruitful collaboration between research communities that focus on PFTs, plant competition, plant allometry, plant physiology, systems ecology and earth system science. Such a collaboration will improve our understanding of how climate and vegetation interact to define the past, current and future distribution of vegetation.

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