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LETTER

Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty

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Abstract

Model-based projections of shifts in tree species range due to climate change are becoming an important decision support tool for forest management. However, poorly evaluated sources of uncertainty require more scrutiny before relying heavily on models for decision-making. We evaluated uncertainty arising from differences in model formulations of tree response to climate change based on a rigorous intercomparison of projections of tree distributions in France. We compared eight models ranging from niche-based to process-based models. On average, models project large range contractions of temperate tree species in lowlands due to climate change. There was substantial disagreement between models for temperate broadleaf deciduous tree species, but differences in the capacity of models to account for rising CO_2 impacts explained much of the disagreement. There was good quantitative agreement among models concerning the range contractions for Scots pine. For the dominant Mediterranean tree species, Holm oak, all models foresee substantial range expansion.

Keywords

Climate change, *Fagus sylvatica*, France, *Pinus sylvestris*, *Quercus ilex*, *Quercus petraea*, *Quercus robur*, species range, vegetation model intercomparison.

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INTRODUCTION

Observations, experiments and models all strongly indicate that rising atmospheric CO_2 concentrations and associated climate change will alter the functioning and distribution of trees over the coming decades (Lenoir *et al.* 2008; Keenan *et al.* 2010). Projected poleward range shifts of forest biomes due to global warming are on the order of several 10's to 100's of km during the 21st century (Fischlin *et al.* 2007). These range shifts will have major economic, ecological and social impacts, especially if characterised by widespread tree mortality (Lindner *et al.* 2010).

There is, however, substantial uncertainty in the extent that climate change will alter tree distributions for four main reasons: (1) high uncertainty in future greenhouse gas emissions, (2) important unknowns in climate sensitivity, (3) lack of understanding of key aspects of tree function, biotic interactions and disturbance and (4) large differences in the simplifying assumptions and parameter choices made in models of tree response to climate (which we refer to as 'model type' uncertainty). Rigorous estimates of these uncertainties are essential if models are to be used as decision support for forest managers, for projections of changes in terrestrial carbon storage, etc. This article focuses on quantitatively assessing model type uncertainty.

Several studies have evaluated emissions scenario and climate model components of uncertainty by running vegetation models with a range of climate projections (Thuiller 2004; Beaumont *et al.* 2011), but few studies have evaluated model type uncertainty across a broad range of models (Beale & Lennon 2012). Model intercomparisons are a powerful means to evaluate uncertainty in projections of biosphere response to global change (Pereira *et al.* 2010). A few recent studies of projected shifts in tree distributions at regional (Bolliger *et al.* 2000; Morin & Thuiller 2009; Keenan *et al.* 2010) and global scales (Sitch *et al.* 2008) show that models of trees and forests vary tremendously in their sensitivity to climate change. It has been suggested there are systematic differences related to model type. For example, niche-based models (NBMs) generally project greater losses of suitable climate at the trailing edge of their ranges and greater increases at the leading edge of ranges than process-based models (Morin & Thuiller 2009). It has also been repeatedly suggested that the effects of atmospheric CO_2 concentrations on photosynthesis and water use efficiency must be accounted for to correctly simulate past and future tree distributions (Wu *et al.* 2007; Galbraith *et al.* 2010; Keenan *et al.* 2010). This is a potentially serious handicap for NBMs that rarely account for CO_2. More generally, phenomenological relationships between climate and distribution may fail to account for future novel

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combinations of climatic factors (Williams *et al.* 2007). Our study goes beyond previous studies by a rigorous intercomparison of a wide range of well-established models to analyse future climate change impacts on tree distributions.

We compared two NBMs (N-NBM and BIOMOD, which uses an ensemble of species distribution models), a simple growth index model (STASH), a process-based species distribution model (PHENOFIT), a process-based tree growth model (CASTANEA) and three dynamic global vegetation models (LPJ, IBIS and ORCHIDEE; see McMahon *et al.* 2011 and Bellard *et al.* 2012 for critical discussions of these types of models). Models generated a wide range of measures of tree performance that we transformed into presence/absence based on quantitative comparisons with current tree distributions from the French National Forest Inventory (NFI).

Model intercomparisons of predicted presence/absence were used to address a range of questions related to understanding and quantifying uncertainty: (1) How well do models simulate current distributions of trees? (2) Are simulations of climate change impacts on spatial distributions similar at mid-century and, if not, why? (3) What can we learn from similarities and differences in model projections to improve our knowledge and reduce model-based uncertainty? (4) How do species differ in terms of the environmental factors mediating range shifts? We interpret projected shifts in tree distributions in the light of recent observations and experiments. Finally, we provide perspectives on using models as decision support tools.

MATERIALS AND METHODS

Model characteristics

Characteristics of the eight models used in this study are outlined in Table 1. Short descriptions of each model are provided in Appendix SA1. Detailed descriptions can be found in the references cited in Table 1. All models were run using a standardised 8-km resolution grid using common regionalised climate, soil and current tree distribution data. Species-based models (Table 1) were applied to five dominant tree species, European beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.), sessile oak [*Quercus petraea* (Matt) Leibl.], Holm oak (*Quercus ilex* L.) and Scots pine (*Pinus sylvestris* L.). We also examined the response of groups of tree species that share similar ecological traits (= plant functional types or PFTs), focusing on temperate broadleaf summergreens (TeBS) and temperate broadleaf evergreens (TeBE; note that Holm oak is the only major representative of this group in France).

Study area, observed species distribution and environmental data

The study area covers France (544 000 km^2), 28% of which is covered by forests. Occurrences of the tree species in this study were extracted from the NFI database and aggregated to obtain presence/absence on the 8-km climate grid. For more information on NFI data see http://www.ifn.fr.

Climate projections were based on the IPCC A1B SRES emissions scenario using the ARPEGE AGCM of Météo-France (Déqué 2007). ARPEGE output was downscaled to a *c.* 8-km grid using a weather type method. This method is based on the idea that large-scale atmospheric circulation (LSC) patterns, which can be simulated with GCMs, are a key determinant of local climate. Multivariate statistics were used to identify clusters (i.e. weather types) of observed LSC and local climate patterns (Boé *et al.* 2009). LSC from ARPEGE projections of future climate where downscaled to 8-km resolution using these weather types (See Appendix SA2). We used two time periods for this study: 'current' climate based on a 1971–2000 time slice and '2055' climate based on a 2046–2065 time slice. The atmospheric CO$_2$ concentration of 530 p.p.m. in 2055 from the A1B SRES scenario lies in the middle of the range of the IPCC SRES scenarios. When averaged over France the 2055 time slice, changes are +2.4 °C in temperature and −20 mm in monthly precipitation during the growing season compared with current climate (Fig. S1). This downscaled annual temperature is close to the mean of downscaled IPCC A1B AR4 multi-model climate projections for France, but precipitation is on the dry end of the range (Fig. S2).

Soil parameters were extracted from the French soil database developed by the INRA [1 : 10 000 000-scale, Infosol Unit, INRA, Orléans, (Jamagne *et al.* 1995)] and aggregated to the 8-km climate grid to provide measures of plant available water capacity and soil depth (Badeau *et al.* 2010).

Model evaluation for current climate

We compared the model accuracy for the current time period to presence/absence data derived from NFI data. Models generated a variety of continuous values as outputs (Table 1), so to compare models with NFI data and facilitate model intercomparison we applied a threshold to transform continuous values into presence/absence. We used thresholds for each species that maximised the goodness-of-fit of each model's output to NFI presence/absence data. Goodness-of-fit was measured using the true skill statistic (TSS), where TSS = sensitivity + specificity-1; sensitivity = correctly predicted presences/(correctly predicted presences + predicted absences, but truly presences) and specificity = correctly predicted absences/(correctly predicted absences + predicted presences, but truly absences) (Allouche *et al.* 2006). Important characteristics of TSS are that it takes into account both omission (i.e. sensitivity) and commission (i.e. specificity) errors, and ranges from −1 to +1, where +1 indicates perfect agreement and values of zero or less indicate performance no better, or worse than random.

Model comparison in the future climate

To compare model predictions in 2055, we applied thresholds as calculated above to transform all model output into presence/absence. We have synthesised the results using 14 bioclimatic regions based on Dupias & Rey 1985. This delineation relies on plant community classifications to define zones of reasonably homogeneous vegetation, geology and climate within France.

For each species and model we generated maps that distinguish four types of grid cells (1) predicted to be present in the current climate, but absent in 2055, (2) predicted to be absent in the current climate, but present in 2055, (3) predicted to be present in the current and 2055 climates and (4) predicted to be absent in the current and 2055 climates. In addition, quantitative estimates of relative and absolute changes in absence/presence were calculated for each of the bioclimatic regions (Appendix SA3, Table S1–S6).

We also carried out sensitivity tests to better understand the mechanisms underlying the projections of future distributions.

Table 1. Characteristics, parameterisation, limitations and outputs of the eight tree models used in the intercomparison

Model name and references	Model type	Model characteristics	Origin of model parameters	Limitations	Species or PFTs	Input climate variables	Output used for distribution
BIOMOD and N-NBM (see SI, Appendix SA1)	Niche-based models (a.k.a. correlative or bioclimatic envelope models)	Correlative plant distribution models based on phenomenological relationships between current species range and climate	Calibrated using a sub-sample of the observed species distribution and evaluated using the remaining part	Not accounted for: CO_2 effects on plants, temporal dynamics of response. Biotic interactions, historical and human legacies implicitly included in abiotic factors	European beech Pedunculate oak Sessile oak Scots pine Holm oak	BIOMOD: mean annual, winter, and summer precipitation. Mean annual T °C and minimum T °C of the coldest month. Growing degree days (GDD > 5 °C). Annual potential evapotranspiration (PET) N-NBM: minimum, maximum and mean T °C. Precipitations. Wind speed. Relative humidity and vapour pressure deficit. Atmospheric pressure. Global solar irradiance. PET. Growing degree days (> 0 °C, > 5 °, > 10 °C). Number of days of frost (< 0 °C, < −5 °C, < −10 °C) Water stress index (intensity and duration)	BIOMOD = committee averaging method (see SI, Appendix SA1) N-NBM = probability of presence
STASH (see SI, Appendix SA1)	Growth index model	Very simple growth index model based on temperature and drought indices	Bioclimatic parameters based on physiological knowledge on native species distribution	Not accounted for: CO_2 effects on plants, biotic interactions and disturbance	European beech Pedunculate oak Scots pine Holm oak	Monthly mean values of temperature, precipitation and percentage of cloudiness	Probability of presence
PHENOFIT (see SI, Appendix SA1)	Process-based species distribution model	Species distribution model based on survival and reproductive success as a function of climate effects on functional traits (phenology, resistance to temperature and water stress)	Measured or fit to observations of the process-trait modeled	Not accounted for: CO_2 effects on plants, biotic interactions, environmental constraints on growth, disturbance	European beech Pedunculate oak Scots pine	Daily temporal scale: maximum and minimum T °C, precipitation, relative humidity, total incoming shortwave radiation, wind speed and the holding water capacity	Fitness (survival and reproductive success)
CASTANEA (see SI, Appendix SA1)	Process-based tree growth model	Process-based model of C, energy and water fluxes of a forest and growth of an 'average' tree in a mono-specific stand. Forest management	Measured fluxes and growth, knowledge of species-specific physiological characteristics	Not accounted for: biotic interactions, disturbance. Highly data intensive for parameterisation	European beech Sessile oak	Hourly temporal scale: global radiation, rainfall, wind speed, air humidity, air temperature and CO_2 air concentration	Harvested aboveground wood during a forest management cycle of 150 years
LPJ (see SI, Appendix SA1)	DGVM but run at the species level for this study	Process-based model of C, water and energy fluxes and dynamic changes in vegetation distribution	Measured fluxes and growth, knowledge of species-specific physiological characteristics and bioclimatic limits fit to species distribution	Not accounted for: intraspecific and interspecific competitions, biotic interactions and disturbance	European beech Pedunculate oak Scots pine Holm oak	Monthly mean values of temperature, precipitation and percentage of cloudiness	Mean values of NPP over the time slice used after 300 years of spin-up
ORCHIDEE & IBIS (see SI, Appendix SA1)	DGVM (PFT)	Process-based models of C, water and energy fluxes and dynamic changes in vegetation distribution, include PFT competition for light and water, dynamics solely based on carbon balance for IBIS	Measured fluxes and growth, knowledge of species-specific physiological characteristics and bioclimatic limits	Not accounted for: Biotic interactions other than competition (nutrient limitations and dispersion only for ORCHIDEE)	PFTs studied: TeBS TeBE	Hourly temporal scale: minimum and maximum air T °C, shortwave and long wave incoming radiations, specific air humidity, precipitations, surface pressure and wind speed	Fraction of PFT for ORCHIDEE NPP for IBIS

Table 2 Goodness-of-fit, sensitivity, specificity and thresholds applied for the eight model types and six species or PFTs using the TSS

	Sensitivity	Specificity	Goodness-of-fit	Output	Threshold
European beech					
BIOMOD	0.99	0.74	0.73	Committee averaging method (see Appendix SA1)	
N-NBM	0.82	0.78	0.60	Probability of presence	0.46
STASH	0.92	0.26	0.18	Probability of presence	0.42
PHENOFIT	0.96	0.20	0.16	Fitness	0.48
CASTANEA	0.93	0.40	0.33	Harvested aboveground wood (m^3 ha^{-1})	649
LPJ	0.74	0.74	0.48	NPP (gC m^2 year^{-1})	665
Pedunculate oak					
BIOMOD	0.88	1	0.88	Committee averaging method (see Appendix SA1)	
N-NBM	0.94	0.71	0.65	Probability of presence	0.66
STASH	0.91	0.65	0.56	Probability of presence	0.56
PHENOFIT	0.93	0.59	0.52	Fitness	0.50
LPJ	0.90	0.36	0.26	NPP (gC m^2 year^{-1})	505
Sessile oak					
BIOMOD	0.61	0.99	0.60	Committee averaging method (see Appendix SA1)	
N-NBM	0.88	0.55	0.43	Probability of presence	0.4
CASTANEA	0.82	0.46	0.27	Harvested aboveground wood (m^3 ha^{-1})	202
Scots pine					
BIOMOD	0.90	0.58	0.48	Committee averaging method (see Appendix SA1)	
N-NBM	0.70	0.60	0.30	Probability of presence	0.42
STASH	0.76	0.49	0.25	Probability of presence	0.04
PHENOFIT	0.86	0.39	0.26	Fitness	0.005
LPJ	0.86	0.40	0.26	NPP (gC m^2 year^{-1})	560
Holm oak and TeBE					
BIOMOD	1	0.89	0.88	Committee averaging method (see Appendix SA1)	
N-NBM	0.87	0.95	0.83	Probability of presence	0.1
STASH	0.54	0.88	0.42	Probability of presence	0.48
LPJ	0.84	0.69	0.53	NPP (gC m^2 year^{-1})	212
IBIS	0.77*	0.92*	0.68*	NPP (gC m^2 year^{-1})	2*
ORCHIDEE	0.72*	0.78*	0.50*	Fraction of PFT	0.04*
TeBS					
BIOMOD	0.90	1	0.90	Committee averaging method (see Appendix SA1)	
N-NBM	0.92	0.70	0.62	Probability of presence	0.78
IBIS	0.94*	0.69*	0.63*	NPP (gC m^2 year^{-1})	419*
ORCHIDEE	0.74*	0.72*	0.46*	Fraction of PFT	0.27*

TSS, true skill statistic.
Asterisks indicate that model output was compared to PFT distributions.

Sensitivity tests for CO$_2$, temperature, precipitation and potential evapotranspiration (PET) were carried out by holding one factor at its current level, whereas all other factors were set to 2055 levels.

RESULTS

Modeled current tree distributions

Comparisons between modeled current distributions and gridded presence/absence data from the NFI show highly variable agreement depending on model and species or functional group (Table 2). The best overall matches are for the NBMs as they are fit to current distributions. BIOMOD generally does better than the N-NBM because BIOMOD uses a multi-model ensemble method (Marmion *et al.* 2009).

The spatial patterns of fits to current distributions of beech are good for BIOMOD, N-NBM and LPJ (Fig. 1a). CASTANEA tends to over-predict presence in the Southwest, the Southern portion of Brittany and centre of the Northwest region, a tendency that is much stronger for STASH and PHENOFIT (Fig. 1a). The fits to current distributions of pedunculate oak are relatively good except for LPJ, which over-predicts presence in general (i.e. specificity is very low, Table 2, Fig. 2a). For sessile oak, CASTANEA over-predicts presence in the Northwest and Brittany (Fig. S4a). For the deciduous broadleaved tree PFT (TeBS), fits to current distributions by BIOMOD, N-NBM and IBIS are good, but ORCHIDEE under-predicts presence in the Southwest and the southern portion of the center region (Fig. 3a, Table 2). All four models predict well TeBE or Holm oak distributions (Table 2). The fits to Scots pine for all models are characterised by high errors of commission (Fig. 4a, Table 2).

Projections of future distributions

Projections for European beech, pedunculate oak and sessile oak

There are large differences in projected range shifts for beech. BIOMOD, N-NBM and STASH project nearly total loss in much of the plains and low altitudes in mountainous regions (Fig. 1b). This is in sharp contrast to PHENOFIT and LPJ that foresee modest losses to substantial gains in the mountains and plains. CASTANEA lies in between these extremes, with projections of substantial range contraction in Southern and central areas, but little change in the Northern tier of France. In mountains, models generally foresee an upward shift of *c.* 100–200 m in altitude.

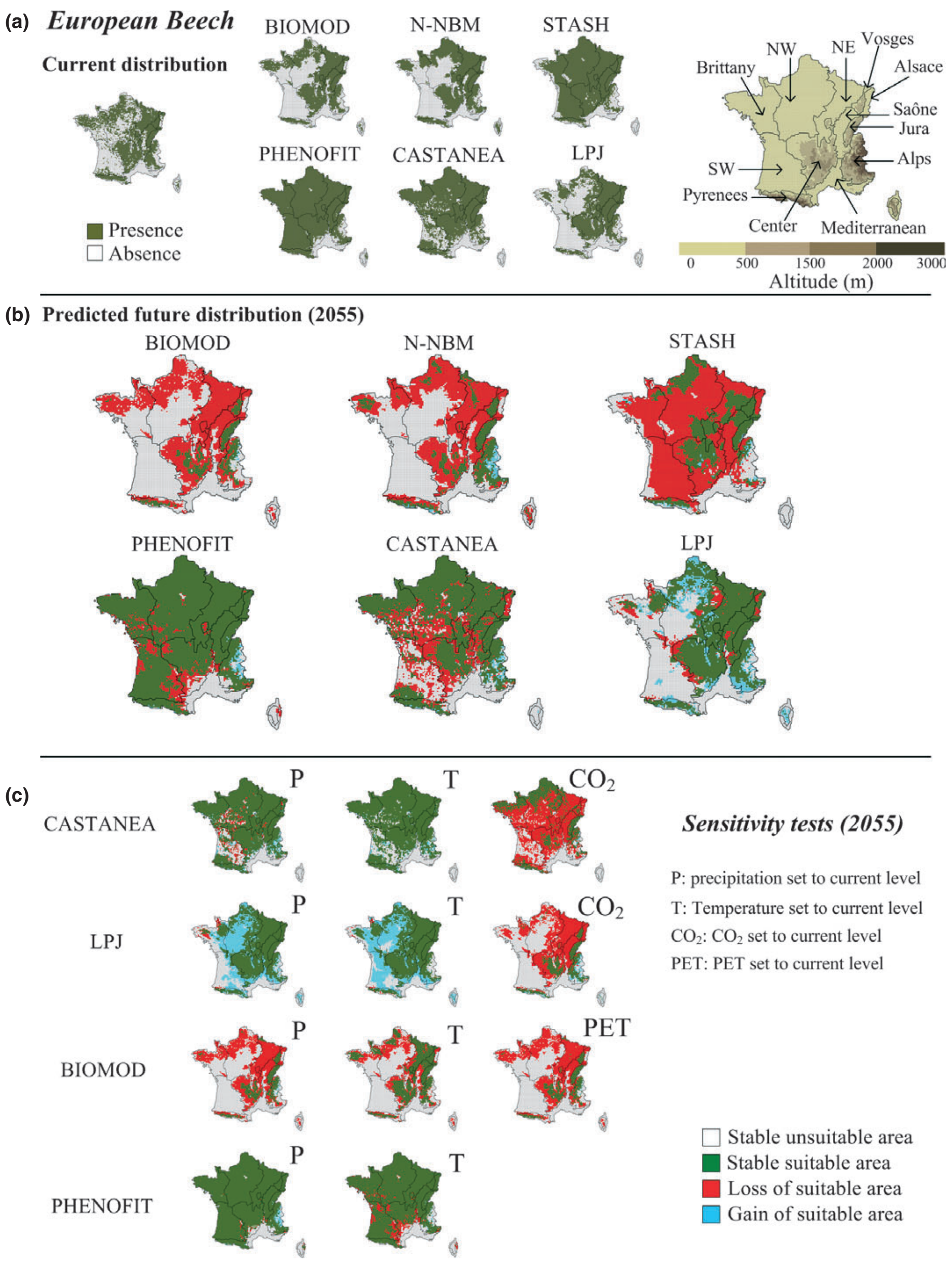

Figure 1 Modeled European beech distribution: (a) Current spatial patterns simulated by models and observed current distribution (NFI data). (b) Changes in distribution by mid-century. Red = predicted to be present in the current climate (CC), but absent in 2055; blue = predicted to be absent in the CC, but present in 2055; green = predicted to be present in the current and 2055 climates and white = predicted to be absent in the current and 2055 climates. (c) Sensitivity tests carried out by setting one climate variable to current levels and all others to 2055 levels. CO_2 = CO_2 concentration set to CC. T = temperature set to CC. P = precipitation set to CC. PET = PET set to CC.

Sensitivity tests show that positive effects of rising CO_2 explain much of the differences between CASTANEA and LPJ and the NBMs, as holding CO_2 concentrations to current levels in the former two models results in losses that approach those of NBMs (Fig. 1c). Sensitivity tests with BIOMOD and N-NBM point to temperature as the primary driver of range contraction in beech (Fig. 1c and S3a), whereas temperature or precipitation interact to drive losses of beech in CASTANEA. LPJ and PHENOFIT respond weakly to the sensitivity tests.

Patterns of modeled response to climate change for pedunculate oak are similar to beech, but with less-severe losses especially in Northern tier of the country (Fig. 2b). As is the case for beech, there is a strong contrast between large losses in the plains simulated by BIOMOD, N-NBM and STASH, and little loss or

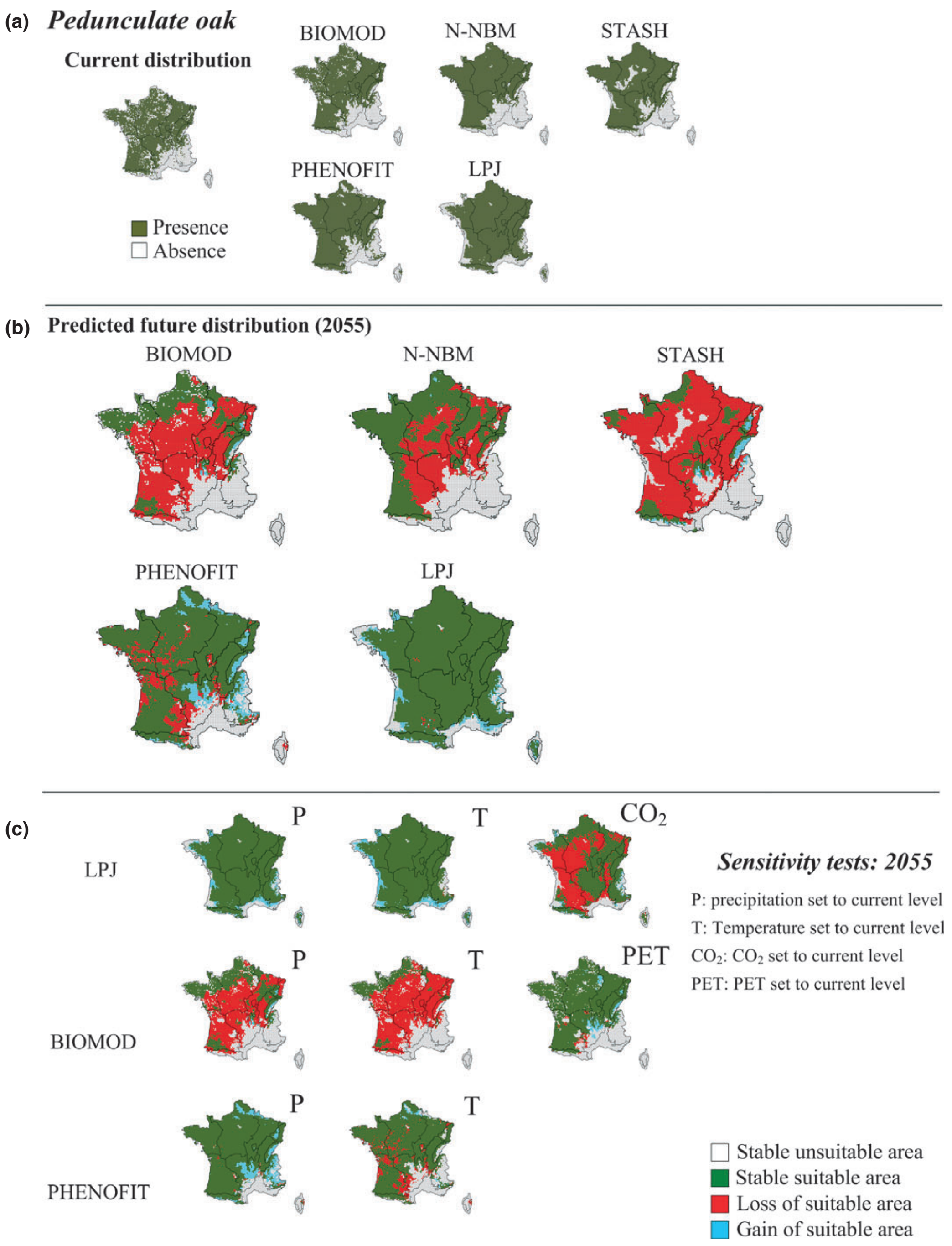

Figure 2 Modeled Pedunculate oak distribution under present and future climate: (a) Current spatial patterns of Pedunculate oak simulated by models and observed current distribution based on NFI data. (b) Model projections of changes in Pedunculate oak distribution forecasted by models by mid-century (see Fig. 1 for detailed explanation of colour code). (c) Sensitivity tests (see Fig. 1 for more detailed explanation of tests).

small gains simulated by PHENOFIT and LPJ (Fig. 2b). The response of pedunculate oak is highly dependent on CO_2 concentrations in the LPJ model and projected losses holding CO_2 constant approach those of the niche models (Fig. 2c). Sensitivity tests show that PET mediates range loss in pedunculate oak in BIOMOD (Fig. 2c) and N-NBM (Fig. S3b), in contrast to the temperature dependence of beech (Fig. 1c and S3a). Sessile oak is also projected to undergo large losses in the plains by BIOMOD and CASTANEA (Fig. S4b), with CASTANEA indicating high CO_2 sensitivity (Fig. S4c). Losses in BIOMOD are primarily driven by temperature (Fig. S4c). In contrast to these two models, N-NBM shows low climate sensitivity (Fig. S3c).

Projections for TeBS

Niche-based models projections are the summed responses of the three dominant temperate broadleaf deciduous species elsewhere. BIOMOD shows substantial range contraction in plains and mountains (Fig. 3b). ORCHIDEE foresees more modest losses of this PFT in all regions; N-NBM and IBIS forecast less change, or even

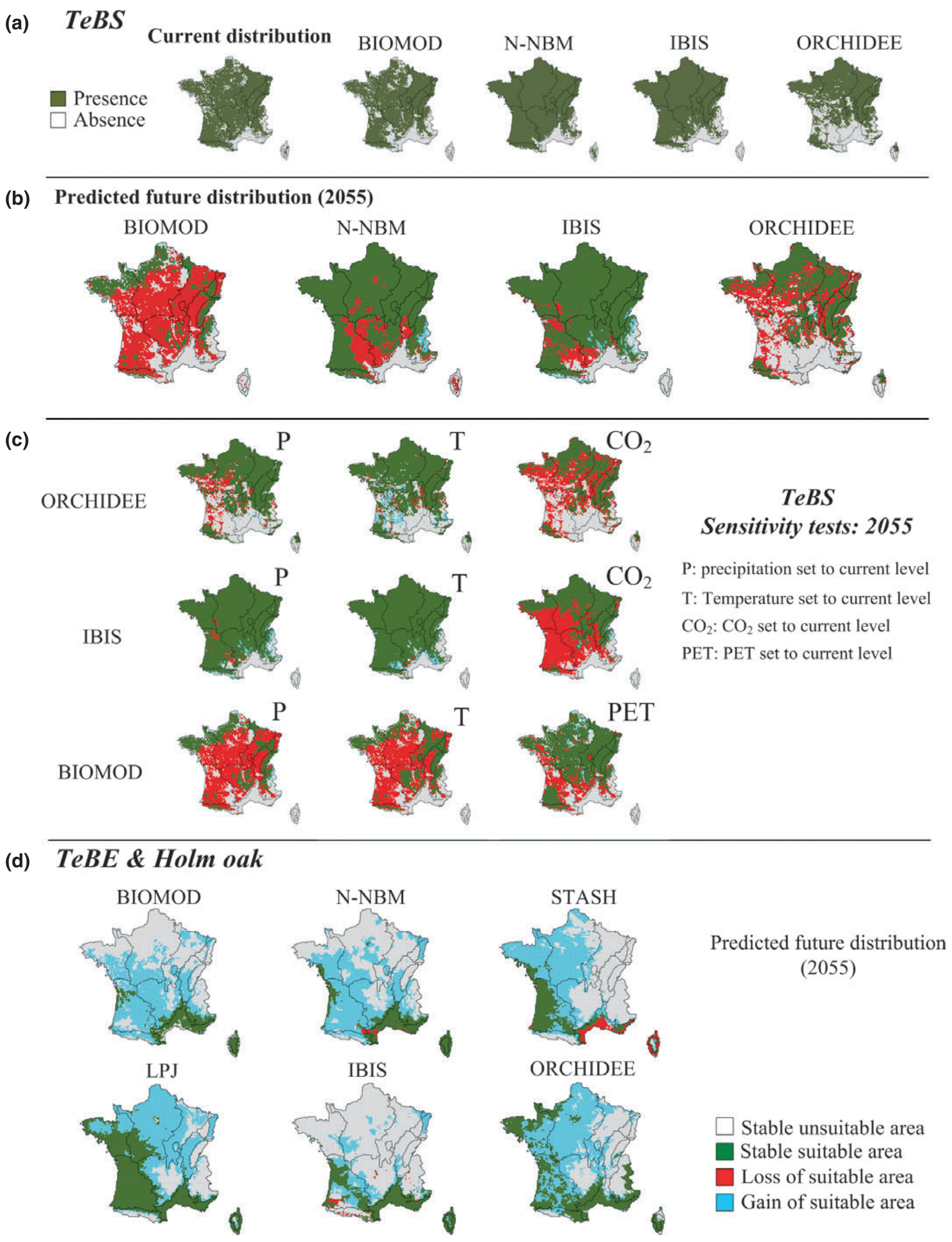

Figure 3 Projected changes in distribution of temperate broadleaf summergreen TeBS (a, b, c) and Holm oak and its PFT (temperate broadleaf evergreen TeBE; d). (a) Current spatial patterns of TeBS simulated by models and observed current distribution based on NFI data. (b) Projected changes in TeBS distribution forecasted by models by mid-century (see Fig. 1 for detailed explanation of colour code). (c) Sensitivity tests for TeBS (see Fig. 1 for more detailed explanation of tests).

slight gains (Fig. 3b). Holding atmospheric CO_2 concentrations to current levels in IBIS brings it closer to the distributions projected by BIOMOD (Fig. 3c). Holding either temperature or precipitation to current levels eliminates loss of range simulated by ORCHIDEE (Fig. 3c). Sensitivity tests indicate BIOMOD is most responsive to changes in PET (Fig. 3c).

Projections for Holm oak and TeBE

All models foresee substantial range expansion by 2055 of Holm oak in the Western two-thirds of France (Fig. 3d). Although there are large quantitative differences between the models, the qualitative response of significant gains is common to all models.

Projections for Scots pine

All models foresee nearly total loss of Scots pine in the Western two-thirds of country with the exception of higher altitudes of the centre region (Fig. 4b). In contrast to temperate broadleaf summergreen trees, rising CO_2 has only modest effects on range contractions in the LPJ model (Fig. 4c). Models are in disagreement concerning the Eastern third of the country with BIOMOD and N-NBM projecting

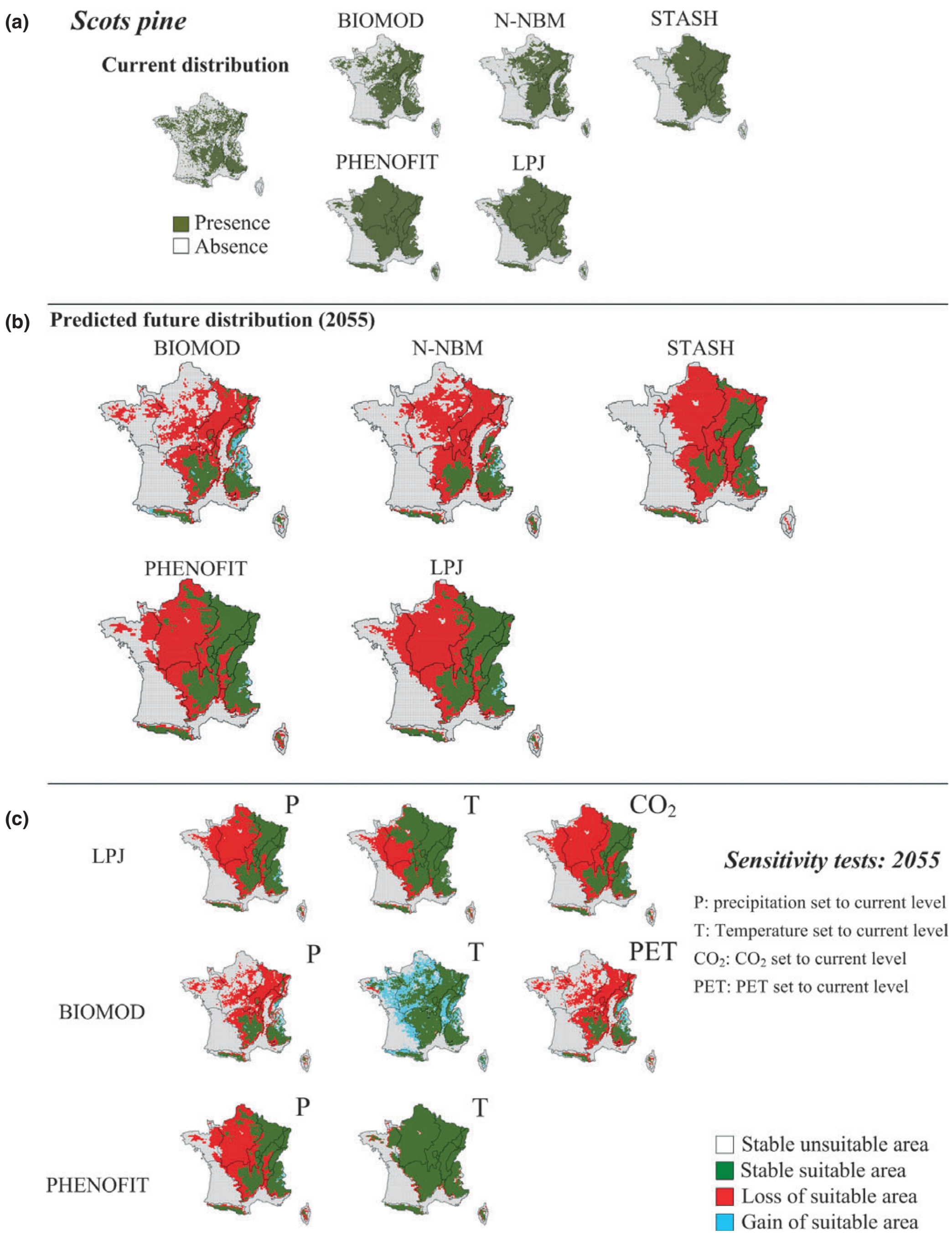

Figure 4 Modelled Scots pine distribution under present and future climate: (a) Current spatial patterns of Scots pine simulated by models and observed current distribution based on NFI data. (b) Projected changes in Scots pine distribution forecasted by models by mid-century (see Fig. 1 for detailed explanation of colour code). (c) Sensitivity tests (see Fig. 1 for more detailed explanation of tests).

near total loss in plains, PHENOFIT and LPJ projecting stability in plains and STASH in between these two extremes.

DISCUSSION

Interpreting modeled current and future distributions

Current distributions

The NBMs BIOMOD and N-NBM were fit to current observed distributions, so even though they only use climate variables as inputs, they implicitly take into account biotic interactions (i.e. simulate the Hutchinsonian realised niche) as well as management effects (Meier *et al.* 2010). On the other hand, CASTANEA, PHENOFIT, LPJ (in the configuration used in this study) and STASH simulate the environmental constraints on trees in the absence of biotic interactions (i.e. simulate the Hutchinsonian potential niche). ORCHIDEE and IBIS fall in the middle of this spectrum because they explicitly account for inter-PFT competition. Assuming that biotic interactions generally limit distributions, we expected that the predicted range size to greatest in CASTANEA, LPJ, PHENOFIT and STASH, smallest in BIOMOD and N-NBM, and in between these extremes in IBIS and ORCHIDEE. In addition, the process-based models account for a limited set of mechanisms controlling potential niche; for example, CASTANEA does not account for climatic limits on regeneration and PHENOFIT does not account for climatic limits on tree growth. Thus, when compared with observed distributions, process-based models potentially make significant errors of commission (low specificity), with hopefully relatively few errors of omission (high sensitivity), which is what we observed (Table 2). These differences complicate model intercomparison, but can be helpful in drawing inferences about the mechanisms driving current and future distributions.

Comparing models with observations for highly managed species poses additional problems. For example, the nearly complete absence of beech in some regions, e.g. lower Saône Valley and Southwest (see regions in Fig. 1), may be due to management practices since historical evidence and charcoal remains indicate that beech may have been present in the recent past at low densities (Delhon & Thiébault 2005; Silva *et al.* 2010). Thus, it is difficult to know to what extent the overprediction of presence in these regions by process-based models is incorrect.

Future distributions

Projected changes in distribution should be interpreted keeping in mind several caveats. First, to facilitate model comparison we have used long-term responses of trees to 2055 climate. BIOMOD, N-NBM, PHENOFIT and STASH simulate tree distributions at quasi-equilibrium with climate. CASTANEA, LPJ, ORCHIDEE and IBIS simulate tree performance in the long-term (150–300 years). Second, transitions from presence to absence mean that the model output falls below a threshold: it does not necessarily indicate increased tree mortality. Third, niche models generally do well at predicting current distributions, but several lines of evidence suggest that inability to account for direct CO_2 effects and novel future climates could make them unreliable for projecting future distributions (Williams *et al.* 2007; Keenan *et al.* 2010; Dawson *et al.* 2011). Fourth, none of the models include dispersal; as such, projections of increased range size should be interpreted as indicating new areas of favourable climate with an unknown time lag for establishment in these areas. Finally, none of the models account for disturbances such as insect outbreaks, pathogens or wind storms that may increase climate change-related mortality (McDowell 2011).

Insights from model comparison

Temperate broadleaf deciduous species

A superficial analysis of model comparisons for the three temperate broadleaf deciduous species and temperate broadleaf summer-green PFT suggests there is too much uncertainty for models to be of substantial help in understanding climate change impacts on their ranges. However, underlying this apparent disagreement is a coherent signal and valuable information about mechanisms of modeled tree response to climate change. First, in the absence of rising CO_2 effects, models agree in projecting widespread range contraction of the three species and their PFT in the plains of France. Second, a key exception to this pattern is the weak climate sensitivity of the PHENOFIT model, which is not necessarily in contradiction with this projection, but rather suggests that range loss is not due to climate limitations on key life stages such as flowering or seed germination. Third, the LPJ, CASTANEA and IBIS models indicate that the range contraction in the absence of CO_2 effects is due to reductions in NPP or wood production. Fourth, when rising CO_2 is accounted for, it leads to improved tree potential performance in France's Northern tier (data not shown) and even induces range expansion in some cases.

The message is therefore clear: the projected fate of broadleaf deciduous forests in France for the climate scenario used in our analysis hinges on the effects of rising CO_2 concentrations on tree performance. This conclusion confirms previous studies (Galbraith *et al.* 2010; Keenan *et al.* 2010), but does so with a substantially wider range of models. Unfortunately, there is insufficient observational evidence for adult trees to determine whether this strong positive effect of CO_2 in models is warranted. Experiments and studies in natural CO_2 springs show that temperate deciduous trees, including European beech and sessile oak, respond to elevated CO_2 with strong increases in leaf photosynthesis and NPP (Norby *et al.* 2005), but this does not always translate to significant growth responses in mature trees (Körner 2006). An analysis of tree growth and C isotopes in North America suggests that rising CO_2 concentrations have not halted recent warming related declines in tree growth despite increased water use efficiency (Silva *et al.* 2010).

Our sensitivity analyses provide additional insights into species-specific responses to climatic factors. Simulated future shifts in beech distributions are dominated by temperature responses in BIOMOD and N-NBM, as opposed to precipitation or PET. The opposite is true for Pedunculate oak as range contractions are driven almost entirely by PET. No clear pattern emerges for sessile oak. In contrast, the process-based models tend not to identify single factors as controlling range contractions: temperature and precipitation play roughly equally important roles. In-depth sensitivity analyses using the CASTANEA model with beech suggests that complex interactions between temperature, precipitation and rising CO_2 create 'novel' future climates for trees (see Fig. 1c and Davi *et al.* 2006). For example, warming is projected to increase growing season length. This can have positive effects on tree growth in the absence of water stress, but increases sensitivity to reduced precipitation because earlier spring activity reduces soil water reserves. Increased temperature can also have negative effects on tree growth due to increased respiration. Rising CO_2 decreases modeled sensitivity to water stress by enhancing photosynthesis and tree C balance. These interactions explain why future beech distributions are sensitive to temperature, precipitation and CO_2 in CASTANEA (Fig. 1c), and illustrate why predicting future tree distributions with models that do not account for these interactions may be problematic.

Scots pine

All models have difficulties predicting current distribution of Scots pine, but this appears to be due to the inability of models to predict scattered presence within its range as opposed to getting range boundaries right. These difficulties may, in part, be due to strong management effects on Scots pine distribution. In contrast to the modeled response of deciduous broadleaved trees, all models agree about future climate impacts on Scots pine in Brittany, Northwest and centre regions: they foresee large range contractions in the plains of the Western two-thirds of the country. In contrast to deciduous broadleaved trees, rising CO_2 appears to provide little protection against range contraction. The relatively strong coherence of the models in some regions is the result of the dominant role that temperature plays in mediating loss (Fig. 4c and S3d), corresponding to well-documented warm temperature limits on Scots pine growth and survival (Reich & Oleksyn 2008).

Holm oak and temperate broadleaved evergreens

For Holm oak and its PFT, all models agree that climate becomes favourable well north of its current range. Models disagree on the extent of this potential range expansion, but this is not an issue over the relatively short-time frame under consideration as dispersal and establishment will certainly be the primary limitation. Range contraction simulated by niche models in the Mediterranean region should not be overinterpreted, because Holm oak distribution in France is not representative of its Southern limit in Europe.

Overall lessons learned

A guideline for understanding part of the diversity of model responses is related to the importance of hard climatic limits such as freezing tolerance in controlling tree distributions. For example, distributions in DGVMs are controlled by productivity and growth, or hard climatic limits. When a range limit of a species is determined by hard climatic factors in these models, elevated CO_2 has little influence and range limit aligns more closely with NBMs (e.g. Scots pine). When range is limited by productivity or growth, then CO_2 can play a large role and responses often diverge significantly, especially with NBMs (e.g. beech).

Model benchmarking

Confidence in model projections depends on testing models with a broad range of data types (Dawson *et al.* 2011). Observed spatial and temporal patterns of tree and ecosystem processes provide an important check for processes-based models. CASTANEA does a good job of reproducing the dynamics of measured forest ecosystem CO_2 and H_2O fluxes and growth for stands of several key European tree species at broad spatial scales (Davi *et al.* 2006). ORCHIDEE (Morales *et al.* 2005), IBIS (Kucharik *et al.* 2000) and the PFT version of the LPJ model (Sitch *et al.* 2003; Morales *et al.* 2005) simulate reasonably well-spatial patterns of water, energy and carbon exchanges and stocks at global scales.

The ability to reproduce changes in tree distributions due to large climate fluctuations during the Holocene is an interesting test of models, notwithstanding the uncertainties associated with reconstructing climate and tree ranges (Dawson *et al.* 2011). Comparisons with pollen records suggest that LPJ (Smith *et al.* 2001) reproduces beech range well for colder climates, tends to overestimate mid-Holocene range, must account for low atmospheric CO_2 to reproduce early Holocene distributions and appears to underestimate drought sensitivity (Garreta *et al.* 2010). NBMs such as BIOMOD (Pearman *et al.* 2008), as well as STASH (Giesecke *et al.* 2007) and PHENOFIT also reproduce observed Holocene pollen distributions of woody species reasonably well, but tend to overpredict beech range in the mid-Holocene.

Interpreting model projections in the light of recent trends

There are conflicting signs concerning tree response to recent climate change. There is ample evidence that tree growth in Northern temperate climates had been increasing over the last several decades driven by a combination of atmospheric N deposition, rising CO_2 concentrations and increased growing season length due to warming (Charru *et al.* 2010; McMahon *et al.* 2010). These trends support the more optimistic projections of some models concerning climate change impacts on tree health and distribution. Other trends are less reassuring. There is growing evidence that tree growth in Northern temperate regions, including France, is beginning to decline with evidence pointing to climate change as the culprit (Charru *et al.* 2010; Silva *et al.* 2010).

There are also numerous signs of climate change related range shifts in European trees. In the Montseny mountains of Spain, beech forest has shifted upwards in altitude by *c.* 70 m over the last 50 years and is being replaced by Holm oak at lower altitudes (Penuelas & Boada 2003). In Scandinavia, several tree species including Scots pine have advanced poleward by hundreds of metres since the early 1950's (Kullman 2002). More generally, forest species optimums in Europe have moved up in altitude by 29 m per decade over the last century, although woody species responses lag those of herbaceous species (Lenoir *et al.* 2008). These observations support the idea that trees have and will continue to move poleward and up in altitude due to climate change.

Scientists and forest managers are increasingly concerned by a recent rise in tree mortality (Allen *et al.* 2010). This includes increased mortality of Scots pine following the 2003 heatwave and rising mortality in deciduous oaks in France due to drought stress (Bréda & Badeau 2008). Increased mortality of Scots pine has also been observed at its southern range limits in Switzerland and Italy (Vertui & Tagliaferro 1998; Bigler *et al.* 2006). More generally, the mortality of many woody species appears to be increasing in a broad arc across the Mediterranean region due to recent dry and warm conditions (Penuelas *et al.* 2001). These observations lend support to projections of range contractions by 2055, but it is too soon to know to if these are the loss of a few fragile populations or early indicators of more widespread tree mortality (Allen *et al.* 2010; McDowell 2011).

Using models as decision support for adaptive management

Several studies have outlined adaptive measures that could be adopted in the face of climate change in France (Legay & Mortier 2006) and elsewhere (Bolte *et al.* 2009; Lindner *et al.* 2010). These recommendations focus on: (1) improving resilience of forests by increasing genetic and species diversity, favoring natural regeneration, culling and minimising impacts of forestry activities on soils, (2) planting fast growing trees to limit the time to harvest or (3) planting species, including exogenous species, or genotypes that are resistant to higher temperatures and greater water stress.

We have discussed preliminary results of this study in numerous forums with private and public foresters, park managers and government representatives. The contrasting cases of Scots pine and beech illustrate the ways we can and cannot address the concerns of these stakeholders. In both cases, uncertainty in the degree and spatial distribution of climate change and its impacts makes it imprudent to provide site-specific forecasts of potential mortality, which is what forest managers would like to have, and this is unlikely to change in the foreseeable future. As such, our recommendations are of a more general nature and focus on regional scales.

The forestry community is particularly concerned about climate change impacts on beech, based on its known drought intolerance and projections of NBMs. Our study suggests that substantial range contraction over the next decades is possible, but there are several sources of high uncertainty. First, projected changes in precipitation are highly uncertain, ranging from −20 to −120 mm change in annual precipitation in France by 2055 for the A1B SRES scenario (Fig. S2). Second, there is little agreement among models about the impacts of the climate on beech. It is of little consolation to practitioners that we have identified the response of beech to rising CO_2 as the principal source of this uncertainty. Without further experimental CO_2 studies on adult trees it will be difficult to increase our confidence in model projections for beech. In the face of this high risk and high uncertainty, strategies focusing on increasing the resilience of beech forests to climate change through site choice and management appear to be the most prudent.

In the case of Scots pine, the forestry community was aware of possible problems at the Southern edge of its distribution, but unaware of the potential climate risk in the centre and in the Northern tier of France. Our analysis suggests that there is a high risk of range contraction for Scots pine over the entire Western two-thirds of France (Fig. S5). There is good agreement among models, range contraction appears to be driven by rising temperature, warming is predicted by a large suite of climate models (range +1.4 to +3.4 °C by 2055, Fig. S2) and experiments and current trends of Scots pine mortality point in the same direction as models. Models and experiments (Reich & Oleksyn 2008) suggest there is little leeway to alleviate this through management as climate change impacts appear to be mediated by direct temperature effects. Replacement by heat and drought tolerant conifers such as Corsican pine (*Pinus nigra* subsp. laricio) seems a sensible strategy, although not without risk if future climate includes more extreme winter temperatures.

Range shifts in trees, especially for dominant species like we have studied, will have large impacts on biodiversity and a wide range of non-provisioning ecosystem services such as ecosystem C storage, nature-based tourism and recreation, etc. (see Lindner *et al.* 2010 for a detailed analysis), but these impacts will heavily depend on the temporal dynamics of tree response to climate. Future study must therefore focus on improving the capacity of models to simulate important processes, such as mortality, dispersal, regeneration, biotic interactions and disturbance (Dawson *et al.* 2011; McDowell 2011; McMahon *et al.* 2011), and on assessing sources of uncertainty in temporal dynamics using a wide range models that include these processes.

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AUTHORSHIP

AC and PL wrote the article, analysed the results and prepared figures and tables; VB transformed original NFI, soil data and bioclimatic regions for this study; JB and CP performed the climate regionalisation; AC, VB, IC, CF, ES.G, ED, CD, WT and NV ran models and analysed results; CF and VB contributed actively to statistical techniques; ML led the dialogue with the forestry community. All authors contributed to the design of the study and provided comments on the manuscript.

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