TECHNICAL ADVANCE

FATE-HD: a spatially and temporally explicit integrated model for predicting vegetation structure and diversity at regional scale

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Abstract

During the last decade, despite strenuous efforts to develop new models and compare different approaches, few conclusions have been drawn on their ability to provide robust biodiversity projections in an environmental change context. The recurring suggestions are that models should explicitly (i) include spatiotemporal dynamics; (ii) consider multiple species in interactions and (iii) account for the processes shaping biodiversity distribution. This article presents a biodiversity model (FATE-HD) that meets this challenge at regional scale by combining phenomenological and process-based approaches and using well-defined plant functional groups. FATE-HD has been tested and validated in a French National Park, demonstrating its ability to simulate vegetation dynamics, structure and diversity in response to disturbances and climate change. The analysis demonstrated the importance of considering biotic interactions, spatio-temporal dynamics and disturbances in addition to abiotic drivers to simulate vegetation dynamics. The distribution of pioneer trees was particularly improved, as were all undergrowth functional groups.

Keywords: abiotic constraints, biodiversity scenarios, biotic interactions, dispersal, dynamic vegetation model, functional diversity, landscape modelling, plant functional groups

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Introduction

Environmental changes impact all components of biodiversity, leading to species extinctions, shifts in species distributions and alterations to species interaction networks (Van der Putten *et al.,* 2009). In this context, modelling tools play a crucial role in simulating the potential consequences of global changes on biodiversity (Thuiller *et al.*, 2008; Bellard *et al.*, 2012). To provide reliable forecasts at regional scale, where dynamic range shifts take place and where biodiversity is managed, there is a necessary modelling trade-off between the number of species modelled and the level of mechanism details implemented. On the one hand, phenomenological models may account for many species (Thuiller *et al.*, 2011) but ignore spatio-temporal dynamics and present extrapolation issues (Dormann *et al.*, 2012). On the other hand, knowledge and data constraints force mechanistic models to focus on a limited extent, number of species and/or mechanisms. For instance, a species-by-species approach may account for species demography and dispersal but usually neglects species interactions (e.g. Dullinger *et al.*, 2012). A forest model (e.g. LANDIS, He *et al.*, 1999) describes tree–tree interactions but ignores herbaceous species.

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A global dynamic vegetation model (e.g. LPJ, Sitch *et al.*, 2003) uses a small number of plant functional types (PFT) representing tree and herbaceous species, but is not detailed enough to encompass plant diversity at regional scale (Harrison *et al.*, 2010). To overcome these limitations, the development of new models should combine approaches, using the latest theoretical advances (Gallien *et al.*, 2010; Dormann *et al.*, 2012; Thuiller *et al.*, 2013).

The first challenge is to consider enough species to represent the whole community dynamics (Kissling *et al.*, 2012). One approach to addressing plant diversity is to only select and model the dominant species, which is typically the case in forest gap models (Bugmann, 2001). However, focusing only on trees is not necessarily suitable for biodiversity assessment, as it does not represent plant diversity across an ecosystem. When several habitat types are considered, regional to global vegetation models traditionally model a limited set of plant functional types (PFTs) to simplify floristic complexity (Foley *et al.*, 1996; Daly *et al.*, 2000; Sitch *et al.*, 2003). However, although model combinations have been developed which integrate more PFTs (e.g. LPJ-GUESS, Hickler *et al.*, 2004), vegetation diversity is still under represented. In an attempt to reconcile vegetation modelling with recent advances in functional and community ecology, Boulangeat *et al.* (2012a) proposed

a theoretical framework to create plant functional groups (PFGs) that can meaningfully represent regional scale vegetation diversity. This is a promising approach for the field of landscape modelling.

The second challenge is to keep an easily parametered model, whilst integrating the three main mechanisms driving species distributions over environmental and disturbance gradients into a single modelling framework, thereby allowing them to interact over time and space:

1 Physiological constraints, each individual's intrinsic limitation to withstand a range of abiotic environmental conditions, are assumed to be most relevant in determining large-scale plant species distribution (Woodward, 1987). The abiotic filtering thereby determines the pool of species that can potentially co-occur and interact in a given location. In forest models, abiotic constraints are usually accounted for using demographic parameters which vary according to environmental variables (e.g. yearly minimum winter temperature and day degree sum influence tree recruitment in TreeMig, Lischke *et al.*, 2006). However, the parameterization of these relationships is highly time-consuming. As an alternative, recent works have used the phenomenological approach of habitat suitability models (HSM) to represent abiotic constraints on species distributions in spatio-temporally explicit models (e.g. Keith *et al.*, 2008; Dullinger *et al.*, 2012).

2 Although biotic interactions are crucial to determine species' local abundances (Boulangeat *et al.*, 2012b; Kunstler *et al.*, 2012), they are often neglected in species distribution models or, at best, included via proxies (e.g. Meier *et al.*, 2010; Giannini *et al.*, 2013). At landscape scale, models implementing plant interactions generally focus on competition for light (Bugmann, 2001). Other existing competition models (e.g. for soil resources) are too complex to be integrated into landscape models.

3 Dispersal is crucial to model species' range changes and source-sink dynamics (Pulliam, 1988). Moreover, seed dispersal interacts with the local population dynamic to determine the species' ability to track favourable environments (Pulliam, 2000). It is therefore vital to account for dispersal using spatially and temporally explicit models. To ensure computational effectiveness, spatially explicit landscape models usually aggregate individuals into cohorts, and use phenomenological representation of processes by stochastic algorithms and semiquantitative rules (Perry & Enright, 2006).

This article presents FATE-HD, a spatially explicit landscape vegetation model addressing the two aforementioned challenges. It integrates the most important mechanisms driving vegetation dynamics, structure and diversity (i.e. biotic interactions, dispersal and abiotic filtering) to simulate species or PFG responses to both environmental variation and disturbance regimes. FATE-HD has been tested in the French Alps, where it was parameterized for 24 PFGs representing plant diversity in a national park. The effect and the importance of each mechanism (abiotic filtering, biotic interaction and dispersal) in predicting vegetation structure and dynamics were analysed. FATE-HD's overall performance in retrieving the dominant vegetation distribution in different habitat types was then compared with that of habitat suitability models. As expected, PFG distributions were more constrained and accurate using FATE-HD as it takes into account biotic interactions, disturbances and temporal dynamics. Accounting for all these mechanisms largely improved the predicted distribution of small trees and undergrowth PFG. However, the effects were minimal for subalpine herbaceous species, which tolerate a large range of biotic conditions and disturbances, as well as for alpine PFGs, which rarely interact with taller plants (better competitors for light) given their specific cold habitat. Finally, FATE-HD performed well enough given the complexity of the modelled system and the described processes, which provides new avenues for future applications such as analysing the spatio-temporal response of the functional plant diversity to combined climate and land-use change scenarios.

Materials and methods

The model

FATE-HD is a dynamic landscape vegetation model that simulates interactions between plant modelling entities (e.g. species or plant functional groups), their population dynamics and dispersal, whilst taking into account external drivers such as disturbance regimes, and environmental variations. The model is built on past conceptual and technical developments (Albert *et al.*, 2008; Midgley *et al.*, 2010) but has been entirely recoded in C++ and revisited. An overview of how it operates is presented below (see Appendix S1 for a detailed description). Four inter-related submodels simulate the overall dynamics:

1 *Succession model*: Based on the 'FATE' model (Moore & Noble, 1990), it describes the within-pixel succession dynamics in an annual time step. Vegetation height is represented by a limited number of strata to incorporate the shading process (Fig. 1a). Within a pixel, the light resource for each stratum is calculated from the total abundance of all PFGs across all the upper strata. Within-pixel spatial heterogeneity in light resources is not taken into consideration, which is an important criterion for selecting the appropriate
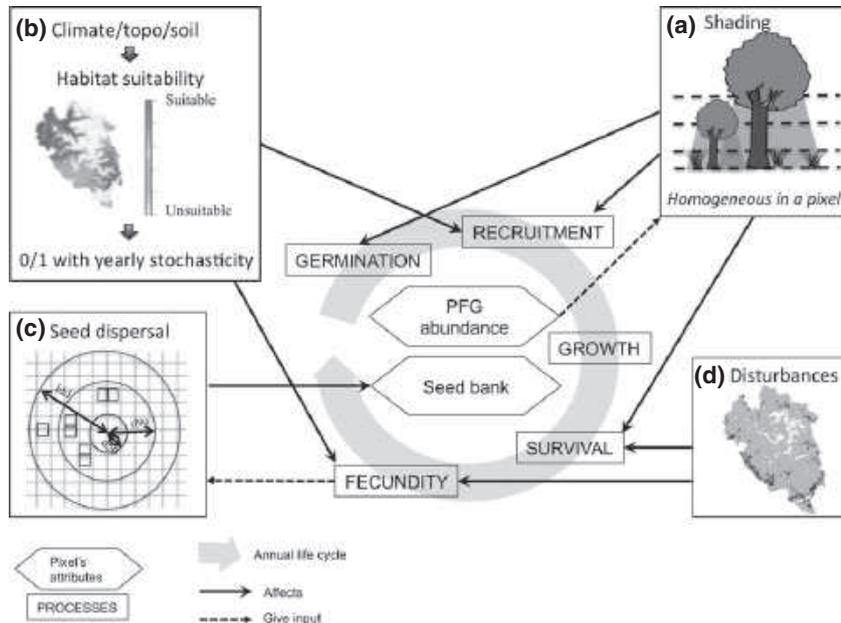
Fig. 1 Conceptual diagram of FATE-HD. The whole area is divided in grid-cells in which an independent succession model (FATE) regulates the PFG life cycle. PFG abundances are structured by age into cohorts and each cohort is attributed to a height stratum according to the growth parameters. Four submodels affect this cycle at various levels. Shading regulates interactions between cohorts affecting germination, recruitment and survival. Habitat suitability affects the recruitment and fecundity rates, and disturbances affect PFG survival and fecundity. The seed dispersal model makes FATE-HD spatially explicit by connecting grid-cells. It depends on the amount of seeds produced by mature plants and affects each PFG's seed bank in each cell.

model resolution. Five processes describe PFG demography (germination, recruitment, growth, survival and fecundity, see Table 1).

2 *Habitat suitability model*: Modelling how habitat suitability affects species population dynamics is tricky given the limited knowledge on the type and form of this relationship. Gallien *et al.* (2010) suggested a parsimonious approach using only presence-absences or a linear link. In FATE-HD, the probability for recruitment and seed production occurring is calculated every year according to the habitat suitability of the PFG in the pixel in question. Over time, the probability of presence is thus linearly related to fecundity and establishment. Accounting for interannual variability allows species coexistence via temporal niches. Mortality does not depend on habitat suitability, as the immediate effects of annual abiotic conditions on plant mortality are not clear in the literature. Habitat suitability for each PFG

can be obtained from various sources such as correlative species distribution models (Guisan & Thuiller, 2005) or mechanistic niche models (Chuine & Beaubien, 2001).

3 *Seed dispersal model*: The quantity of produced seeds depends on the abundances of mature PFGs and their habitat suitability. A seed dispersal model determines seed inflow in each pixel (Fig. 1c). From the source, three circles of influence are defined using distance parameters. In the first circle, 50% of the seeds are distributed uniformly. In the second circle, 49% of the seeds are distributed with the same concentration as in the first circle but by pairs of pixels, simulating the spatial autocorrelation of dispersed seeds. In the third circle, 1% of the seeds fall into a random pixel. This seed dispersal model behaves similar to a continuous kernel function (see Fig. S1a) but is very effective and requires only a few parameters (Vittoz & Engler, 2007).

Table 1 Demographic processes. Each demographic process is listed with its dependent variables and species traits required for the parameterization

Process	Response variable	Dependent variable	Species specific trait used for the parameterization
Germination	Germinants	Light conditions, seed bank	Shade tolerance, woodiness
Recruitment	Seedlings	Light conditions, habitat suitability, germinants	Shade tolerance, number of years at maturity
Growth	Height	Age	Longevity, maturity age, plant canopy height
Survival	Cohort abundance	Age, light conditions	Longevity, shade tolerance
Fecundity	New seeds	Mature abundance, habitat suitability	–

4 *Disturbance model*: Several disturbance models can be parameterized to remove vegetation, affect fecundity, kill seeds or activate dormant seeds according to each PFG's tolerance or sensitivity to the given disturbance. (Fig. 1d).

Case study - plant functional groups (PFGs) and parameterization

This study took place in the French Alps, in the Ecrins National Park (hereafter 'PNE') (Fig. 2) which covers a surface area of 178 400 hectares and is characterized by mountainous to alpine ecosystems (669 m to 4102 m a.s.l) with a majority of open habitats (60%), hosting a rich flora (around 2000 species). The agricultural activity consists of extensive grazing (50%), some crop fields and mown grasslands (15%), and forest management (10%).

We used the plant functional group classification proposed and validated in Boulangeat *et al.* (2012a) for the same study area. It was built using an emergent group approach based on six plant characteristics involved in the most important coexistence mechanisms when modelling vegetation dynamics: bioclimatic niche, competitive effect and response for light resources, dispersal ability, demography and response to disturbance. The 24 groups obtained (Table 2) proved to contain most of the information required to estimate vegetation biodiversity including species richness and functional diversity.

FATE-HD was run over a regular grid containing 258 582 pixels at a resolution of 100 m (Fig. 2). We defined five strata to calculate plant interactions (0–1.5 m; 1.5–4 m; 4–10 m; 10–20 m; above 20 m), which can be linked to field data (presence of three layers: 0–1 m; 1–4 m; >4 m). Demographic parameters (Table 1) were derived from the literature and expert assessment (see Appendix S2). Seed dispersal distance classes were assigned to all representative species from each PFG, from an available database built by Vittoz & Engler (2007) and other
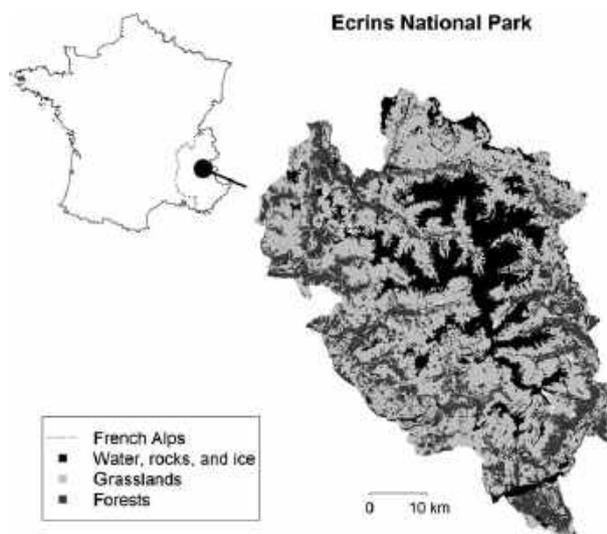
Table 2 List of the 24 plant functional groups used in the simulations to represent vegetation structure and diversity in the study area. These groups have been defined according to the species' dispersal abilities, canopy height, shade tolerance, bioclimatic niche and palatability. H1 to H10 represent herbaceous plants (mostly Hemicryptophyts). C1 to C6 represent Chamaephyts. P1 to P8 represent Phanerophyts. The interpretation was made *a posteriori* based on expert knowledge of determinant species and the PFG's average attributes

PFG	Interpretation
H1	Alpine species (which do not tolerate shade, and have a short dispersal distance)
H2	Mountainous species which tolerate nitrophilous soils and have a long dispersal distance
H3	Mountainous to lowland species found in wet niches and which have a long dispersal distance
H4	Undergrowth and shadow species which do not tolerate full light
H5	Mountainous to subalpine species which have a short dispersal distance and tolerate dry soils
H6	Tall plants typical of megaphorbiaies which can form undergrowth
H7	Plants species found in rocky habitats and undergrowth at all elevations
H8	Subalpine to alpine species not usually grazed and which have a short dispersal distance
H9	Short subalpine to alpine species which have long dispersal distance
H10	Mountainous species which have a long dispersal distance and tolerate shade
C1	Thermophilous chamaephytes which have a long dispersal distance
C2	Alpine and subalpine chamaephytes species
C3	Chamaephytes which have a short dispersal distance
C4	Tall shrubs
C5	Mountainous to subalpine heath found in dry climates
C6	Mountainous to subalpine heath found in wet climates
P1	Thermophilous pioneer trees (deciduous trees and pines)
P2	Small deciduous pioneer trees (e.g. colonizing riversides)
P3	Tall forest edge trees
P4	Tall pioneer (larch)
P5	Late succession trees found in wet climates
P6	Intermediate succession trees found in dry climates
P7	Small forest edge trees
P8	Small pioneer found in cold climates (white birch)

Ecrins National Park

French Alps
Water, rocks, and ice
Grasslands
Forests

0   10 km

Fig. 2 The study area. The Ecrins National Park is located in the geographic centre of the French Alps. For the simulations we excluded any body of water, rocks and ice (black zones).

experts. The median class was given to the group and the associated parameters were found in Vittoz & Engler (2007) and Engler & Guisan (2009) (see Appendix S2).

We considered the two ongoing annual disturbances (domestic grazing and mowing) in the park, located and characterized in the 'DELPHINE' database. This database is a comprehensive landscape mapping of the park including vegetation type, structure and associated disturbances (http://www.ecrins-parcnational.fr/telechargements/doc_

download/157-latlas-delphine.html). Following the available classification (light, extensive and intensive grazing), we built three grazing disturbance models which affected an increasing proportion of PFGs at determined locations. Five response classes were considered, depending on the age of the PFG (1 year old trees, other trees below 1.5 m, juvenile herbs, mature herbs and senescent herbs). The responses were either death or 'resprouting' that prevents mature plants from producing seeds. The proportion of affected individuals was related to the PFG's palatability class. A fourth disturbance model was created to represent mowing, and was associated to the removal of all trees above 1.5 m (see Appendix S2).

Habitat suitability was modelled for each PFG using the *biomod2* package in R (Thuiller *et al.*, 2009). The presences and absences of species representative of each PFG were extracted from the CBNA database, which includes relevés from inside the park and from the whole French Alps (Boulangeat *et al.*, 2012a), and pooled together to obtain PFG distribution. These were then related to seven environmental variables: slope, percentage of calcareous soil and five 'BIOCLIM' variables (Hutchinson *et al.*, 2009). Five different statistical models were chosen to cover a range of techniques from standard regression (e.g. Generalized Linear Model) to advanced machine learning (e.g. Generalized Boosted Models). We combined all predictions into one single output estimated as the weighted sum of predictions, the weights reflecting the models' performance (Thuiller *et al.*, 2009). The models were calibrated over the whole French Alps to avoid extrapolation issues (Thuiller *et al.*, 2004) (see Appendix S3 for details and data sources).

Simulations workflow

Our simulations aimed to reconstruct the current vegetation distribution. The landscape was first initialized with annual seeding (addition of seeds from each PFG at all locations across the map), which allows the forest canopy to form and undergrowth PFGs to settle. The seeding lasted 300 years, which was enough for all PFG distributions to reach quasi-equilibrium (Appendix S5, Fig. S5a). A stabilization phase requiring 500 additional years (Fig. S5b) was then necessary to restore a realistic demography (limited fecundity). Finally, to compare model outputs to current observations, current disturbance regimes were applied during the last 200 years of the stabilization phase (Fig. S5c). Trees above 1.5 m were first cut from all areas currently disturbed (representing past deforestation) and then annual grazing and mowing disturbances were applied. Before recording the outputs (years 10, 20, 30, 40 and 50 years after initialization), trees were again removed from managed areas mimicking the impact of regular grassland maintenance. The simulations were replicated three times and this workflow was used for all the variations presented below.

Sensitivity analyses

We first analysed the contribution of the three coexistence mechanisms (abiotic filtering, biotic interactions and dispersal) to the vegetation structure (forest cover and strata). To assess the importance of the abiotic filtering, we compared the baseline simulation to a simulation in which habitat suitability was equal to one throughout (i.e. no habitat suitability constraint) for all PFGs. The importance of biotic interactions was assessed by comparing the baseline simulation to a simulation where all species tolerated all light conditions (i.e. no mortality due to light conditions). We confronted simulated tree cover (above 1.5 m) with empirical observations in 3345 plots (covering 20% of the studied area) where the observed vegetation structure was assumed to be homogeneous at a resolution of 100 m. As observed tree cover has been estimated on plots covering on average 9000 m^2, we applied a focal statistic to both observed and simulated maps which assigned each cell with the average value of the nine adjacent cells. The results are presented separately for seven habitat types (alpine natural grasslands, subalpine unexploited habitats, exploited grasslands and meadows, mountainous forests, mountainous open habitats, lowlands and rocky habitats, see Appendix S4). We also confronted the simulated abundance of three layers (0–1.5 m; 1.5–4 m; above 4 m) with the observed layer's presence or absence in nonopen habitats (2189 plots).

Finally, the effect of dispersal limitations was tested using two additional simulation scenarios. Dispersal distance limitations were released in a simulation where dispersal distance was considered to be unlimited, but the production of seeds was still determined by population size. The effect of seed production on dispersal limitations was investigated with a simulation where a seeding (seeds added at all locations across the map) occurred every 5 years. For all simulations, the colonization dynamic was followed using the percentage of tree cover (above 1.50 m) recorded every 5 years, for disturbed and undisturbed areas separately.

Model accuracy

Measuring the accuracy of biodiversity models for a region where the modelled entities (PFGs) are not explicitly recorded in the field is challenging. In coherence with the simulations' spatial grain, we used the 'DELPHINE' database, which describes vegetation composition and structure for 18 381 plots covering the whole park. We removed wetlands, lakes and villages from the analysis. We established a correspondence table between the 90 vegetation types described in DELPHINE and our 24 PFGs (Appendix S4). For each vegetation type, a PFG was either considered as expected absent, or surely present (i.e. representative of the vegetation type), or potentially present.

Simulated PFG abundances were converted into presence-absences with a threshold chosen to maintain prevalence at the same level as in the observed plots. Model performance (sensitivity, specificity and error rate) was assessed using 8841 sampled plots where vegetation types have been described. These plots constitute a completely independent data set from the one used to calibrate the HSMs. For each PFG, we also compared the HSM predictions to the FATE-HD predictions to test the overall effect of including biotic interactions, dispersal and disturbances in addition to the abiotic filter.

Results

Sensitivity of the vegetation structure to biotic and abiotic forcing

In the baseline simulation, tree cover was, on average, slightly overestimated (+4%, Fig. 3). However, it varied amongst habitat types. Tree cover in lowlands and mountainous forests was underestimated (−10% and −4% respectively) but was overestimated in rocky and alpine habitats (+7%). In forests, the abundance of each stratum was higher in the pixels where it was observed (Fig. 4). However, the difference in simulated abundances between locations where the stratum has been observed or not was small for the lowest stratum (herbaceous) (Fig. 4a).

The removal of competition for light did not significantly change the tree cover simulations (15% overestimation on average). However, in this case, abundance in the lower strata (<1.5 m) was similar across pixels regardless of whether the layer was observed or not (Fig. 4a). Removing the abiotic constraint generally led to more pixels being colonized by the forest. In particular, rocky and alpine habitats were largely colonized by trees (Fig. 3). In consequence, in this case the whole forest structure was wrongly predicted (Fig. 4).

Effects of dispersal limitations

In the baseline simulation, tree cover stabilized around 250 years after the seeding phase (Fig. 5a). This broadly corresponds to the average life span of phanerophyt PFGs. At low elevations (below 1800 m a.s.l.), average tree cover slightly decreased over time, suggesting a potential edge effect (no seeds are received from outside of the study area). Tree cutting (to create managed areas) had a similar effect given that sources (mature trees) established in managed areas were removed, which disturbed the source-sink dynamic and decreased the abundance of adjacent forests (Fig. 5a). Under current management, the simulated trees slowly colonize pastures and meadows. This is consistent with the known regular human interventions on tree seedlings in grazed or mown areas.

Both unlimited dispersal distance and regular seeding scenarios showed deviations from the baseline simulation, highlighting the importance of dispersal limitation to obtain realistic vegetation dynamics. With an unlimited dispersal distance, tree abundance significantly decreased after seeding or tree cutting, dropping to a lower level than in the baseline simulation. Indeed, because the seeds of each PFG are regularly dispersed over the whole grid, a higher proportion of seeds fell into unsuitable grid-cells with no chance of
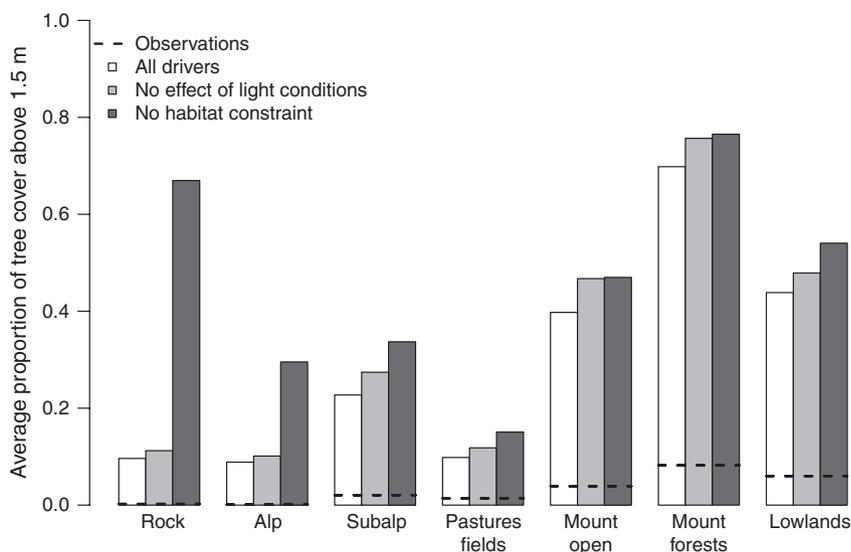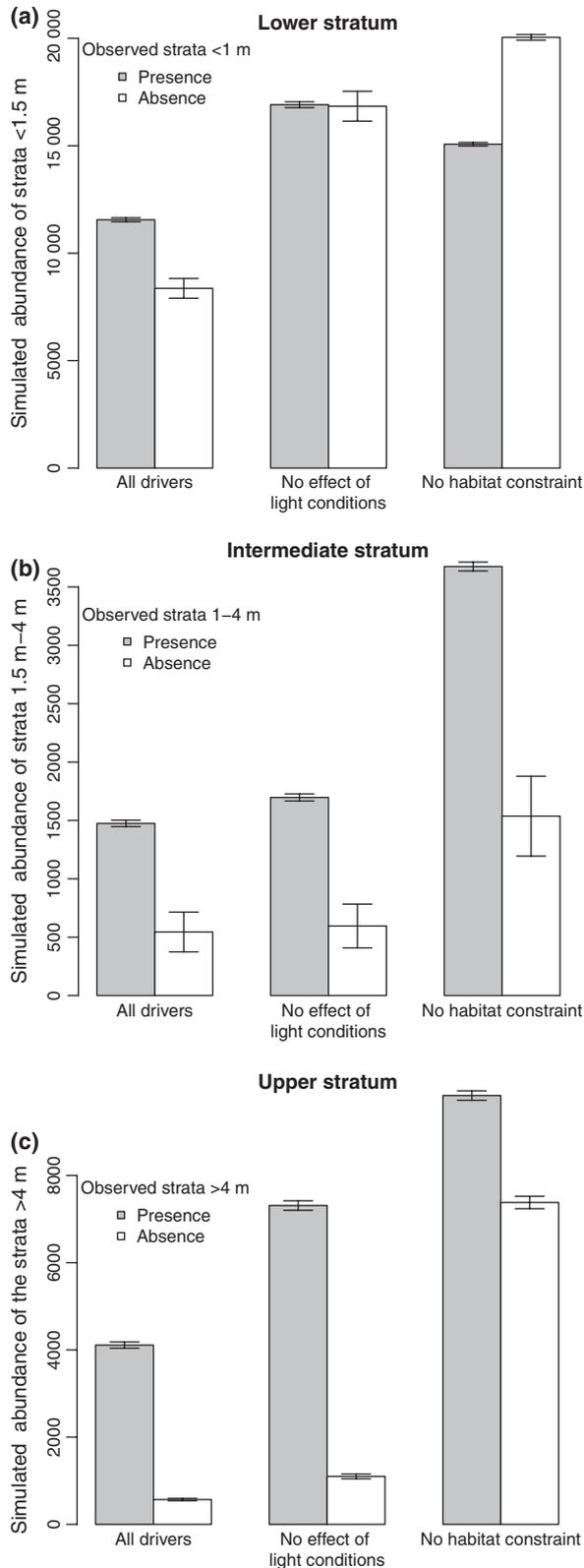

Fig. 3 Observed and simulated tree cover across habitat types. Three simulations are compared with observations. (i) A baseline simulation (All drivers), (ii) a simulation without the light conditions constraint and (iii) a simulation without the habitat constraint. The results are given for seven habitats: rocky habitats (rocks, 21 444 pixels); alpine unexploited habitats including snow-packs, crests on calcareous and silica and other grasslands (alp, 1395 pixels); subalpine unexploited habitats (subalp, 2909 pixels); grazed and mown habitats at all elevations (pastures and fields, 1420 pixels); open habitats of the mountainous belt (mount open, 367 pixels); young and mature mountainous forests (mount forests, 3246 pixels); Mediterranean and colline vegetation (lowlands, 100 pixels). The dashed line corresponds to the observations.

(a)

Lower stratum

(b)

Intermediate stratum

(c)

Upper stratum

Fig. 4 Observed presence or absence vs. simulated abundance of forest strata. The average simulated abundance for each stratum across analysed pixels is confronted with the recorded presence or absence of each stratum. Three simulations are compared: (i) a baseline simulation (all drivers), (ii) a simulation without light condition constraints and (iii) a simulation without the habitat constraint. (a) Lower stratum (b) Intermediate stratum (c) Upper stratum. Note that there is a small discrepancy for the first height threshold between the observations (1 m) and the simulations (1.5 m).

colonization rate was both limited by dispersal distance and tree demography which determines the production of seeds by mature plants.

Accuracy: FATE-HD vs. HSM

On average, FATE-HD predicted PFG distributions better (error rate = 0.32) than HSMs (error rate = 0.38), although the difference varied across PFGs. FATE-HD improved the simulated distributions of most PFGs with a restricted tolerance to light levels (H3, H4, H9, C3, P3, P4, P5, P6, P7) by refining their distribution (higher specificity, see Table 2; Fig. 6). However, the biotic constraints applied by FATE-HD appeared too stringent for some PFGs (H3, P3 and P7) resulting in low sensitivity (Table 3). FATE-HD also performed better than HSM for phanerophyt PFGs sensitive to the grazing disturbance, whether restricted by shade tolerance or not (P1, P2, P4). On the contrary, simulated distributions of PFG unconstrained by disturbance, shade tolerance or dispersal limitation as expected did not improve using FATE-HD (e.g. H7, Fig. 6).

Discussion

Integrating the different processes shaping biodiversity into a single modelling framework is crucial as it makes it possible to assess their interacting effects (Thuiller *et al.*, 2013). The substantial work in landscape ecology to build mechanistic plant succession models based on life history traits and competition for light constitutes a strong basis from which this goal can be achieved (Noble & Slatyer, 1980). The model presented here expands the one proposed by Moore & Noble (1990), including abiotic constraints, spatially explicit seed dispersal and disturbance regimes (Albert *et al.*, 2008; Midgley *et al.*, 2010).

Abiotic constraints

The effects of abiotic constraints (e.g. climate) are integrated into the succession model as environmental forcing, influencing both fecundity and recruitment.
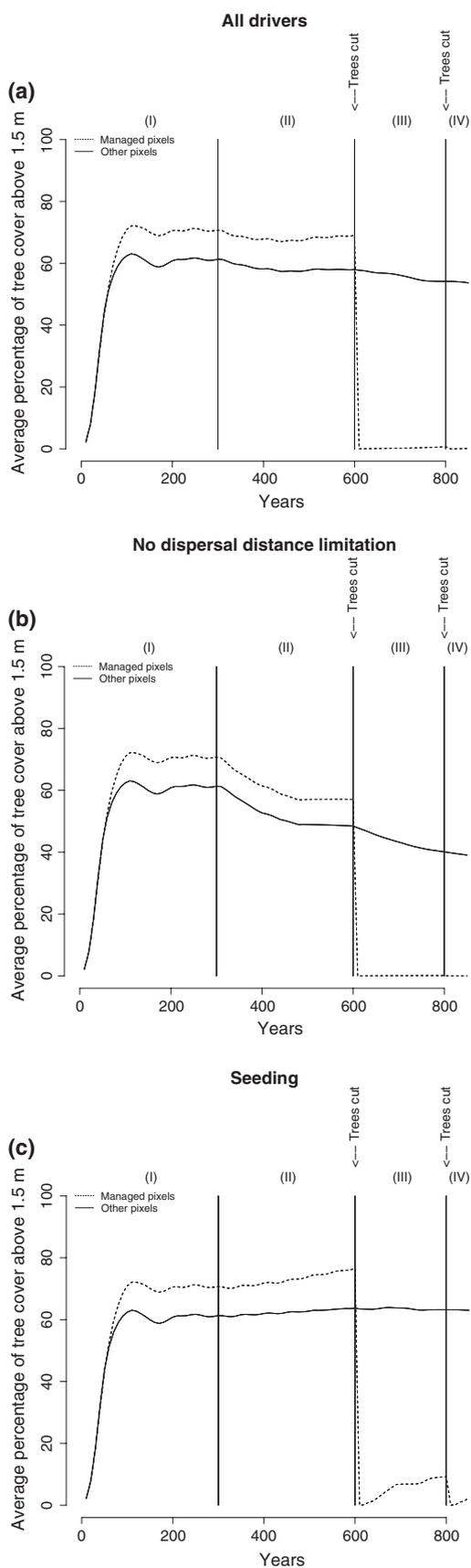
recruitment. Conversely, with regular seeding, tree cover after disturbance increased faster than in the baseline simulation. These results suggest that the tree

(a) All drivers

(b) No dispersal distance limitation

(c) Seeding

Fig. 5 Temporal change in tree cover above 1.5 m during the simulations. The simulation encompasses four phases: (I) Seeding (continuous addition of seeds of all PFG everywhere), (II) Stabilization (no seeding anymore), (III) Current disturbance regime is set up, (IV) Quasi-equilibrium; outputs are recorded. All trees located in areas currently grazed or mown were cut prior to settling current grazing and mowing regimes that occur where the forest has been removed in the past. Trees were cut again prior to recording results because the current grazing pressure is unable to maintain open the grasslands, which are then regularly maintained open through human intervention. Results from the three repetitions are overlaid. Grid-cells are grouped if they are disturbed (mown or grazed) or not (a) Simulation with regular parameters. (b) Simulation with unlimited dispersal distance for all PFGs (c) Simulation with seeding every 5 years in the last two phases which gives an unlimited seed production in addition to unlimited dispersal distance (III and IV).

Abiotic constraints are modelled at regional scale to determine the suitability of the abiotic environment in each grid-cell. Community dynamics then occur within the grid-cells, with an appropriate level of detail for landscape modelling. The integration of this physiological aspect, although treated using correlative HSM in our example, means FATE-HD is applicable under climate change scenarios and takes into account all the abiotic drivers relevant at the study grain (100m). Our simulations have shown that the climate and soil drivers used limit tree colonization in the alpine belt (Fig. 3), particularly in siliceous alpine crests (details not shown). Alternatively, habitat suitability could be determined based on expert knowledge or a process-based model.

As in Conlisk *et al.* (2013), we found that habitat suitability models had a high impact on model outputs. It is particularly crucial to minimize type II errors (false negatives) because the way FATE-HD integrates habitat suitability makes it possible to refine PFG distributions within their habitat limits (see Fig. 6). Conversely, false positives might be tolerated in the habitat model as other processes are involved in limiting PFG distributions. In our example, specificity (proportion of correct absences) generally increased when additional constraints to HSM were applied, and error rates were consequently reduced (Table 3). Similarly, HSMs have been shown to overpredict species richness, especially at intermediate climatic conditions (Pineda & Lobo, 2012; Pottier *et al.*, 2013). However, as in Pottier *et al.* (2013), we show that this pattern varies across species, depending on if the species is subject to competition for light (e.g. P1), or if its distribution is mainly determined by abiotic constraints (e.g. H7). The recurring conclusion is that additional factors such as species interactions and disturbances should be accounted for.
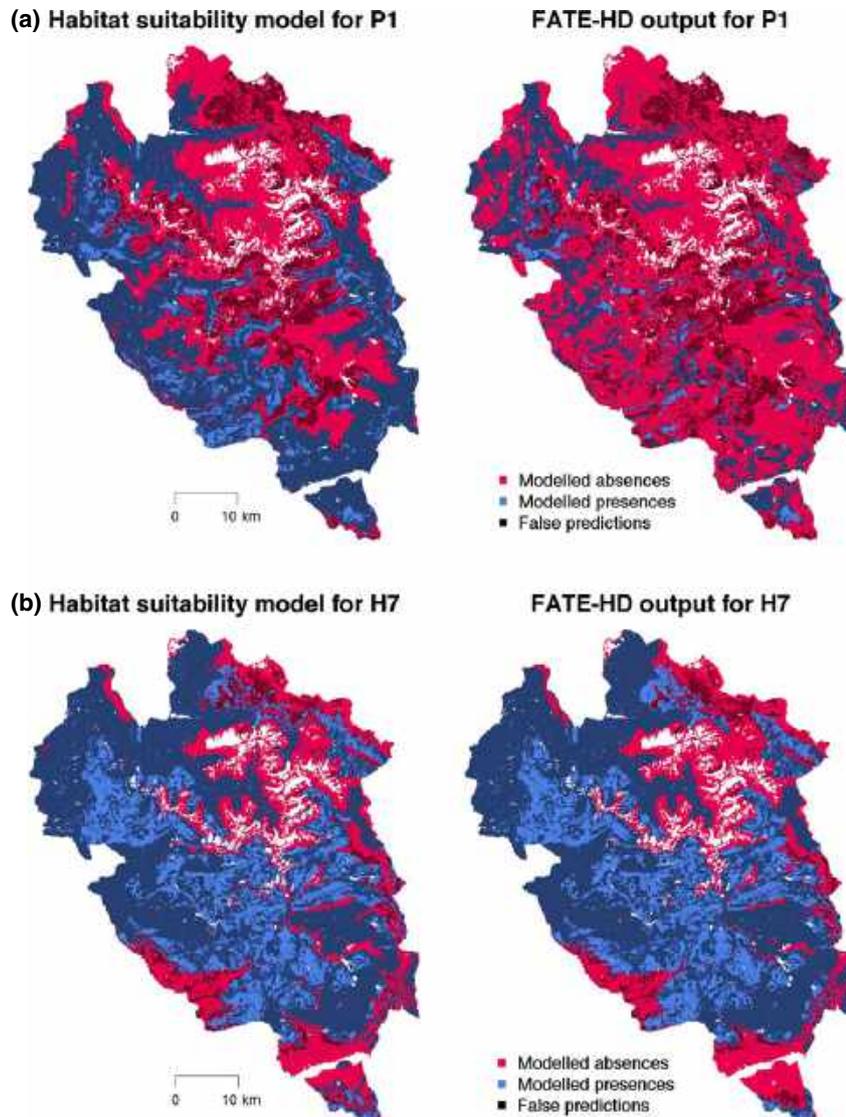
(a) Habitat suitability model for P1   **FATE-HD output for P1**

■ Modelled absences
■ Modelled presences
■ False predictions

(b) Habitat suitability model for H7   **FATE-HD output for H7**

■ Modelled absences
■ Modelled presences
■ False predictions

Fig. 6 Habitat suitability maps and FATE-HD outputs vs. for two PFGs. Given that there is very little variation from one repetition to another, the map presented here is from one repetition. Modelled absences (red) and presences (blue) are darkened where false predictions have been detected (a) Distribution of P1 (Thermophilous pioneer trees) (b) Distribution of H7 (Plants species found in rocky habitats and undergrowth at all elevations).

Biotic interactions

The simulations have shown that biotic interactions through competition for light are necessary to model a realistic forest structure (Fig. 4). Including both abiotic and biotic constraints in landscape dynamics thereby improves predictions for many PFGs, especially phanerophyts, undergrowth species or shade intolerant species (Table 3). On the other hand, the vegetation structure analysis suggests that herbaceous PFG distributions are not sufficiently restricted (Fig. 4a). This is unsurprising as no competition occurs between herbaceous PFGs, which share the same stratum. However,

producing a more comprehensive representation of these competitive interactions is a genuine challenge. As this is an annual model, a herbaceous species that grows late in the season would not compete for light with an early-season species. Taking competition for soil resources into account would be a major improvement but existing soil resource models require numerous parameters which are not necessarily fully available on large spatial scales. Temporal niches may also be relevant, because they may counterbalance a species' competitive ability (Alexander *et al.*, 2012). FATE-HD may include seed dormancy (Appendix S1), but the major issue is again the lack of data to

Table 3 Predictive accuracy of FATE-HD and traditional habitat suitability models used to model PFG distributions. FATE-HD outputs are compared to simple habitat suitability models (HSM). Bold numbers represent the model with the best performance. Observed absences correspond to vegetation types where a PFG is unexpected. Observed presences are located where a PFG is characteristic of the vegetation type. Model performance indices do not vary from one repetition to another. Sensitivity and specificity represent the proportion of PFGs correctly predicted present or absent, respectively

PFG	Specificity (% correct absences)		Sensitivity (% correct presences)		Error rate		Nb observed absences	Nb observed presences
	FATE-HD	HSM	FATE-HD	HSM	FATE-HD	HSM		
H1	0.36	**1.00**	**0.90**	0.00	0.45	**0.36**	3306	1827
H2	0.12	**0.20**	0.92	**0.93**	0.67	**0.60**	1965	737
H3	**0.95**	0.44	0.06	**0.78**	**0.18**	0.51	3996	717
H4	**0.89**	0.62	0.18	**0.57**	**0.19**	0.38	5696	729
H5	0.26	**0.32**	0.88	0.88	0.58	**0.54**	2454	840
H6	0.55	**0.59**	**0.65**	0.61	0.43	**0.40**	4131	1006
H7	**0.36**	0.33	0.66	**0.72**	**0.57**	0.59	4102	1104
H8	0.60	**0.71**	**0.58**	0.52	0.40	**0.30**	4378	190
H9	**0.66**	0.58	0.25	**0.63**	**0.36**	0.42	6053	391
H10	0.59	**0.61**	0.46	**0.52**	0.42	**0.40**	5333	506
C1	0.42	**0.51**	0.82	**0.87**	0.53	**0.44**	3160	501
C2	0.57	**1.00**	**0.84**	0.00	0.38	**0.19**	4288	994
C3	0.47	0.47	0.94	**0.96**	0.32	**0.31**	3253	2632
C4	**0.90**	0.64	0.40	**0.75**	**0.19**	0.34	3529	827
C5	**0.75**	0.57	0.26	**0.52**	**0.31**	0,44	3179	478
C6	0.57	**0.60**	0.59	**0.64**	0.43	**0.40**	4953	551
P1	**0.89**	0.56	0.32	**0.75**	**0.15**	0.43	3448	225
P2	**0.85**	0.64	0.30	**0.56**	**0.17**	0.36	5811	171
P3	**0.97**	0.66	0.10	**0.64**	**0.06**	0.34	5182	210
P4	**0.77**	0.66	0.35	**0.62**	**0.27**	0.34	5743	702
P5	**0.84**	0.78	0.57	**0.60**	**0.17**	0.22	7482	320
P6	**0.68**	0.47	0.46	**0.63**	**0.32**	0.53	5157	180
P7	**0.94**	0.81	0.08	**0.22**	**0.08**	0.21	6342	171
P8	0.90	**0.98**	**0.15**	0.06	0.12	**0.04**	8044	171

parameterize dormancy for all PFGs. Model performance might also be improved by adding local stochastic disturbances such as avalanches or rock falls that would allow shade intolerant PFG and trees to coexist. Indeed, FATE-HD overpredicts tree cover in subalpine, alpine, rocky and open mountainous habitats where avalanches and rock falls are common.

Spatio-temporal dynamics

Population dynamics and dispersal are modelled in FATE-HD in the same way as in other landscape models. The individuals are grouped into cohorts to model species demography, and dispersal kernel functions are used to disperse the produced seeds over the gridded study area. Nevertheless, FATE-HD integrates simplified algorithms. It uses a simple semiquantitative approach to describe plant succession (FATE, Moore & Noble, 1990), and proposes a stochastic dispersal algorithm that is on average similar to a traditional kernel function but more computationally efficient

(Appendix S1). This strategy means the model can include numerous functional groups and uses available data (e.g. Vittoz & Engler 2007).

Our work is the first to present and test a spatially explicit model involving multiple entities capable of representing vegetation diversity, whilst integrating the main coexistence mechanisms. In protected areas, it would make it possible to forecast both final and transient vegetation states in response to climate and land use change scenarios. It could also be used to test community ecology theories. For instance, FATE-HD models neutral community dynamics when PFGs have the same functional traits except dispersal ability. Conversely, including differences in terms of recruitment, survival and growth, but not in dispersal ability would lead to an extreme case of pure niche theory.

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References

Albert CH, Thuiller W, Lavorel S, Davies ID, Garbolino E (2008) Land-use change and subalpine tree dynamics: colonization of Larix decidua in French subalpine grasslands. *Journal of Applied Ecology*, **45**, 659–669.

Alexander HM, Foster BL, Ballantyne F, Collins CD, Antonovics J, Holt RD (2012) Metapopulations and metacommunities: combining spatial and temporal perspectives in plant ecology. *Journal of Ecology*, **100**, 88–103.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecology letters*, **15**, 365–377.

Boulangeat I, Gravel D, Thuiller W (2012a) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology letters*, **15**, 584–593.

Boulangeat I, Philippe P, Abdulhak S et al. (2012b) Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and comunity ecology. *Global Change Biology*, **18**, 3464–3475.

Bugmann H (2001) A review of forest gap models. *Climatic Change*, **51**, 259–305.

Chuine I, Beaubien EG (2001) Phenology is a major determinant of tree species range. *Ecology Letters*, **4**, 500–510.

Conlisk E, Syphard AD, Franklin J, Flint L, Flint A, Regan H (2013) Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. *Global change biology*, **19**, 858–869.

Daly C, Bachelet D, Lenihan JM, Neilson RP, Parton W, Ojima D (2000) Dynamic simulation of tree-grass interactions for global change studies. *Ecological Applications*, **10**, 449–469.

Dormann CF, Schymanski SJ, Cabral J et al. (2012) Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, **39**, 2119–2131.

Dullinger S, Gattringer A, Thuiller W et al. (2012) Extinction debt of high-mountain plants under 21st-century climate change. *Nature Climate Change*, **2**, 619–622.

Engler R, Guisan A (2009) MigClim: predicting plant distribution and dispersal in a changing climate. *Diversity and Distributions*, **15**, 590–601.

Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, Sitch S, Haxeltine A (1996) An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Global Biogeochemical Cycles*, **10**, 603–628.

Gallien L, Münkemüller T, Albert CH, Boulangeat I, Thuiller W (2010) Predicting potential distributions of invasive species: where to go from here? *Diversity and Distributions*, **16**, 331–342.

Giannini TC, Chapman DS, Saraiva AM, Alves-dos-Santos I, Biesmeijer JC (2013) Improving species distribution models using biotic interactions: a case study of parasites, pollinators and plants. *Ecography*, **36**, 649–656.

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

Harrison SP, Prentice IC, Barboni D, Kohfeld KE, Ni J, Sutra J-P (2010) Ecophysiological and bioclimatic foundations for a global plant functional classification. *Journal of Vegetation Science*, **21**, 300–317.

He HS, Mladenoff DJ, Boeder J (1999) An object-oriented forest landscape model and its representation of tree species. *Ecological Modelling*, **119**, 1–19.

Hickler T, Smith B, Sykes MT, Davis MB, Sugita S, Walker K (2004) Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA. *Ecology*, **85**, 519–530.

Hutchinson M, Xu T, Houlder D, Nix H, Mcmahon J (2009) *ANUCLIM 6.0 User's Guide.* Fenner School of Environment and Society, Australian National University, Canberra.

Keith DA, Akçakaya HR, Thuiller W et al. (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560–563.

Kissling WD, Dormann CF, Groeneveld J et al. (2012) Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, **39**, 2163–2178.

Kunstler G, Lavergne S, Courbaud B et al. (2012) Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology letters*, **15**, 831–840.

Lischke H, Zimmermann NE, Bolliger J, Rickebusch S, Löffler TJ (2006) TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling*, **199**, 409–420.

Meier ES, Kienast F, Pearman PB et al. (2010) Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography*, **33**, 1038–1048.

Midgley GF, Davies ID, Albert CH et al. (2010) BioMove - an integrated platform simulating the dynamic response of species to environmental change. *Ecography*, **33**, 612–616.

Moore AD, Noble IR (1990) An individualistic model of vegetation stand dynamics. *Journal of Environmental Management*, **31**, 61–81.

Noble IR, Slatyer RO (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Plant Ecology*, **43**, 5–21.

Perry GLW, Enright NJ (2006) Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. *Progress in Physical Geography*, **30**, 47–72.

Pineda E, Lobo JM (2012) The performance of range maps and species distribution models representing the geographic variation of species richness at different resolutions. *Global Ecology and Biogeography*, **21**, 935–944.

Pottier J, Dubuis A, Pellissier L et al. (2013) The accuracy of plant assemblage prediction from species distribution models varies along environmental gradients. *Global Ecology and Biogeography*, **22**, 52–63.

Pulliam HR (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652–661.

Pulliam HR (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.

van der Putten WH, Bardgett RD, de Ruiter PC et al. (2009) Empirical and theoretical challenges in aboveground-belowground ecology. *Oecologia*, **161**, 1–14.

Sitch S, Smith B, Prentice IC et al. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.

Thuiller W, Brotons L, Araújo MB, Lavorel S (2004) Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, **27**, 165–172.

Thuiller W, Albert CH, Araújo MB et al. (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 137–152.

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD - a platform for ensemble forecasting of species distributions. *Ecography*, **32**, 369–373.

Thuiller W, Lavergne S, Roquet C, Boulangeat I, Lafourcade B, Araujo MB, Araújo MB (2011) Consequences of climate change on the tree of life in Europe. *Nature*, **470**, 531–534.

Thuiller W, Münkemüller T, Lavergne S, Mouillot D, Mouquet N, Schiffers K, Gravel D (2013) A road map for integrating eco-evolutionary processes into biodiversity models. *Ecology letters*, **16**, 94–105.

Vittoz P, Engler R (2007) Seed dispersal distances: a typology based on dispersal modes and plant traits. *Botanica Helvetica*, **117**, 109–124.

Woodward FI (1987) *Climate and Plant Distribution*. Cambridge University Press, Cambridge.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed model description.
Appendix S2. PFG Parameterization for the submodels.
Appendix S3. Habitat suitability models.
Appendix S4. PFGs to vegetation types correspondence table.
Appendix S5. Initialization.