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Incorporating the effects of changes in vegetation functioning and CO_2 on water availability in plant habitat models

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The direct effects of CO_2 level changes on plant water availability are usually ignored in plant habitat models. We compare traditional proxies for water availability with changes in soil water (fAWC) predicted by a process-based ecosystem model, which simulates changes in vegetation structure and functioning, including CO_2 physiological effects. We modelled current and future habitats of 108 European tree species using ensemble forecasting, comprising six habitat models, two model evaluation methods and two climate change scenarios. The fAWC models' projections are generally more conservative. Potential habitats shrink significantly less for boreo-alpine and alpine species. Changes in vegetation functioning and CO_2 on plant water availability should therefore be taken into account in plant habitat change projections.

Keywords: soil water content; BIOMOD; habitat models; CO_2 effect; climate change; ensemble forecasting

1. INTRODUCTION

Current climate change is causing shifts in plant species habitats, potentially causing range shifts or extinctions (Parmesan & Yohe 2003; Parmesan 2006). The impacts of climate change depend on each species' ability to migrate or adapt, phenologically or physiologically (Menzel & Fabian 1999). Migration ability partly depends on the extent of habitat shift that can be studied using habitat models (see reviews by Guisan & Zimmermann 2000 and Guisan & Thuiller 2005). The main problems limiting the accuracy of habitat models include the assumptions of equilibrium between species distribution and climate (Araújo & Pearson 2005), control of species range distributions mainly by climate (Thuiller *et al.* 2004; Araújo & Luoto 2007) and difficulties in incorporating mechanistic understanding of plant species' responses to rising atmospheric CO_2 (Woodward & Lomas 2004).

The effects of increased atmospheric CO_2 usually appear indirectly in habitat models, via their impact on global climate. However, CO_2 also affects plant physiological processes directly. Higher CO_2 concentrations generally decrease stomatal conductance (Ainsworth & Long 2005), potentially leading to lower transpiration and increased soil water availability (Gerten *et al.* 2005; Gedney *et al.* 2006). On the other hand, vegetation productivity increases with CO_2 (Norby *et al.* 2005), which may cause more transpiration through larger leaf areas (McCarthy *et al.* 2006). Vegetation structure and functioning also respond to other drivers, such as longer growing seasons in the north (Lucht *et al.* 2002; Morales *et al.* 2007). Until now, these effects have been ignored in species habitat models.

Hickler *et al.* (submitted) showed that changes in soil water projected by a process-based ecosystem model, which accounts for changes in vegetation structure and functioning due to modified climate and CO_2, can be fundamentally different from those of the traditional water availability measures of habitat models.

Are these changes sufficiently important to affect species habitat change (SHC) models? We address this question by incorporating ecosystem model-derived water availability estimates into species habitat modelling. We compare the results with models using traditional measures of water availability.

2. MATERIAL AND METHODS

We used the presence/absence data for 108 European tree and tall shrub species (Jalas & Suominen 1972–1996), split into five classes (= groups of chorotypes from the dataset): EURopean (43, temperate/pan); MEDiterranean (30); ALPine (19); BOReo-ALPine (9); and BOReal (7). We used two sets of bioclimatic data. The first ('TRAD') included only traditionally used variables: annual aridity (equilibrium evapotranspiration minus precipitation); annual precipitation; winter precipitation; mean annual temperature; mean winter temperature; and growing degree days until April and August. The bioclimatic variables were derived from a high-resolution ($10' \cong 16$ km) climate grid of Europe, including the recent past (1901–2000) and future scenarios (2001–2100; Mitchell *et al.* 2004). We averaged the bioclimatic variables for two time frames (1971–2000 and 2050–2080) and two emission scenarios (A2 and B1; Nakicenovic & Swart 2000) based on the HadCM3 global circulation model (Mitchell *et al.* 2004).

In the second dataset ('CO_2' for short, though it includes vegetation effects), aridity and precipitation were replaced by the average fraction of plant-available soil water-holding capacity (fAWC) during the growing season (daily temperature more than 5°C) in two soil layers (0–0.5 and 0.5–1.5 m). This was simulated with the LPJ-GUESS vegetation dynamics model (Smith *et al.* 2001), using parameters for European potential natural vegetation and including both CO_2 and vegetation effects (appendix I in the electronic supplementary material).

Using the BIOMOD framework (Thuiller 2003), implemented in the R software (R_Development_Core_Team 2004), we fitted six models (classification tree analysis, generalized additive model, generalized boosted model, generalized linear model, mixture discriminant analysis and randomForest) relating tree species distributions to climate, using a random subset (70%) of the data. We used the remainder to evaluate the models using Cohen's κ and the area under the curve (AUC) of a receiver-operating characteristic plot.

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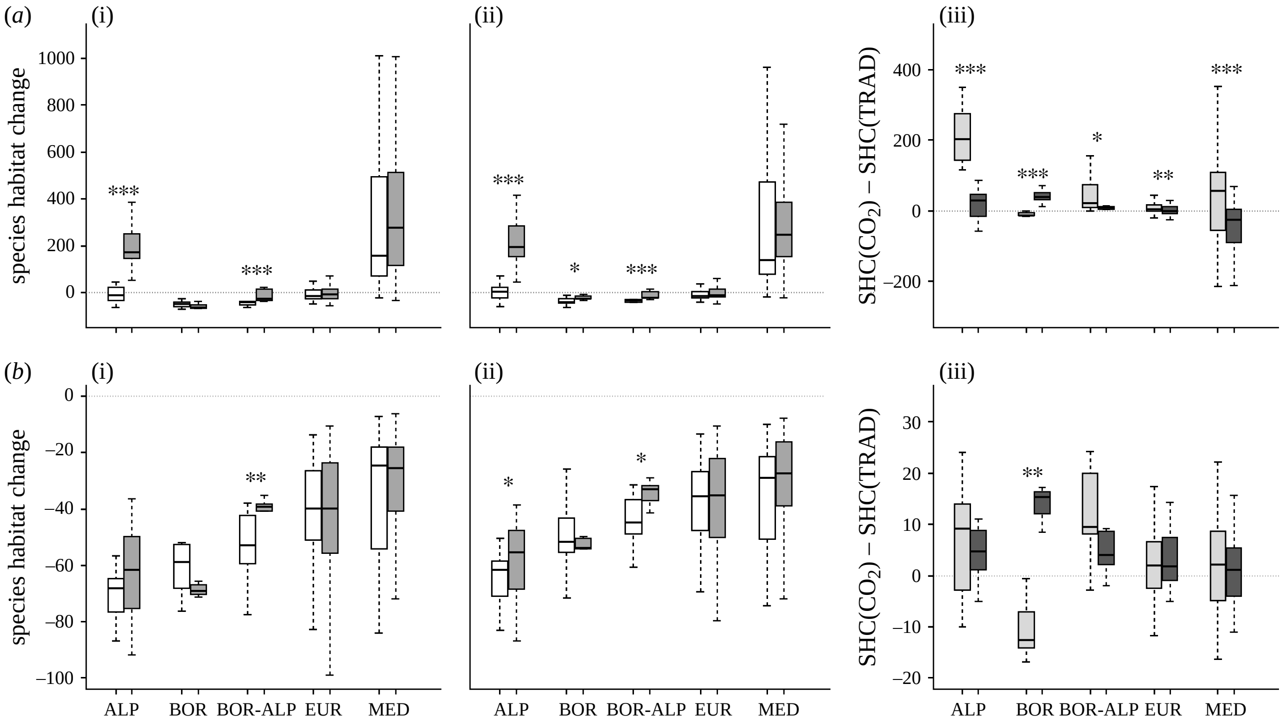


Figure 1. SHC (percentage of current distribution) in 2080, by IPCC scenarios (A2 and B1), climate dataset (TRAD and CO_2 boxes) and chorotype (ALPine, BOReal, BOReo-ALPine, temperate/pan-EURopean and MEDiterranean), with (*a*) unlimited migration or (*b*) no migration. (i)(ii) Average values per species of all the model/evaluation method combinations for A2 and B1, respectively; white boxes, TRAD; grey boxes, CO_2. (iii) SHC difference between the two datasets; light grey boxes, A2; dark grey boxes, B1. (*a*(iii),*b*(iii)) The SHC difference between the two sets of climate data. Differences between pairs of boxes were evaluated with a Wilcoxon rank sum test. ($^{***}p < 0.01$, $^{**}p < 0.05$ and $^{*}p < 0.1$.)

We projected the species current and future potential habitats with/without CO_2 and with the A2/B1 scenarios. We transformed the current occurrence probabilities into presences/absences, using the thresholds that maximize both the percentage of presences/absences correctly predicted and Cohen's κ statistic; we used the same thresholds to convert future occurrence probabilities. There are 48 model combinations per species: six models × two evaluation methods × two climate datasets × two scenarios. We calculated SHC as the proportion of new habitat respective to current habitat.

To constrain model uncertainty, we calculated a consensus projection (Araújo & New 2007) by stacking, that is, average of the 12 model combinations per climate datasets (TRAD and CO_2) and scenarios (A2 and B1), weighted according to each model's AUC score.

3. RESULTS

When unlimited migration is assumed, changes in potential habitats for plants by 2080 (figure 1*a*) vary among chorotypes: large expansions for alpine and Mediterranean species, little change or slight contractions for boreal, boreo-alpine and temperate/pan-European species. With no migration outside the current habitat (figure 1*b*), models project severe losses of potential habitat for alpine and boreal species. Including vegetation and CO_2 effects in the models gives less pessimistic projections (smaller losses/larger expansions) except for boreal species, though the difference is only significant for alpine and boreo-alpine species. The difference in projected SHC between the CO_2 and TRAD datasets are scenario dependent with unlimited migration, but not significantly so with the 'no migration' assumption. The SHC values for some selected species (table 1) also illustrate the greater difference between climate datasets than between scenarios.

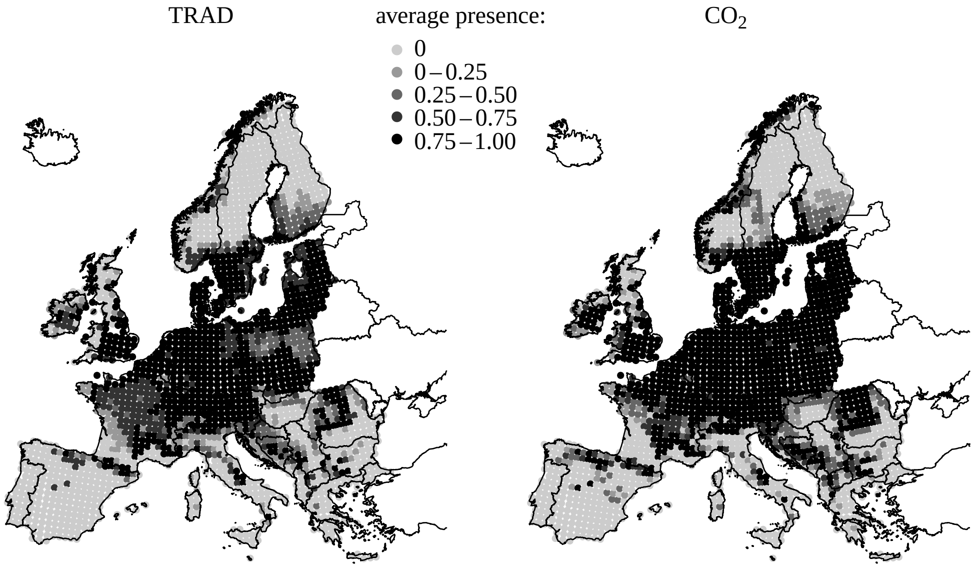
The consensus projections of potential habitats in 2080 under scenario A2 (figure 2) show a possible expansion of the *Quercus ilex* across part of western Europe with the new water availability proxies. For *Fagus sylvatica*, the difference is smaller but the eastern and western edges of the habitat range show higher presence probabilities.

4. DISCUSSION

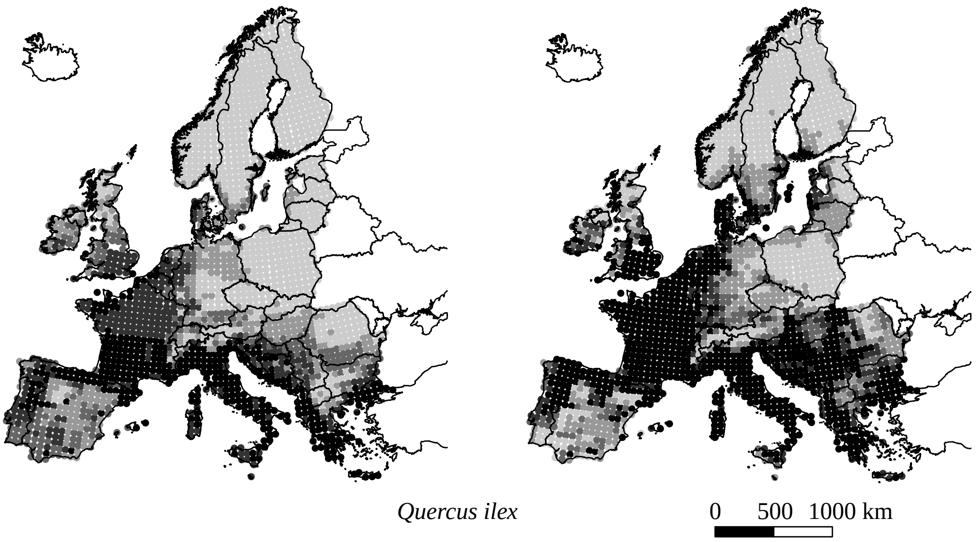
Our results show marked differences in model projections of tree species habitats when vegetation and CO_2 effects on water availability are used instead of traditional proxies. These differences are generally larger than those between the two climate change scenarios, at least for 2080. The boxplots by chorotype with unlimited migration (figure 1*a*) show that including CO_2 effects is particularly important when modelling the habitat of alpine and boreo-alpine species. This remains true when no migration is assumed (figure 1*b*), despite values changing drastically from a habitat increase to a large decrease, especially for alpine species. This difference is due to new suitable habitats appearing in regions which species cannot colonize due to migration constraints (e.g. Scandinavia for alpine species). Although Mediterranean and temperate species seem less sensitive to the new input variables, there can still be large changes in the potential habitat for some species, e.g. *Q. ilex* (MED; figure 2). The outcome of including vegetation and CO_2 in the water availability calculation depends on the net effect of changes in stomatal conductance and vegetation structure, particularly leaf

Table 1. SHC (percentage of current distribution) for six common European tree species (representing three chorotypes: ALPine; temperate/pan-EURopean; and MEDiterranean), per scenario and climate dataset. (The values are the mean and standard deviation for all models (six) and evaluation methods (two), weighted by the models' AUC scores. For all other species, see appendix II in the electronic supplementary material.)

	unlimited migration				no migration			
	A2		B1		A2		B1	
	TRAD	CO_2	TRAD	CO_2	TRAD	CO_2	TRAD	CO_2
Larix decidua (ALP)	−64±53	52±82	−59±58	47±89	−76±11	−67±13	−74±12	−65±13
Fagus sylvatica (EUR)	−25±18	−9±12	−25±23	−10±19	−42±11	−34±8	−41±15	−32±13
Pinus sylvestris (EUR)	−48±4	−44±4	−34±4	−30±4	−50±4	−46±3	−37±3	−35±3
Quercus petraea (EUR)	−14±10	−6±7	−14±17	−11±29	−33±8	−27±6	−30±13	−28±22
Quercus robur (EUR)	−5±9	−4±11	−8±8	−7±12	−22±6	−21±8	−22±6	−22±9
Quercus ilex (MED)	70±67	180±44	77±51	171±43	−18±10	−12±11	−14±10	−9±5



Fagus sylvatica



Quercus ilex

Figure 2. Future habitat projections for *F. sylvatica* and *Q. ilex* (typical of EUR and MED, respectively) by 2080, for scenario A2. These are ensemble forecasts, that is, weighted averages of the presence/absence predictions from all the combinations (six models × two thresholds), which show the presence likelihood. A value of 1 means all models predicted a presence, while 0 means all predicted an absence. To a certain extent, intermediate values represent the level of agreement across models, though they are also influenced by the weights. See electronic supplementary material for a colour version.

area. Both are affected by climate and CO_2 changes (Hickler *et al.* submitted). Stomatal closing has a stronger effect in warm dry climates where transpiration is high and water availability is low (Morales *et al.* 2007). Leaf area generally increases in cold areas as growing seasons lengthen and CO_2 rises, but in some Mediterranean areas, it decreases due to reduced water availability (Schröter *et al.* 2005; Morales *et al.* 2007; Hickler *et al.* submitted).

We conclude that the effects of changes in vegetation and CO_2 should be considered when modelling the future potential habitats of plant species. Further research should determine more precisely which species or species types are most sensitive to these effects and how these may vary over time and investigate other direct physiological effects of CO_2 changes. It would also be desirable to include land-use changes in ecosystem models to represent vegetation structure effects more realistically.

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