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SPECIAL ISSUE

Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model

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ABSTRACT

Aim To assess the extent to which climate change might cause changes in potential natural vegetation (PNV) across Europe.

Location Europe.

Method We parameterized a generalized dynamic vegetation model (LPJ-GUESS) for the most common European tree species, and, for the first time, modelled large-scale vegetation dynamics using a process-based model explicitly representing tree species, age cohorts, gap dynamics and biogeochemical cycles in a single framework. For projections, the model was driven with climate scenario data from two atmosphere–ocean general circulation models (AOGCMs), downscaled to $10 \times 10'$ spatial resolution (*c.* 18.5×12 km at 50° N).

Results At a general level, modelled present-day PNV corresponded better with an expert reconstruction of the PNV than most earlier plant functional type (PFT)-based simulations, but at a finer scale the model and the expert map showed substantial discrepancies in some areas. Simulations until 2085 showed considerable successional shifts in vegetation types in most areas: 31–42% of the total area of Europe was projected to be covered by a different vegetation type by the year 2085. In the long term, equilibrium changes are substantially larger: simulations with one climate scenario suggest that 76–80% of the European land surface could exist within another PNV if climate was stabilized by the end of the century and vegetation had unlimited time to achieve equilibrium with the new climate. 'Hotspots' of change include arctic and alpine ecosystems, where trees replace tundra in the model, and the transition zone between temperate broad-leaved and boreal conifer forest. In southern Europe, the model projected widespread shifts from forest to shrublands as a result of drought.

Main conclusions The model presents a considerable advance in modelling dynamic changes in natural vegetation across Europe. Climate change might cause substantial changes in PNV across Europe, which should be considered in the management of reserves and forestry.

Keywords
Biodiversity, climate change, dynamic vegetation modelling, Europe, forest response, LPJ-GUESS, nature conservation, vegetation shifts.

INTRODUCTION

During the coming decades and centuries, climate change will strongly affect the distribution of species, habitats and biodiversity (Fischlin *et al.*, 2007). Despite uncertainties in future greenhouse gas (GHG) emissions, their atmospheric concentrations and the resulting regional climate change, projections of the possible extent of these impacts are essential for climate adaptation.

Existing projections of the effects of climate change on species and biodiversity are based on one of three different approaches. Firstly, analyses of shifts in climate space have shown that European climatic zones might, on average, move northwards by 272–645 km by 2100 (compared with pre-warming conditions – average climate for 1931–60), depending on the climate scenario (Ohlemüller *et al.*, 2006). Secondly, bioclimatic envelope models have been widely used for projecting changes in species distributions and biodiversity (e.g. Bakkenes *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005). Using this technique, Thuiller *et al.* (2005) estimated that more than half of the 1350 European plant species studied could be vulnerable in their present locations or threatened by 2080. Envelope modelling has also been used to assess reserve-selection methods under climate change (Araújo *et al.*, 2004), but the realism of projections of species-specific geographic distributions based upon the bioclimatic envelope concept has been questioned (Pearson & Dawson, 2003; Botkin *et al.*, 2007). The criticism has particularly concerned the implicit assumption of equilibrium between species distributions and climate (Svenning & Skov, 2004). Furthermore, biotic interactions, the effects of increasing levels of atmospheric CO_2 on plant productivity (Ainsworth & Long, 2005) and terrestrial water cycling (Gerten *et al.*, 2005) are not accounted for in bioclimatic envelope models.

The third approach is to use process-based dynamic vegetation models, either based on tree species and including detailed representations of competition, tree population dynamics and forest succession (Bugmann, 2001), or so-called dynamic global vegetation models (DGVMs), which simulate changes in the distribution of plant functional types (PFTs), yielding broad vegetation types or biomes (Prentice *et al.*, 2007). Tree species-based dynamic models are often parameterized for particular study sites or regions and have rarely been applied for projecting large-scale changes in vegetation (Badeck *et al.*, 2001; but see Koca *et al.*, 2006). Most DGVMs simulate transient changes in vegetation and ecosystem properties, including the effects of increasing CO_2 and competition between different types of plants. The parameterization is based as much as possible on general physiological principles, rather than being site- or region-specific. Physiological parameters are estimated from laboratory or field experiments that are independent from – and are often obtained at a lower level of biological hierarchy than – the model output of interest, which often concerns high-level ecosystem processes such as net carbon uptake or release. The vegetation is, however, represented in terms of a small number of PFTs, and vegetation dynamics are generally highly simplified. Furthermore, DGVMs might underestimate future changes

because many species have narrower niches than the broadly defined PFTs, which summarize large numbers of species (Fischlin *et al.*, 2007), and the vegetation classification in the PFT-based DGVMs is too coarse for inferring regional-scale guidelines for adaptation.

For this study, we have parameterized a generalized dynamic vegetation model (LPJ-GUESS; Smith *et al.*, 2001), which integrates ecophysiological process descriptions from the LPJ-DGVM (Sitch *et al.*, 2003) with detailed representations of vegetation dynamics, as commonly used by tree species-based forest gap models (Bugmann, 2001), for the most common European tree species and additional PFTs, in order to represent the potential natural vegetation (PNV) of Europe. We applied the model with present-day climate and compared the modelled current vegetation with an independently derived expert map (Bohn *et al.*, 2003). Then we used the model to project transient (until the year 2085) and equilibrium changes in PNV across Europe. As an example of potential implications for climate change adaptation, the modelled vegetation shifts were overlaid on a gridded dataset of the Europe-wide Natura 2000 protected area network.

MATERIALS AND METHODS

Vegetation model

LPJ-GUESS (Smith *et al.*, 2001) combines the generalized representations of the physiological and biophysical processes embedded in the widely used global model LPJ-DGVM (Sitch *et al.*, 2003) with detailed representations of tree population dynamics, resource competition and canopy structure, as generally used in forest gap models (Bugmann, 2001). LPJ-GUESS can be run in different modes, with different levels of abstraction of the population and community processes. For this study, the more detailed 'cohort' mode was used, in which individuals, patches and vertical canopy structure are represented explicitly, but living individuals within a cohort (age class) of a given tree species in a given patch are assumed to be identical (in terms of all state variables, such as height and stem diameter). Not accounting for differences within cohorts increases the computational efficiency. A complete description is given in Smith *et al.* (2001) and Gerten *et al.* (2004), the latter describing updates of the hydrology scheme. A summary, details of recent updates and species parameters are given in the Supporting Information (Appendix S1).

Parameterizing European tree species and PFTs

LPJ-GUESS has been parameterized for a set of PFTs representing woody vegetation across Europe (Smith *et al.*, 2001; Morales *et al.*, 2007) as well as tree species in the north-eastern USA (Hickler *et al.*, 2004) and Scandinavia (Koca *et al.*, 2006; Miller *et al.*, 2008; Smith *et al.*, 2008; Wolf *et al.*, 2008). For this study, we parameterized the main tree species as well as other PFTs yielding an appropriate representation of European vegetation, including only tree and shrub species that are widely distributed

across Europe and can become dominant in some areas. Nomenclature follows the Atlas Florae Europaeae (http://www.luomus.fi/english/botany/afe/index.htm). Species with restricted distributions were not included because many of these may be limited by factors other than climate (Svenning & Skov, 2004). Using widely distributed tree species also has the advantage that their physiology and ecology is relatively well understood. The dominance criterion was used in order to focus on species that are commonly used to distinguish major vegetation types. In the case of closely related and ecologically similar species (e.g. *Quercus robur* and *Quercus petraea*), the species with the wider distribution and ecological tolerance was used (*Q. robur* in this example). Mediterranean rain-green small shrubs with shallow roots (e.g. *Lavendula* spp., *Rosmarinus* spp.) and alpine/arctic shrubs (e.g. *Vaccinium* spp.) were represented as PFTs in the model. As in earlier applications of LPJ-GUESS, herbaceous vegetation was represented by two 'generic herb' PFTs, with C_3 and C_4 photosynthesis, respectively. The final set of species and PFTs (Table S1.1 in Appendix S1) included 16 tree species, two mediterranean tall shrubs, one mediterranean shrub PFT, one boreal/alpine shrub PFT, and two herbaceous PFTs. This set is similar to the set of species used to distinguish major classes of the PNV of Europe by Bohn *et al.* (2003; see below). The model did not represent vegetation classes restricted to waterlogged soil conditions, usually caused by topographic conditions and the proximity to rivers, and classes with very restricted distribution.

Model parameters for the species and PFTs were based on parameters for corresponding PFTs in the original version of the model (Smith *et al.*, 2001; Sitch *et al.*, 2003), with a number of updates and species-specific variations, as outlined below and summarized in Tables S1.1 & S1.2 in Appendix S1. As bioclimatic limits, we only used variables that are clearly linked to known physiological mechanisms: minimum winter temperature for survival ($T_{c,min}$), minimum requirement for yearly sum of temperatures above 5 °C (growing degree days; GDD_5) and maximum winter temperatures for establishment were taken from Sykes *et al.* (1996). For those species that were not included in Sykes *et al.* (1996), bioclimatic limits were derived by visual comparison between species distributions and the values of bioclimatic variables, averaged for 1950–80 from a global gridded 0.5° climate dataset (Mitchell & Jones, 2005). As a measure of a species' ability to endure drought at the sapling stage, we included a minimum average growing season (where daily temperatures are above 5 °C) fraction of plant-available water holding capacity (fAWC) in the first soil layer as an additional bioclimatic limit for establishment. Changes in fAWC also reflect effects of elevated CO_2 on transpiration, and thereby water availability (Gerten *et al.*, 2005; Hickler *et al.*, 2009), which is not the case for most traditionally used drought indices. The different shade-tolerance classes (Table S1.2 in Appendix S1; Smith *et al.*, 2001; Hickler *et al.*, 2004) were reparameterized by reassessing the literature concerning physiological and population dynamics differences between trees with different shade tolerance and by reparameterizing them within uncertainty bounds, such that the model reproduced known patterns of

forest development through time in a general sense (see Appendix S2 for details). The capability of the model to reproduce site-scale vegetation structure and composition for different forest types across Europe was then evaluated by comparing model output with observational data from 10 European pristine forests (Appendix S2). The results from this evaluation suggest that the model is indeed capable of simulating vegetation composition and structure for a variety of forest types in Europe. For example, the model predicted the correct vegetation class in eight out of ten forests, and the right dominant species for seven forests.

Further parameters that differed between species included the maximum non-stressed longevity, resistance to fire disturbance, relative allocation of roots to different soil layers, leaf area to sapwood cross-sectional area ratio and needle or leaf longevity (see Table S1.1 in Appendix S1).

Environmental driving data and modelling protocol

We used a gridded climate dataset of mean monthly temperature, precipitation and cloud cover for the European land surface from 1901–2100 at $10 \times 10'$ spatial resolution (*c.* 18.5×12 km at 50° N; Fronzek *et al.* 2010). The period 1901–2000 was constructed from interpolated observations. Climate input for 2001–2100 was derived from two atmosphere–ocean general circulation models (AOGCMs; HadCM3 and NCAR-PCM) driven with the SRES A2 emission scenario, corresponding to the ALARM scenario BAMBU ('business as might be usual') (Spangenberg *et al.*, 2012). These two climate scenarios were selected to be representative of larger ensembles of temperature and precipitation projections for Europe. Using HadCM3 with the B1 GHG emission scenario [ALARM scenario 'sustainable European development goal' (SEDG); with lower GHG emissions than A2], for example, yields stronger impacts on vegetation and more warming than using the colder NCAR-PCM with the high emission scenario A2 (results not shown). However, they nevertheless span only a part of the uncertainty range (Fronzek *et al.*, 2010). Key characteristics of the climate scenarios are described in Table 1, and more details are given in Appendix S3.

Model input in terms of soil texture was derived by disaggregating a 0.5° global soil texture dataset (Sitch *et al.*, 2003). His-

Table 1 Key characteristics of the climate change scenarios. Changes in temperature (ΔT) and precipitation (ΔP) for the period 2071–2100 relative to 1961–90 for all of Europe, northern Europe and southern Europe (divided at 47.5° N latitude), from two atmosphere–ocean general circulation models (AOGCMs).

	All Europe		Northern Europe		Southern Europe	
AOGCM	ΔT (°C)	ΔP (%)	ΔT (°C)	ΔP (%)	ΔT (°C)	ΔP (%)
HadCM3	4.9	−2.5	4.9	6.0	4.8	−13.0
NCAR-PCM	2.9	2.0	3.2	8.7	2.6	−6.4

Table 2 Dominant species or plant functional types (PFTs), rules for vegetation type classification in addition to the text, and the classes in the potential natural vegetation (PNV) map (Bohn *et al.*, 2003) corresponding with the vegetation classes used in this study.

	Bohn class[1]	GDD$_5$ (°C)	Total LAI	Tree LAI	Woody LAI	Herb LAI	Dominant species
Arctic/alpine desert	A	< 1200	< 0.2				Herbaceous, BES
Arctic/alpine tundra	B	< 1200		< 0.5			Herbaceous, BES
Boreal/alpine mixed woodland	C			> 0.5			
Boreal/alpine conifer forest	D[3]			> 2.0			*Picea abies, Pinus sylvestris*[2]
Hemiboreal mixed forest	D8			> 2.0			
Temperate mixed broad-leaved forest	F[4],G1			> 2.0			
Temperate beech and mixed beech forest	F5			> 2.0			*Fagus sylvatica*[5]
Thermophilous mixed broad-leaved forest	G[6]			> 2.0			
Mediterranean sclerophyllous forest/ woodland	J1-3,5,6			> 1.5			*Quercus ilex, Pinus hallepensis*
Mediterranean sclerophyllous shrubland[7]	J4,7,8				> 0.5[8]		
Steppe woodland	L	> 1200			> 0.5	> 0.5	
Steppe	M	> 1200	> 0.2				
Desert	O	> 1200	< 0.2				

LAI, leaf area index; GDD$_5$, growing degree days above 5 °C; BES, boreal evergreen shrub.

[1]The following Bohn classes were excluded (see text for explanation): xerophytic coniferous forest scrub (K), oroxerophytic vegetation (N), tall reed vegetation and tall sedge vegetation and aquatic vegetation (R), swamp and fen forests (T), vegetation of flood plains, estuaries and fresh water polders and other moist or wet sites (U).

[2]In some rare cases (depending on the stochastic patch-destroying disturbance), the shade-intolerant *Betula pubescens*, which generally only dominates more open forest, achieves the highest cover of all tree species.

[3]Excluding D8.

[4]Excluding F5.

[5]*Fagus sylvatica* had highest LAI among trees.

[6]Except G1.

[7]$LAI_{mediterranean\ species/PFTs} > 0.5 \times LAI_{woody\_species/PFTs}$ and $LAI_{mediterranean\ species/PFTs} > LAI_{herbaceous}$.

[8]Applied to mediterranean species/PFTs.

torical CO_2 concentrations for 1901 to 2000 were taken from McGuire *et al.* (2001) and TRENDS (http://cdiac.esd.ornl.gov/trends/co2/contents.htm) for the years 1999 and 2000. CO_2 concentrations for 2001–2100 were taken from simulations with the Bern-CC fast carbon cycle model (Appendix II in Prentice *et al.*, 2001).

The simulations were initialized with 'bare ground' conditions (no biomass) and the model was spun up for 400 years until the modelled vegetation was in approximate equilibrium with the climate and CO_2 around the year 1900 (Smith *et al.*, 2001). Thereafter the model was run from 1901 to 2100 using the climate and CO_2 datasets described above.

In order to assess longer-term equilibrium vegetation changes, we also carried out one model run representing vegetation changes that would occur if the climate at the end of the 21st century prevailed until the year 2500. For this (necessarily artificial) 'abrupt stabilization scenario', we used the same set-up as for the HadCM3 climate scenario until 2100, followed by a repeated series of climate scenario data between 2071 and 2100 (detrended for temperature) and the atmospheric CO_2 concentration in the year 2100 (836 p.p.m.v.) until the year 2500. In order to save computation time, the model was run with only 20 replicate patches until 2800, and the simulated vegetation was averaged over 2501–2800, thus assuming that equilibrium with the future climate was reached by the year 2500. The long-term development of the climate is highly uncertain and most probably climate won't stabilize after 2100, but such a simulation can be instructive as it shows the vegetation that would be in equilibrium and thus optimally adapted by the end of the century.

Potential natural vegetation

To evaluate the ability of the model to reproduce current vegetation, we compared simulated modern-day vegetation with a map of the PNV of Europe, constructed by a geobotanical expert assessment (Bohn *et al.*, 2003). For comparison with the model results, we extracted the major zonal vegetation types (i.e. those determined by climatic factors), which are characterized by the dominance of selected species (Table 2). The PNV mapping units represent plant associations that include many woody and herbaceous species, their distribution being mostly based on expert estimates, in particular in areas where the natural vegetation has been modified by humans for hundreds to thousands of years (e.g. the mediterranean garrigue). Furthermore, the map depicts more environmental heterogeneity, such as small-scale topographical variations, than represented by the vegetation

model and the environmental driver data. For these reasons, the PNV map cannot be considered as a true observation of natural vegetation, and it cannot straightforwardly be compared with output from the vegetation model. However, the vegetation model should be able to reproduce the main general patterns in the PNV map.

Designation of vegetation classes

Model output was translated into vegetation classes that can be compared to the PNV map by using a set of ad hoc rules, which are described below (further details in Table 2). We distinguished three general geographical forest/woodland types: boreal/alpine, temperate and mediterranean. Model output was assigned a particular type where trees and shrubs belonging to this type together contributed 80% of the total woody leaf area index (LAI) in the grid cell. Assignments of species and PFTs to geographical vegetation types are given in Table S1.1 in Appendix S1.

We also defined two transitional forest types: hemiboreal mixed forest and thermophilous mixed broad-leaved forest. Grid cells were assigned one of these vegetation types if the modelled LAI of trees was sufficiently high for a forest (Table 2) and none of the three main geographical types reached the 80% dominance criterion. Where the woody LAI of boreal species and PFTs was higher than the woody LAI of mediterranean and supra-mediterranean species or PFTs, the hemiboreal forest type was assigned; where boreal types had a lower LAI than mediterranean types, the thermophilous mixed broad-leaved forest type was assigned.

In the PNV map, hemiboreal forests are only distinguished for northern latitudes, excluding Britain and Ireland. Therefore, we only distinguished this vegetation class for areas north of 52° N and east of 3° E. Outside this window, at the transition between temperate and boreal/alpine forests, 50% dominance by either temperate or boreal species or PFTs was taken as a criterion to distinguish these two vegetation types. The model does not distinguish arctic/alpine and warm-temperate herbaceous vegetation. Predominantly herbaceous vegetation was therefore classified based upon GDD_5 (Table 2).

Protected areas

The projected changes in vegetation were laid over a 100 × 100 m resolution gridded dataset of Natura 2000 (http://ec.europa.eu/environment/nature/natura2000/index_en.htm), the European Union's system of protected areas established under the 1992 Habitats Directive (http://ec.europa.eu/environment / nature / legislation / habitatsdirective / index _ en. htm). Up to a third of the habitat types earmarked for protection depend on low-intensity agricultural management to maintain their conservation status (Ostermann, 1998). These and other habitats, such as wetlands, are not represented by the vegetation model, and the simulations of the PNV are of limited relevance for these. Our results are more applicable

to forest reserves, many of which are managed with minimum intervention (EEA, 2006, 2008). Forest reserves were distinguished by overlaying the Corine 2000 land-cover data (CLC2000; http://dataservice.eea.europa.eu/dataservice/metadetails.asp?id=822) and the protected area database. The countries of Malta and Cyprus, as well as the Azores, which belong to Portugal, were not included in the analyses, because these areas were represented by only a very small number of grid cells.

RESULTS

Current vegetation

The model generally reproduces the overall vegetation across Europe (Fig. 1). The vegetation model and the PNV map show the same vegetation type for 86% of the area classified in the PNV map, when comparing the two maps using coarse aggregated vegetation types (arctic/alpine; boreal and hemiboreal; temperate and thermophilous, mediterranean; steppe woodland and steppes). But the model does not simulate the same fine-scale mosaic of the 12 vegetation types that is shown in the map. This mismatch is to a large extent the result of the different approaches to defining vegetation types in both maps. For example, the PNV map shows a mosaic of boreal/alpine conifer forests and hemiboreal mixed forests in the Baltic States and Russia, which is partly based on variations in species composition of the understorey vegetation (Bohn *et al.*, 2003), while the species composition of the understorey is not represented by the vegetation model.

Notable discrepancies between the modelled vegetation and the constructed PNV map occur at the transition between hemiboreal and boreal forest in southern Finland, where the modelled northern border of hemiboreal vegetation expands further to the north than shown in the map. The model also predicts a smaller extent of steppe or steppe woodland vegetation at the north-eastern shore of the Black Sea and in the Pannonian Basin than shown in the map. In central Spain, the model simulates mediterranean sclerophyllous shrublands in some areas that would naturally be covered by woodland and forest vegetation according to the PNV map. Turkey is not included in the PNV map. The modelled transgression from mediterranean shrubland at the western cost of Turkey to sclerophyllous forest/woodland vegetation and thermophilous mixed forest further inland and at higher altitudes corresponds well to an earlier version of the PNV map (Bohn, 1993).

Vegetation changes by 2085

According to our simulations, 31% (NCAR-PCM) or 42% (HadCM3) of the study area would undergo a change in PNV by 2085 (Fig. 1). Similar fractions apply to the Natura 2000 network: 30% with NCAR-PCM, 44% with HadCM3 (respectively 25% or 39% of the forested Natura 2000 sites), though the affected area is relatively small in central Europe (Fig. 2).
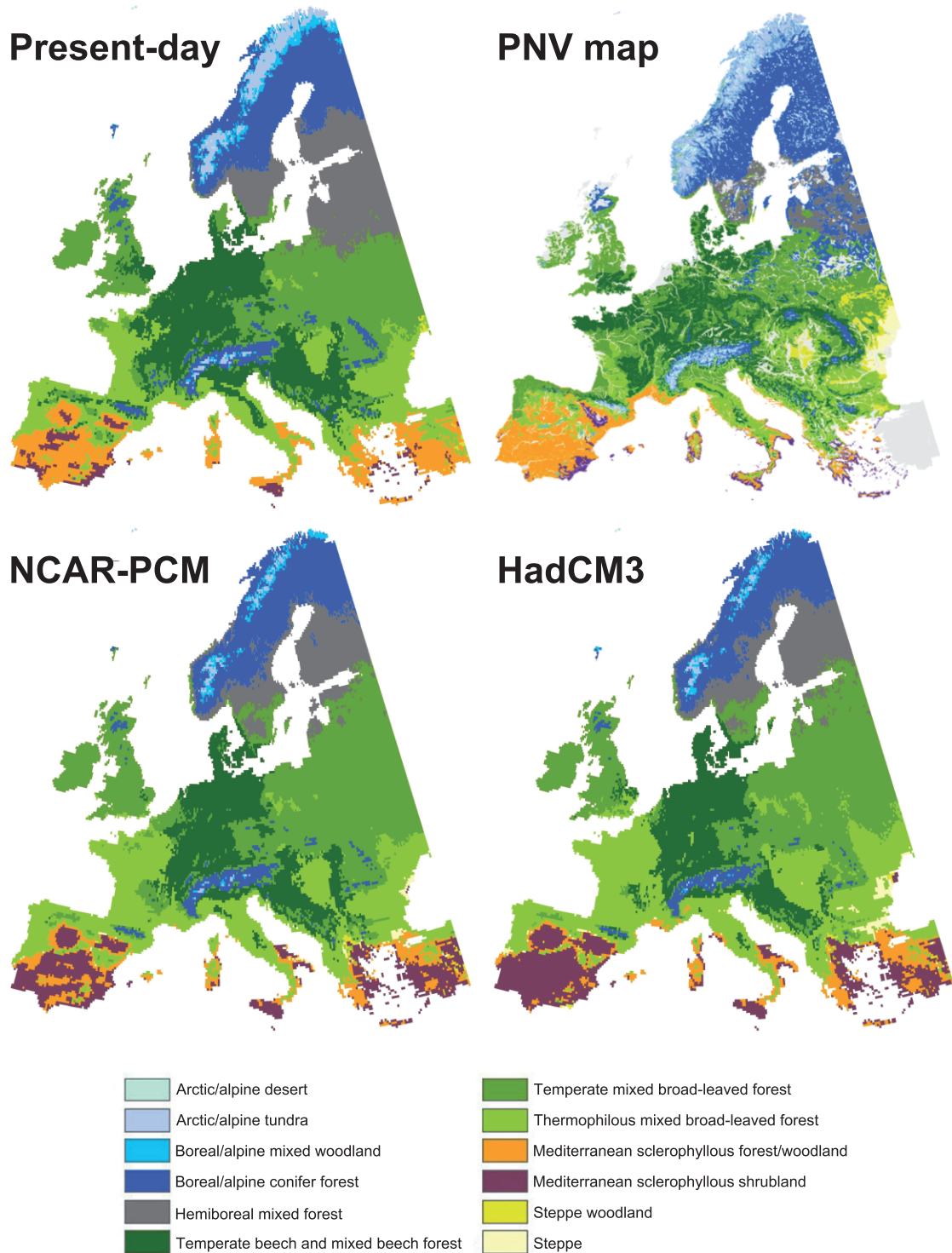
Figure 1 Modelled present-day (averaged for 1961–90) and future (averaged for 2071–2100) potential natural vegetation (PNV) in Europe, compared with an expert reconstruction of the European PNV ('PNV-map'; Bohn *et al.*, 2003), using two atmosphere–ocean general circulation models (AOGCMs; NCAR-PCM and HadCM3) and the A2 SRES emission scenario (ALARM scenario 'business as might be usual', BAMBU). Light grey areas on the PNV map denote areas that were not included by Bohn *et al.* (Turkey) and areas covered by vegetation types that were not represented by the vegetation model (Table 2), such as wetlands.
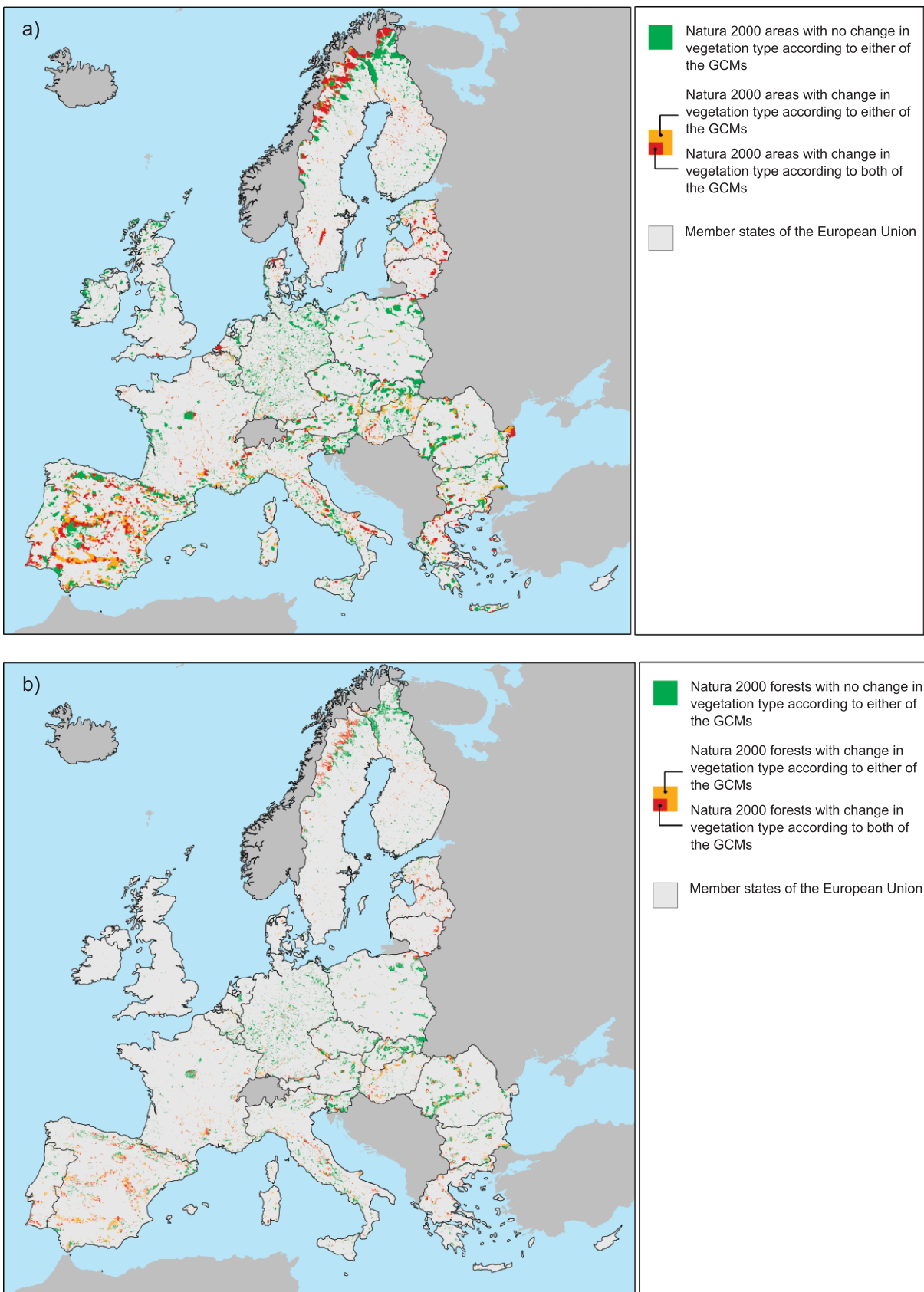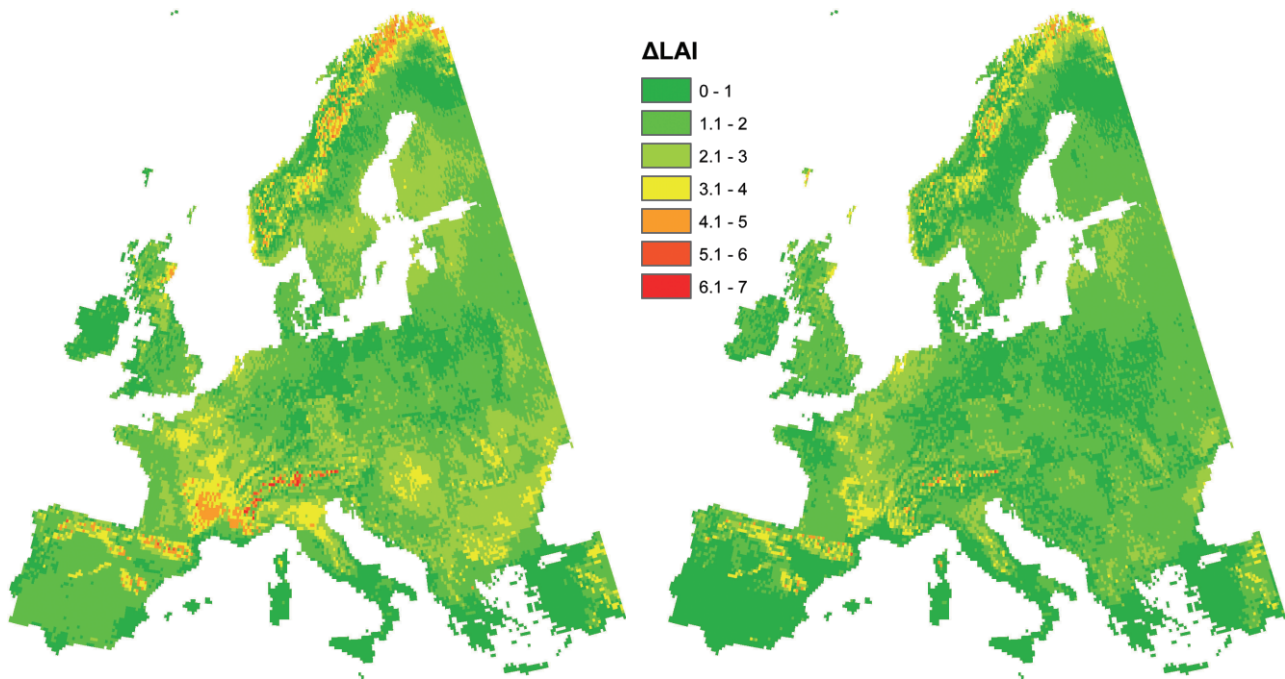
Figure 2 Natura 2000 areas that are projected to undergo a shift in vegetation: (a) all Natura 2000 areas, (b) forested Natura 2000 areas.

Figure 3 The sum of the absolute values of the projected changes in leaf area index (LAI) over all N species and plant functional types (PFTs) $\left(\Delta \text{LAI} = \sum_{i=1}^{N} |\Delta \text{LAI}_i| \right)$ as a continuous measure of vegetation change, for two climate change scenarios.

In both scenarios, the northern boundaries of temperate forests and hemiboreal forests in southern Scandinavia and north-eastern Europe would move northwards (by about 300–500 km), and most of the arctic/alpine tundra would be replaced by forests. The projected changes are relatively small in central Europe. In the Mediterranean, the model predicts substantial shifts from forested to shrubland vegetation as a result of increased drought (Fig. 1). Under the HadCM3-based scenario, the vegetation model predicts replacement of forests by steppe at the western coast of the Black Sea. Within the temperate zone, the model predicts that thermophilous mixed forests increase their range north of the current distribution, in particular in France, while beech forests contract towards the centre of their current distribution.

The sum of the absolute values of the projected changes in LAI over all species and PFTs (ΔLAI), a continuous measure of vegetation change, looks similar for both climate scenarios, but with more pronounced changes under the HadCM3 scenario (Fig. 3). According to this index, the largest changes occur in arctic and alpine areas, in other mountain areas, such as the Pyrenees, south-central France, and on the Black Sea coast. Under the HadCM3 scenario, the transition zone between temperate and boreal forests, northern Italy and the Pannonian Basin also undergo substantial vegetation change (Fig. 3).
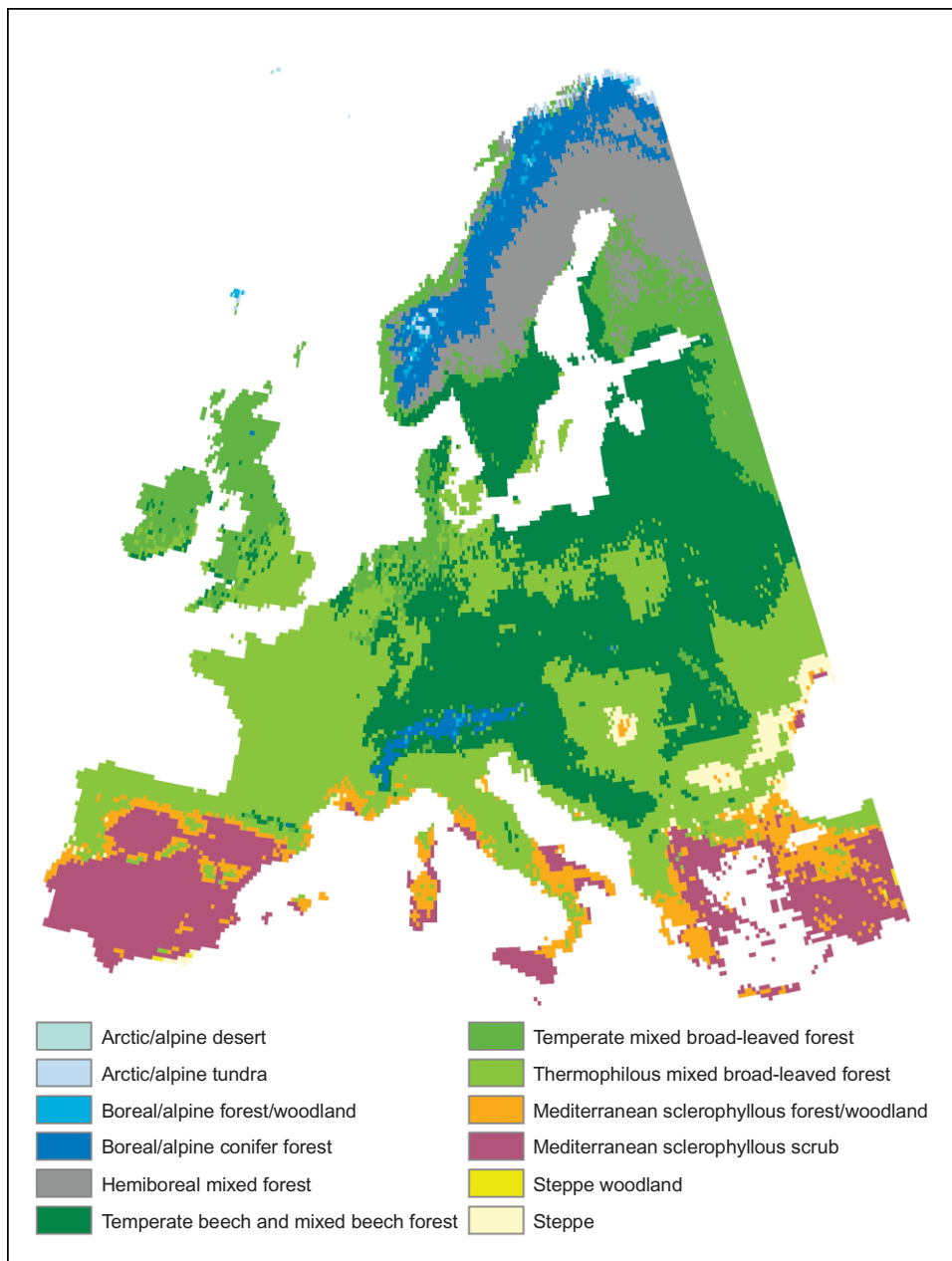
Long-term equilibrium vegetation changes

In most areas, the simulated vegetation takes approximately 300 years to achieve equilibrium with climate and CO_2 after stabili-
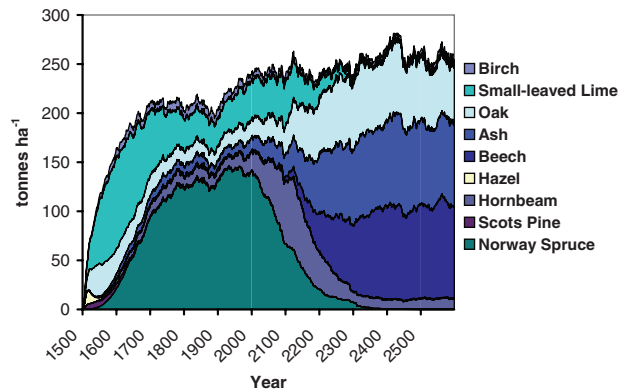
Figure 4 Modelled species composition in terms of the above-ground biomass for a forest in central southern Sweden (15°08′ E; 58°09′ N), starting after disturbance in the year 1500, using the HadCM3 climate scenario and assuming future climate (2091–2100) for the years 2101 to 2600.

zation in 2100 (Fig. 4). These 'equilibrium' PNV shifts affect much larger areas than the transient shifts up to 2085 (Fig. 5); under the HadCM3 scenario, the model predicts that 76% of the study area would be covered by a different potential vegetation type by the year 2500 (Fig. 5). In this simulation, most of the mediterranean forest is replaced by shrublands, forests in the Pannonian Basin and along the Black Sea coast are replaced by steppe, most currently treeless arctic/alpine areas become forested, temperate forests dominate in southern Scandinavia and along the Scandinavian coast, and *Fagus sylvatica* expands its

Figure 5 Modelled long-term equilibrium vegetation distribution, using the HadCM3 climate scenario and assuming future climate (2071–2100) for the years 2101 to 2500.

dominance far into Russia and southern Scandinavia. The area undergoing vegetation change according to the model increases to 80% if the last 10 years of the scenario period (2091–2100) are used repeatedly (instead of the last 30 years).

DISCUSSION

For the first time, we present a tree species-based assessment of dynamic future climate-driven changes in PNV across Europe. The study presents an advance compared with earlier PFT-based dynamic simulations at a similar scale. Projected changes in

PNV are so large, in particular in northern and southern Europe, that they are relevant for discussions concerning adaptation to climate change.

Current vegetation

The representation of current European PNV (Fig. 1) has been substantially improved compared with earlier dynamic vegetation modelling studies. Previously, the only dynamic vegetation modelling results available at this scale have been from DGVMs using PFTs only, and using coarser-resolution climate input

(about 50 × 50 km or larger), while species-based modelling has been performed at the site scale (e.g. Badeck *et al.*, 2001) or for more limited regions, such as Scandinavia (Koca *et al.*, 2006) or the Baltic (Wolf *et al.*, 2008). DGVMs have often not been able to reproduce major vegetation zones across Europe. A number of DGVMs, including the LPJ model which is closely related to the model applied here, overestimated the extent of needle-leaved evergreen forests in temperate western Europe (Friend & White, 2000; Kucharik *et al.*, 2000; Cramer *et al.*, 2001; Sitch *et al.*, 2003), probably because shade-tolerance classes are not distinguished in these models. Hybrid and LPJ also incorrectly predicted grasslands or savannas in central and southern Spain (Friend & White, 2000; Cramer *et al.*, 2001; Sitch *et al.*, 2003). The individual-based LPJ-GUESS performed better than LPJ-DGVM in predicting PNV at selected sites across Europe (Smith *et al.*, 2001), but this is the first time the approach has been taken for the whole of Europe, and the potential vegetation is represented better and in more detail than in earlier DGVM-based studies.

Notable discrepancies between the vegetation predicted by LPJ-GUESS in the present study and the vegetation classes in the reconstructed PNV map occur along the Black Sea coast and in the Pannonian Basin, where the model simulated more forest cover than shown in the map, and some areas in Spain, where the model simulated shrublands while the map suggests potential forest cover. In both cases, however, the PNV map itself must be considered highly uncertain. In the 'steppe' areas, nearly all natural vegetation was cleared for agriculture hundreds to thousands of years ago, which makes it difficult to infer the exact extent of naturally occurring steppes (Bohn *et al.*, 2003). Likewise, the mediterranean vegetation has a long history of human intervention through clearance, grazing and anthropogenic fires, and the extent to which forest would prevail naturally is still debated (Bohn *et al.*, 2003). In southern Finland, the modelled northern border of hemiboreal forests follows the modelled northern boundaries of a number of temperate broad-leaved trees, such as *Tilia cordata* and *Q. robur*. According to the model, conifers, *Picea abies* in particular, dominate in this area, but the criterion of 80% fractional tree cover by conifers for boreal conifer forests (see 'Designation of vegetation classes') is not met. Temperate broad-leaved trees occur in this area in warmer locations and on nutrient-rich soils (Bohn *et al.*, 2003), but the model might slightly overestimate their abundance.

Major vegetation changes and their drivers

The projected expansion of temperate trees into the hemiboreal and boreal forests is consistent with observed recent altitudinal vegetation shifts in undisturbed forests (Beckage *et al.*, 2008), with other simulation studies concerning range shifts (Prentice *et al.*, 1993; Sykes *et al.*, 1996) and with the known northward expansion of temperate forests during the mid-Holocene, when summers in southern Scandinavia and north-eastern Europe were considerably warmer than today (Prentice *et al.*, 1996). The competitive replacement of boreal trees by temperate species is primarily driven by longer growing seasons and warmer winters, which no longer restrict the northern distribution of temperate trees (Woodward, 1987).

The projected shifts in latitudinal and altitudinal tree lines are in line with historical shifts in the Swedish Scandes, but in other mountain areas land-use change could be a more important driver of tree-line dynamics than climate. The *Pinus sylvestris* tree line in the Swedish Scandes has generally risen by 150–200 m during the 20th century, most probably because of warmer winters which decrease tree mortality and increase establishment success (Kullman, 2007). At one Scandinavian study site, the altitudinal range margins of *Picea abies*, *Pinus sylvestris*, *Betula pubescens*, *Sorbus aucuparia* and *Salix* spp. have advanced by 120–375 m since the 1950s (Kullman, 2002). These changes were associated with changes in temperature that were much smaller than anticipated for the coming century; summer temperatures at the site only increased by 0.8 °C between 1901 and 2000 (Kullman, 2002). However, browsing by animals such as reindeer and orographic variations can counteract the development of climatic tree lines (Cairns & Moen, 2004; Dullinger *et al.*, 2004), and not all tree lines have shown a consistent response to recent climate warming (Dullinger *et al.*, 2004). In the Swiss Alps, land abandonment has, during recent decades, been a more important driver of tree-line shifts than climate change (Gehrig-Fasel *et al.*, 2007).

Changes in water availability are also an important driver of the projected vegetation changes. According to both climate scenarios, spring and summer precipitation decrease over most of southern Europe, with more pronounced changes in the HadCM3 scenario (Appendix S3). As potential evapotranspiration increases with rising temperature, plants may experience substantial reductions in water availability under climate warming, even in the absence of growing-season precipitation changes. Many areas in the Mediterranean, and areas along the Black Sea coast in the case of the HadCM3 scenario, become so dry that forest is replaced by shrubland or steppe vegetation in the model simulations (Figs 1 and 5). These results confirm that the Mediterranean is particularly vulnerable to climate change because of an increasing risk of drought (Schröter *et al.*, 2005; Fischlin *et al.*, 2007). They are consistent with observed increased canopy mortality in a 5-year drought experiment in a *Quercus ilex* forest in Spain (Ogaya & Peñuelas, 2007) and modelled changes in net primary productivity (NPP) predicted by LPJ-GUESS when driven by a number of regional climate models (RCMs), bounded by two AOGCMs (Morales *et al.*, 2007). However, tree mortality is a very complex process; in most cases it is the result of multiple stress factors such as drought, storms leaving deadwood as breeding grounds for pests, and insect outbreaks. Therefore, mortality events are difficult to predict with a process model (Keane *et al.*, 2001).

In western Europe, the competitiveness of *Fagus sylvatica* is reduced because the mild winters delay budburst in this species which has a high chilling requirement (Sykes *et al.*, 1996). This projection, however, is uncertain because the main controls of the north-western boundary of the distribution of *F. sylvatica* are not totally understood (Kramer *et al.*, 2010). Different popu-

lations may have different chilling requirements, and *F. sylvatica* has recently been reported to be invasive in some forests in Ireland (R. Bradshaw, Department of Geography, University of Liverpool, Liverpool, UK, pers. comm.).

Long-term equilibrium vegetation changes

Because of the long life spans of most tree species, forest succession and the replacement of one forest type by another typically takes several centuries. The long-term changes simulated by the model (Fig. 5) are therefore much larger than the transient changes shown in Fig. 1. In most cases, the directions of the transient and long-term simulated changes coincide, but the long-term changes are much more pronounced. The strong north-eastern expansion of temperate beech forests seen in Fig. 5, however, has not even started by 2085 (Fig. 1). The north-eastern boundary of the distribution of *F. sylvatica* is currently mainly defined by cold winters (Huntley *et al.*, 1989), and according to LPJ-GUESS summer dryness also plays a role in some areas. During the final 30 years of the HadCM3 scenario, winter temperatures become warm enough and summers wet enough to allow the establishment of *F. sylvatica* in large parts of north-eastern Europe. As a late-successional shade-tolerant tree, *F. sylvatica* then benefits from higher NPP and a denser forest canopy – a result of a longer growing season and higher atmospheric CO_2 concentrations (Morales *et al.*, 2007) – which tends to suppress more light-dependent competitors.

The nature of long-term climate is highly uncertain, and the assumption in the present study of a constant, stable long-term climate just after 2100 is of course purely arbitrary. Only a limited number of studies have attempted to project climate or vegetation to periods beyond 2100. Results from a multi-model AOGCM experiment suggest that temperature would increase by 0.5 °C between 2100 and 2200 and a bit less than that between 2200 and 2500 if GHG concentrations were stabilized in the year 2100 (Meehl *et al.*, 2007; for the A1B emission scenario). Using one AOGCM, Solomon *et al.* (2009) concluded that, even if GHG concentrations decrease after 2100, as fossil fuels become depleted and the ocean continues to take up CO_2, climate change is largely irreversible for 1000 years after emissions stop because of the long time lags in ocean temperature changes. The results from the long-term experiment in this study nevertheless illustrate the magnitude of the long-term 'commitment' of potential vegetation change.

Implications for climate adaptation

The projected changes in PNV are so large that they would have a considerable impact on many protected areas and the forestry sector. Regarding conservation areas, our projections are only relevant for certain types of reserves, namely those with low levels of management that harbour the vegetation types represented by the model. This excludes, for example, wetlands, agricultural areas and heavily managed forests. Furthermore, the model only captures regional-scale vegetation patterns; finer-scale variations that are caused by topography (southern or

northern aspect, slope) or a mosaic of soil types, are not represented. Therefore, further analyses are necessary in order to evaluate if the vegetation shifts are relevant for a particular site. In those cases where our simulations are relevant, shifts in the dominant tree species and PFTs used in this study are likely to affect large number of associated species across organism groups (Leemans & Halpin, 1992; Fischlin *et al.*, 2007). Conservation objectives currently focus predominantly on current habitat type and species composition, but a more dynamic vision accounting for potential effects of climate change is needed (Fischlin *et al.*, 2007).

Regarding forestry, the simulations suggest that closed forest is likely to remain the dominant natural vegetation over most of Europe. This also applies if physiological effects of increasing levels of atmospheric CO_2 (CO_2 fertilization and decreasing stomatal conductance; Hickler *et al.*, 2008) are switched off in the model (Appendix S1 in Hickler *et al.*, 2009). A change from forests to more open vegetation because of decreasing water availability occurs according to the model only in parts of the Mediterranean and along the Black Sea coast and in the Pannonian Basin (Figs 1 & 5). Across the rest of the continent, the model simulations suggest that the climate will also in the future be favourable for forests, but in some areas not the same kind of forests. Even though many commercial tree species can successfully be planted outside their natural range, which is often defined by constraints during the establishment phase, planting outside the natural range can only be successful to a certain, species-specific degree. Planting for future climate is also limited because saplings and young trees are most susceptible to variations in climate. Therefore, many trees establishing today are likely to face a climate as adult trees that they are not adapted to. Such a disequilibrium state might lead to an increased susceptibility to storm damage, pest attacks and other stress factors (Bradshaw *et al.*, 2000; Kozlowski & Pallardy, 2002).

Further guidance for interpreting the results

LPJ-GUESS could still overestimate the rate at which vegetation changes occur because propagules are assumed to be available if the climate is suitable for a certain species or PFT (Smith *et al.*, 2001). We nevertheless consider our results to be relevant because forest management has a long tradition of planting trees beyond their natural ranges in Europe, providing seed sources long before the climate is optimal. With limited efforts, reserve managers could introduce tree species to provide sufficient seed sources for near-natural regeneration. Even without human facilitation, Beckage *et al.* (2008) found little inertia to climatically induced range shifts in mountain forests in Vermont, USA, where the hardwood–boreal forest ecotone has shifted about 100 m upslope since 1962. Studies of migration rates during the last glaciation have shown that trees could migrate by between 200 and 2000 m year^{-1}, with six taxa achieving rates of more than 1 km year^{-1} (Huntley & Birks, 1983). It is unclear, however, to what extent the current fragmentation of the landscape will hinder migration of trees in the future (Fischlin *et al.*, 2007). In some areas, such as the transition zone between temperate and

boreal forests, the modelled vegetation shifts would not be possible without migration rates considerably larger than observed for most species in the past.

Model results for particular species should be treated as scenarios, not predictions, because a model like LPJ-GUESS cannot include all aspects of a species' ecology. Furthermore, there exists considerable uncertainty in the climate projections. The choice of the AOGCM influences the magnitude of the simulated vegetation changes more than the emission scenario (when comparing A2 and B1), and the climate scenarios used here do not account for changes in extreme events, such as prolonged periods of drought, heavy rainfall events and storms (Christensen & Christensen, 2003; Schär *et al.*, 2004). Finally, a number of European trees, such as *Fraxinus excelsior*, have been severely affected by diseases, which in some cases have occurred very rapidly and are therefore difficult, if not impossible, to predict. Therefore, any adaptation strategy must be flexible, dynamic and potentially responsive to the development of climate change and new research on its impacts.

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SUPPORTING INFORMATION

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

Appendix S1 Summary of the LPJ-GUESS model and parameter values for tree species and plant functional types (PFTs).
Appendix S2 Evaluation of LPJ-GUESS at the site scale.
Appendix S3 Description of the climate scenario data.

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BIOSKETCH

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