An ecosystem model-based estimate of changes in water availability differs from water proxies that are commonly used in species distribution models

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ABSTRACT

Aim To assess whether the water availability measures commonly used in species distribution models might be misleading because they do not account for the hydrological effects of changes in vegetation structure and functioning.

Location Europe.

Methods We compared different methods for estimating water availability in species distribution models with the soil water content predicted by a process-based ecosystem model. The latter also accounted for the hydrological effects of dynamic changes in vegetation structure and functioning, including potential physiological effects of increasing CO_2.

Results All proxies showed similar patterns of water availability across Europe for current climate, but when projected into the future, the changes in the simpler water availability measures showed no correlation with those projected by the more complex ecosystem model, even if CO_2 effects were switched off.

Main conclusions Results from species distribution modelling studies concerning future changes in species ranges and biodiversity should be interpreted with caution, and more process-based representations of the water balance of terrestrial ecosystems should be considered within these models.

Keywords

Bioclimatic envelope models, biodiversity projections, climate change, CO_2 fertilization effects, drought effects, hydrology, LPJ-GUESS ecosystem model, species distribution modelling, vegetation response, water availability.

INTRODUCTION

Ongoing climate change has caused considerable shifts in the 20th-century distributions of plant and animal species and greater changes are forecast for the 21st century (Fischlin *et al.*, 2007). Species distribution models using bioclimatic envelopes, also referred to as bioclimatic envelope models, have been widely applied to project changes in species distributions and biodiversity under climate change (e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Schwartz *et al.*, 2006). The results from these models have been used for guiding policies for adaptation to climate change (e.g. Harrison *et al.*, 2006; Hannah *et al.*, 2007).

Some envelope model studies have identified changes in water availability as one of the major drivers of future changes in

species distributions (Thuiller *et al.*, 2005; Araújo *et al.*, 2006), but the effects of changes in vegetation structure and functioning on the water balance of terrestrial ecosystems are not accounted for in the measures of water availability currently used in envelope models. Changes in productivity and leaf area under climate change, for example, might influence transpirational water losses from ecosystems. The potential effects of increasing atmospheric CO_2 have received particular attention in the recent literature (Gerten *et al.*, 2005; Norby *et al.*, 2005; Betts *et al.*, 2007). Increasing CO_2 tends to decrease stomatal conductance (Ainsworth & Long, 2005), potentially leading to lower transpiration and increased soil water content (Körner, 2006; Reich *et al.*, 2006) and runoff (Betts *et al.*, 2007). At least in herbaceous vegetation and young forest stands, elevated CO_2 also increases vegetation

productivity (Ainsworth & Long, 2005; Norby *et al.*, 2005) and thereby potentially the leaf area from which water losses through transpiration occur (Norby *et al.*, 2005; McCarthy *et al.*, 2006). The net effect of stomatal closing and increased leaf area on available water can also be negative (Wullschleger *et al.*, 2002). However, it has never been quantified to what extent measures of water availability that account for the effects of changes in vegetation structure and functioning differ from traditionally used water availability proxies.

In this study, we compare four proxies of water availability that are commonly used in species distribution modelling and the soil water content predicted by a process-based ecosystem model (LPJ- GUESS), which accounts for changes in vegetation structure, such as leaf area index (LAI), and functioning (e.g. effects of changes in photosynthetic demand and CO_2 on stomatal conductance) in response to climate change. We used a gridded climate dataset for calculating water proxies for Europe under present-day climate conditions and one climate change scenario. To account for uncertainties in our projections of direct physiological CO_2 effects, we also computed future changes in soil water content while keeping the CO_2 concentration constant at the current value.

MATERIALS AND METHODS

Environmental driver data

The gridded climate dataset consisted of mean monthly temperature, precipitation and cloud cover fields for the European land surface from 1901–2100 at 10′ spatial resolution (about 16 km; Mitchell *et al.*, 2004). The climate scenarios were derived by combining information on observed climate from the Climatic Research Unit (CRU) at the University of East Anglia (New *et al.*, 2002) with changes in climate variables simulated by an Atmosphere–Ocean General Circulation Model (AOGCM; Mitchell *et al.*, 2004). The AOGCM-derived climate anomalies were superimposed onto the high-resolution observed climate data (see Mitchell *et al.*, 2004, for details), implying that present-day biases in the AOGCM simulation were removed. Daily climate data were derived by linear interpolation between monthly means.

We used a simulation of the Hadley Centre Coupled Model, version 3 (HadCM3) AOGCM (Gordon *et al.*, 2000) forced by the Special Report on Emission Scenarios (SRES) A2 emission scenario (Nakićenović & Swart, 2000). The average annual temperature increases by 3.2 °C between the time periods 1971–2000 and 2051–2080, and the total annual precipitation increases by 0.2% [+18.8% in winter (December, January, February) and −15.4% in summer (June, July, August)].

Ecosystem model input in terms of soil texture was derived by disaggregating a 0.5° global soil texture dataset (Sitch *et al.*, 2003), i.e. soil texture was assumed to be homogeneous within 0.5° grid cells. Historical CO_2 concentrations for 1901–2000 were taken from McGuire *et al.* (2001) and TRENDS (http://cdiac.esd. ornl.gov/ trends/co2/contents.htm). Scenario CO_2 concentrations were taken from a simulation of the Bern-CC carbon-cycle model, with an increase up to 682 p.p.m. by volume (p.p.m.v.) by 2080 for the A2 simulation (Houghton *et al.*, 2001).

Commonly used measures of water availability

As proxies of water availability, we used the total annual precipitation ($PRECIP_{year}$); the total precipitation during the period of the year when water is commonly most limiting (June, July and August; $PRECIP_{JJA}$); the annual water deficit (WD) calculated as the annual sum of the monthly differences between potential evapotranspiration (PET) and precipitation for those months when PET exceeds precipitation; and the growing-season sum of actual evapotranspiration divided by equilibrium evapotranspiration (AET/EET), whereby the growing season was defined by daily mean temperatures above 5 °C. For AET and EET, we used the algorithms described by Prentice *et al.* (1993), with the soil water holding capacity set at 150 mm (Sykes *et al.*, 1996). In these algorithms, AET is calculated as the minimum of the supply of water and the atmospheric demand in terms of EET, whereby the latter is driven by the amount of energy provided to the atmosphere through radiation (Jarvis & McNaughthon, 1986). The water supply is proportional to soil moisture (Federer, 1982), calculated for a one-layer bucket model (Prentice *et al.*, 1993). Estimating PET is more complex, as PET also is driven by water pressure gradients between the surface and the air masses above, which dynamically interact with AET and depend on the amount of water transported away from the surface by wind (Hobbins *et al.*, 2001). On large scales (such as grid cells with an extent of several kilometres), PET can be estimated by multiplying EET with a constant of about 1.3 (Hobbins *et al.*, 2001), which was also applied in this study. The chosen variables or similar indices have been used in a large number of envelope modelling studies (e.g. Hill *et al.*, 1999, 2002; Bakkenes *et al.*, 2002; Thomas *et al.*, 2004; Beaumont *et al.*, 2005; Thuiller *et al.*, 2005, 2006; Araújo *et al.*, 2006; Elith *et al.*, 2006; Franco *et al.*, 2006; Luoto *et al.*, 2006; Menéndez *et al.*, 2007; Pompe *et al.*, 2008).

Soil water content predicted by ecosystem model

We used the LPJ-GUESS model (Smith *et al.*, 2001) to calculate the average fraction of the plant-available soil water-holding capacity (fAWC) in the first soil layer (0–0.5 m) during the growing season (average daily temperature > 5 °C). In LPJ-GUESS, AWC is calculated by subtracting the water-holding capacity at wilting point from the total water-holding capacity. A general wilting point of −1.5 MPa is assumed, and water-holding capacities depend on soil texture (Sitch *et al.*, 2003). In order to distinguish the effects of CO_2 from those of vegetation changes that are driven by other climatic variables, we also computed fAWC with a constant atmospheric CO_2 value from the year 2000 onwards ($fAWC_{noCO2}$).

Ecosystem model

LPJ-GUESS is a generalized, process-based model of vegetation dynamics and biogeochemistry designed for regional to global applications. It combines features of the widely used Lund–Potsdam–Jena Dynamic Global Vegetation Model (LPJ-DGVM; Sitch *et al.*, 2003) with those of the General Ecosystem Simulator

(GUESS; Smith *et al.*, 2001) in a single, flexible modelling framework. The models have identical representations of ecophysiological and biogeochemical processes, including the hydrological cycle updates described in Gerten *et al.* (2004). They differ in the level of detail with which vegetation dynamics and canopy structure are simulated: simplified but computationally efficient representations are used in the LPJ-DGVM, while in LPJ-GUESS a more detailed and mechanistic approach, distinguishing individual trees, population age and size structure, and patch-scale heterogeneity is adopted. In this study, the more detailed approach was used, and the original version of LPJ-GUESS (Smith *et al.*, 2001, including the hydrological updates described in Gerten *et al.*, 2004) was parameterized for 16 major European tree species, two shrub plant functional types (PFTs) and two PFTs representing herbaceous vegetation in order to adequately represent the potential natural vegetation (PNV) of Europe (see Appendix S1 in Supporting Information).

LPJ-GUESS and LPJ-DGVM have been developed and applied by a large number of scientists and have, for example, been shown to reproduce high northern latitude greening trends (Lucht *et al.*, 2002), global and regional patterns of vegetation and tree species distributions (Sitch *et al.*, 2003; Hickler *et al.*, 2006; Koca *et al.*, 2006), variations in net primary productivity (NPP) across different biomes (Zaehle *et al.*, 2005; Hickler *et al.*, 2006), forest stand structure and development (Smith *et al.*, 2001; Hickler *et al.*, 2004) and the magnitude of the response of NPP to elevated CO_2 observed in free air CO_2 enrichment (FACE) experiments (Hickler *et al.*, 2008).

Vegetation dynamics in LPJ-GUESS and model set-up

Vegetation is represented as a mixture of species or PFTs, which are differentiated by bioclimatic limits and physiological, morphological, phenological and life-history criteria. Bioclimatic limits, such as minimum winter temperature for survival and the thermal energy available during the growing season expressed in terms of the growing degree day sum above 5 °C (GDD_5; Sykes *et al.*, 1996), determine which species or PFTs can establish and survive in a given climate. Other ecological characteristics, such as leaf type (needles or broad-leaved), phenology (evergreen or summergreen), general geographical range (which affects base respiration rates), shade-tolerance class and root distribution govern competition for light and water between co-occurring species and determine which species become dominant and the structure of the vegetation under given environmental conditions (see Smith *et al.*, 2001, and Hickler *et al.*, 2004, for details). The modelling of population dynamics in LPJ-GUESS is based upon the gap dynamics concept (Watt, 1947). The model simulates the establishment, growth and mortality of individual trees in a number of replicate patches, each corresponding in size to the approximate area of influence of one adult tree. If one large canopy tree dies, a gap is formed and the establishment of other trees increases, including shade-intolerant species, which cannot establish under a closed canopy. Individual tree establishment, mortality and patch-destroying disturbance (representing, for example, wind storms) are modelled stochastically (Smith *et al.*,

2001). In order to represent the average vegetation of a larger area, such as a grid cell, all state variables and processes, such as LAI and water fluxes, are averaged over a number of replicate patches (here 50).

LPJ-GUESS is driven by daily values of temperature, precipitation and percentage sunshine hours, information on latitude (used for calculating radiation as function of percentage sunshine hours) and soil texture, and a global annual atmospheric CO_2 concentration value. Model simulations in this study followed a standard procedure, described in Sitch *et al.*, 2003), with 400-years spin-up until the modelled vegetation was in approximate equilibrium with the climate. Land use was not accounted for in this study. The model was run so as to simulate PNV vegetation. We simulated transient vegetation changes, implying that the vegetation between 2051 and 2080 was not in equilibrium with the climate scenario data for this period.

Photosynthesis and CO_2 effects

A modified Farquhar photosynthesis scheme (Collatz *et al.*, 1991; Haxeltine & Prentice 1996a,b) calculates vertically integrated canopy photosynthesis analytically as a function of absorbed photosynthetically active radiation, temperature and atmospheric CO_2 concentration. The scheme explicitly calculates light-limited and Rubisco-limited rates of photosynthesis, and leaf respiration as a function of enzyme content. The photosynthetic gain is optimized under the assumption of optimal nitrogen allocation to leaves at different levels in the canopy (Haxeltine & Prentice, 1996b). More details concerning the response of photosynthesis and productivity to elevated CO_2 and other environmental drivers are given in Haxeltine and Prentice (1996b) and Hickler *et al.* (2008).

If the water supply, which is a function of a maximum transpiration rate, the soil water content in both soil layers and the relative distribution of plant roots across soil layers (Smith *et al.*, 2001), is lower than the atmospheric demand, which is calculated based upon the leaf conductance associated with an unstressed (optimal water supply) photosynthesis rate, canopy conductance is reduced until transpiration equals supply. Under these circumstances the diffusion of CO_2 into the leaf is also decreased, resulting in lower photosynthesis rates. The dynamic coupling between photosynthesis and the diffusion of water and CO_2 through stomata is described in equation 1 (Haxeltine & Prentice, 1996a, Eqn. 20)

$$g_c = g_{min} + \frac{1.6 A_{dt}}{c_a (1 - \lambda)} \qquad (1)$$

where g_c is the total daytime canopy conductance, g_{min} is a PFT-specific minimum canopy conductance, A_{dt} is the total daytime net photosynthesis, c_a is the ambient mole fraction of CO_2 and λ is the ratio of intercellular to ambient partial pressure of CO_2. Decreasing CO_2 diffusion into the leaf under water stress is represented through a reduction in λ. Stomatal closing results in a drier atmosphere and thereby potentially higher atmospheric demand for water, which can lead to high transpiration rates in spite of more closed stomata. The coupling between transpiration
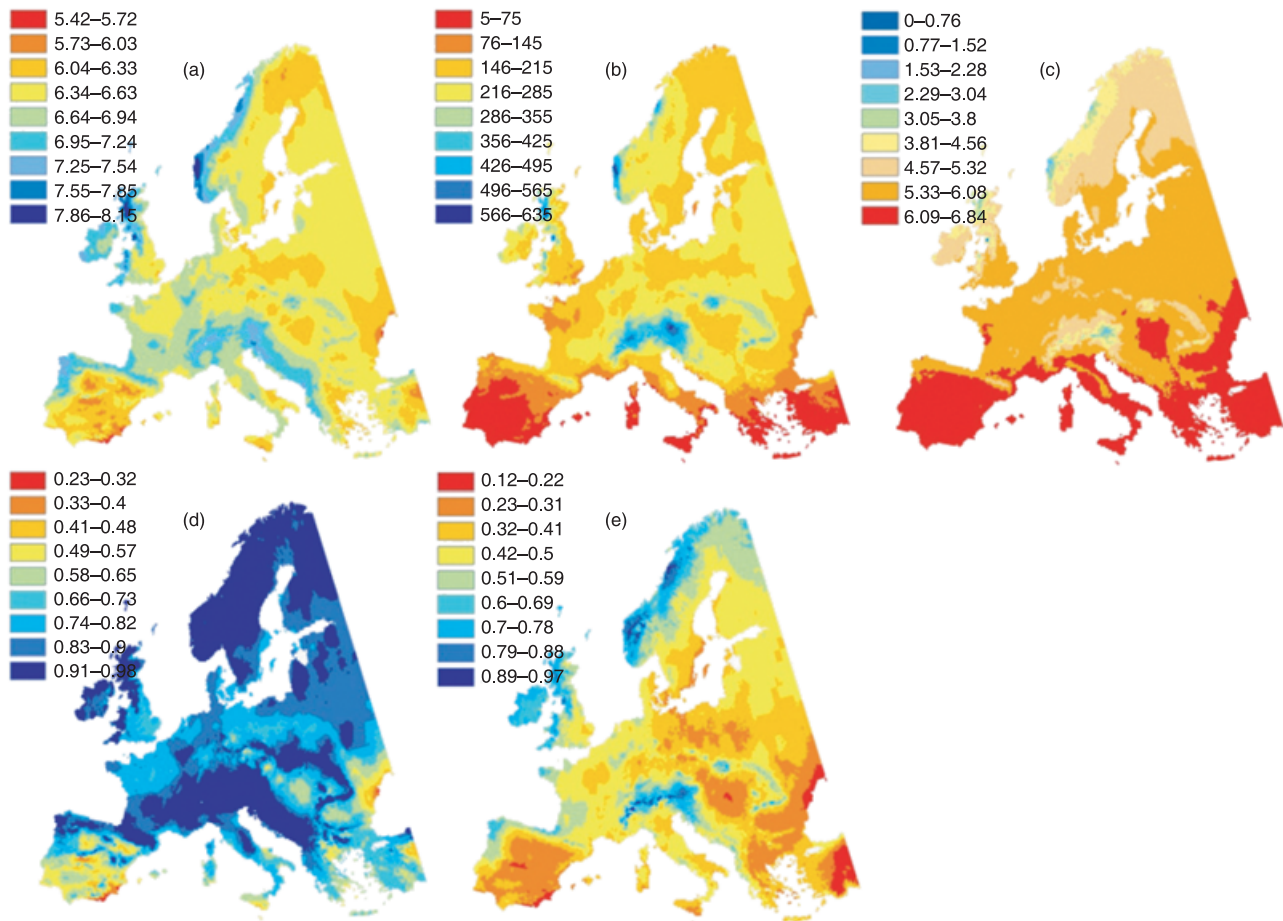
Figure 1 Measures of water availability under present-day climate (average for 1971–2000): (a) total precipitation per year (PRECIP$_{year}$; mm); (b) total summer (June, July, August) precipitation (PRECIP$_{JJA}$; mm); (c) water deficit calculated as annual sum of the monthly differences between potential evapotranspiration (PET) and precipitation for those months when PET exceeds precipitation (WD; mm); (d) total growing season (daily temperature > 5 °C) evapotranspiration/equilibrium evapotranspiration (AET/EET); (e) fAWC [average growing season (daily temperature > 5 °C) fraction of plant-available soil water holding capacity; with (here) and without direct physiological effects of atmospheric CO_2 (fAWC$_{noCO2}$; e.g. Fig. 2)]. For PRECIP$_{year}$ and WD, log values are shown because distributions were highly skewed, in the case of WD after multiplying all values with −1. Classes were divided with equal intervals. High values denote high water availability, except for WD, for which high values denote lower water availability. Albers equal area conic projection (ArcGIS 9.2).

and the characteristics and behaviour of the atmospheric boundary layer is accounted for in LPJ by an empirical relationship between surface conductance and transpiration (Huntingford and Monteith, 1998).

RESULTS

Current water availability measures show similar patterns across Europe (Fig. 1). All variables consistently identify parts of the Mediterranean and the north-western coast of the Black Sea as the driest parts of Europe. According to fAWC, PRECIP$_{year}$, PRECIP$_{JJA}$ and WD, the wettest areas occur along the Atlantic coastal mountains of Norway and Scotland, and in the Alps. AET/EET is less sensitive to changes in water availability under relatively wet conditions (Fig. 1; see also Appendix S2). As the visual impression from the maps indicates, all variables are correlated with each other (Table 1), whereby the correlation between PRECIP and WD is weakest ($R^2 = 0.12$), and PRECIP$_{JJA}$ and WD show the strongest correlation ($R^2 = 0.77$; Table 1). Scatter plots and equations for all correlations are given in Appendix S2.

Projected changes in the water availability measures show marked differences between the commonly used measures PRECIP$_{year}$, PRECIP$_{JJA}$, AET/EET and WD on the one hand, and fAWC on the other (Fig. 2). PRECIP$_{year}$ increases in most of Scandinavia and large parts of central Europe, while PRECIP$_{JJA}$ mainly increases in Scandinavia. WD and AET/EET indicate that the net effect of increasing temperature, and in many areas also annual rainfall, will be drying over most of Europe. fAWC suggests a very different picture. When comparing AET/EET and fAWC, for example, the sign of the change (plus or minus) differs in 32% of the total study area, and fAWC tends to suggest wetter conditions than AET/EET (76% of the area with disagreement).
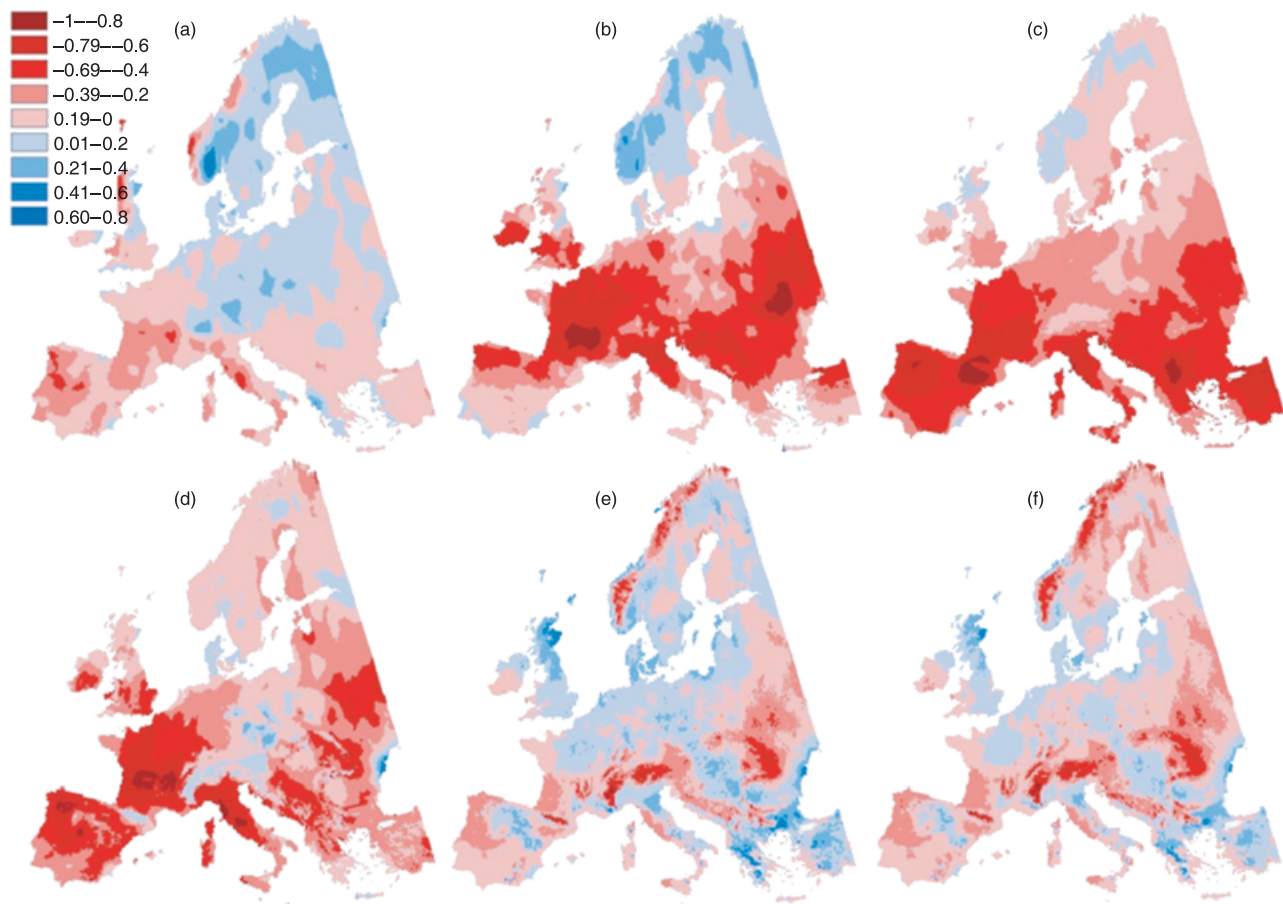
Figure 2 Projected changes in water availability (averages for 2051–2080 minus averages for 1971–2000): (a) total annual precipitation (PRECIP$_{year}$); (b) total precipitation during June, July and August (PRECIP$_{JJA}$); (c) annual water deficit (WD); (d) growing-season sum of actual evapotranspiration divided by equilibrium evapotranspiration (AET/EET); (e) average fraction of the plant-available soil water-holding capacity (fAWC); (f) computed fAWC with a constant atmospheric CO_2 value from the year 2000 onwards (fAWC$_{noCO2}$). All changes were normalized to the maximum change for a given variable. Albers equal area conic projection (ArcGIS 9.2).

Table 1 Squared linear correlation coefficients (R^2) between present-day (averaged for 1971–2000) proxies of water availability. Linear, exponential ($y = ae^{bx}$), and logarithmic ($y = b \ln(x) + a$) relationships were applied. The highest R^2 is presented; if through an exponential or logarithmic relationship marked with an asterisk (*). Scatter plots for all relationships and equations are given in Appendix S2.

	PRECIP$_{year}$	PRECIP$_{JJA}$	WD	AET/EET	fAWC
PRECIP$_{year}$					
PRECIP$_{JJA}$	0.33				
WD	0.12*	0.77*			
AET/EET	0.26*	0.53	0.69		
fAWC	0.48*	0.35	0.50*	0.62*	

PRECIP$_{year}$, total annual precipitation; PRECIP$_{JJA}$, total precipitation during June, July and August; WD, annual water deficit; AET/EET, growing-season sum of actual evapotranspiration divided by equilibrium evapotranspiration; fAWC, average fraction of the plant-available soil water-holding capacity.

fAWC$_{noCO2}$ shows a similar spatial pattern to fAWC, but with drier conditions (an average decrease in fAWC by 3.3%, compared with 0.4% if CO_2 effects are enabled). The changes projected by PRECIP$_{year}$, PRECIP$_{JJA}$, AET/EET and WD are correlated with each other (Table 2), but the changes projected with these variables show no or very weak correspondence with the two ecosystem model-derived proxies of changes in water availability (Table 2). Note that the strong discrepancy only applies to the 'changes' in water availability, not to the totals. However, the magnitude of the projected changes is considerable (Table 3) and, thus, of importance for species distributions.

Despite marked differences between different water proxies, some areas are consistently simulated to be drier in the future when comparing those water measures that account for changes in precipitation and temperature (through its effect on PET; Fig. 2(c)–(f)): large parts of south-western Europe, the Karpatian and Dinarian (Balkan) mountains, south-western Italy and the parts of Russia and Ukraine that are covered here (Fig. 3).

All scatter plots and equations are given in Appendix S3. The heterogeneous spatial pattern in the results from the ecosystem

Table 2 Squared linear correlation coefficients (R^2) between future changes in proxies of water availability (averages for 2051–2080 – averages for 1971–2000; Fig. 2). All changes were normalized to the maximum change for a given variable. Scatter plots for all relationships and equations are given in Appendix S3.

	$PRECIP_{year}$	$PRECIP_{JJA}$	WD	AET/EET	fAWC	$fAWC_{noCO2}$
$PRECIP_{year}$						
$PRECIP_{JJA}$	0.30					
WD	0.46	0.52				
AET/EET	0.41	0.46	0.51			
fAWC	0.05	0.04	0.01	0.03		
$fAWC_{noCO2}$	0.01	<0.01	<0.01	<0.01	0.94	

$PRECIP_{year}$, total annual precipitation; $PRECIP_{JJA}$, total precipitation during June, July and August; WD, annual water deficit; AET/EET, growing-season sum of actual evapotranspiration divided by equilibrium evapotranspiration; fAWC, average fraction of the plant-available soil water-holding capacity; $fAWC_{noCO2}$, computed fAWC with a constant atmospheric CO_2 value from the year 2000 onwards.

Table 3 Means and standard deviations (SD) of the changes in water availability measures are expressed as a percentage. (For the calculation of the means, values were weighted by grid cell size, which decreases to the north, but not for SD.)

	Means	SD
$PRECIP_{year}$	−0.5	7.5
$PRECIP_{JJA}$	−15.4	17.3
WD	−29.3	21.6
AET/EET	−6.9	6.0
fAWC	−0.4	8.6
$fAWC_{noCO2}$	−3.3	8.3

$PRECIP_{year}$, total annual precipitation; $PRECIP_{JJA}$, total precipitation during June, July and August; WD, annual water deficit; AET/EET, growing-season sum of actual evapotranspiration divided by equilibrium evapotranspiration; fAWC, average fraction of the plant-available soil water-holding capacity; $fAWC_{noCO2}$, computed fAWC with a constant atmospheric CO_2 value from the year 2000 onwards.

model is to some extent caused by stochastic variations (see model description). The general picture, however, is independent of the number of replicate patches.

DISCUSSION

The results show that future projections of changes in water availability by the commonly used water availability proxies differ substantially from those that include the effects of changes in vegetation structure and functioning on the water balance. Therefore, projections of altered species distributions based purely on commonly used variables should be interpreted with caution. This is particularly true when changes in water availability
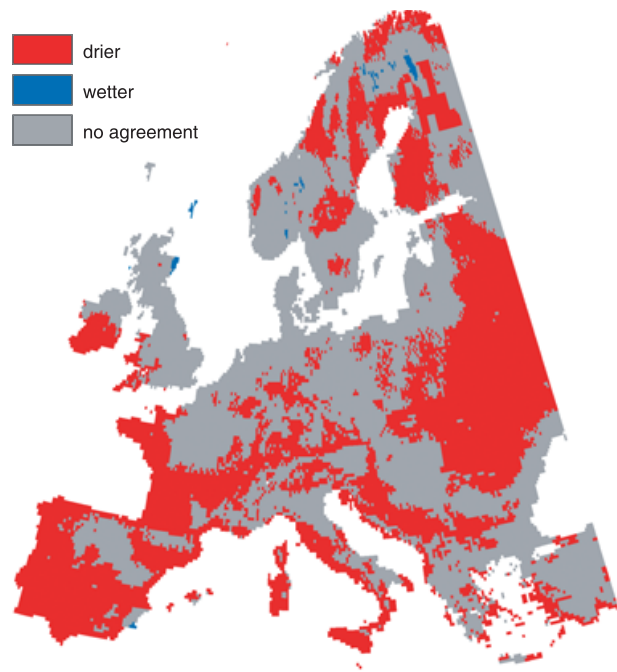
Figure 3 Agreement (wetter or drier) and disagreement amongst those variables that account for changes in precipitation and PET: WD, AET/EET, fAWC and $fAWC_{noCO2}$ (PET, potential evapotranspiration; WD, annual water deficit; AET/EET, growing-season sum of actual evapotranspiration divided by equilibrium evapotranspiration; fAWC, average fraction of the plant-available soil water-holding capacity; $fAWC_{noCO2}$, computed fAWC with a constant atmospheric CO_2 value from the year 2000 onwards). Albers equal area conic projection (ArcGIS 9.2).

have been identified as the main drivers of change in species distributions and biodiversity (e.g. Thuiller *et al.*, 2005; Araújo *et al.*, 2006).

At least for plants, the water content in the soil predicted by an ecosystem model is a more direct measure of water availability than variables that are purely based on climate. The capability of LPJ-GUESS and the closely related LPJ-DGVM to adequately simulate water fluxes in ecosystems has been demonstrated by comparing model output to observations of soil water content (Sitch *et al.*, 2003), stand-scale AET (Morales *et al.*, 2005), continental and global runoff (Gerten *et al.*, 2004) and latitudinal variations in AET across the globe (Gerten *et al.*, 2004). The implemented scheme for coupling photosynthesis, the CO_2 concentration in the atmosphere and canopy conductance is based on physiological principles (Farquhar *et al.*, 1980) and very similar approaches have been adopted by many biosphere and earth system models (e.g. Cramer *et al.*, 2001; Betts *et al.*, 2007). LPJ-GUESS also reproduces the magnitude of NPP enhancement under elevated CO_2 observed in forest FACE experiments (Hickler *et al.*, 2008), but the relevance of these experiments in primarily young forest stands to long-term NPP responses is still debated, in particular because of interactions with nutrients (Körner 2006; Hickler *et al.*, 2008).

Factors that are only accounted for by the ecosystem model

LPJ-GUESS includes a number of factors that influence water availability and are not accounted for in simpler water proxies. These include the potential of vegetation to adapt to drier conditions by decreasing LAI, and thereby water losses, from ecosystems through evapotranspiration; increased photosynthesis and NPP at high altitudes and northern latitudes in response to longer growing seasons (Lucht *et al.*, 2002; Morales *et al.*, 2007) and increased atmospheric CO_2 if there is ample supply of water; shifts in vegetation, for example, as trees can grow at higher altitudes and further to the north (Kullman, 2002) or replacement of boreal conifers by temperate broad-leaved trees (Appendix S1); and potential effects of increasing levels of atmospheric CO_2 on the water balance of ecosystems and plant water use efficiency.

Potential ecosystem adaptation to drier conditions through reductions in leaf area has been discussed by foresters as a measure to reduce the vulnerability of forests to climate change. In our simulations, this 'ecosystem adaptation' occurs, for example, in the Mediterranean part of the Iberian Peninsula, where shrublands replace evergreen forests (Fig. S1.1 within Appendix S1). Shifts of the tree line in response to climate warming (Appendix S1) are causing higher transpiration and interception, thereby decreasing soil water in many mountain areas according to the model (Fig. 2). In LPJ-GUESS, the tree line shifts as GDD_5 and minimum winter temperatures increase under climate change. Tree establishment at the tree line is primarily limited by GDD_5 (with a minimum of 350 for the most northern trees), with species-specific minimum winter temperatures for survival only being important in areas with very cold winters (Sykes *et al.*, 1996). Pronounced tree line shifts have been observed under only moderate climate change. Kullman (2002), for example, reported observed historical tree line shifts of 100–150 m (depending on the species, up to 375 m) since the 1950s in the Swedish Scandes, driven by a slight temperature increase of 0.8 °C between 1901 and 2000. However, the model simulates potential tree line shifts, not accounting for browsing animals, steep topographic gradients and dispersal limitations, which can all exert a strong influence on tree lines (Cairns & Moen, 2004; Dullinger *et al.*, 2004). Therefore, the true response will be smaller in most areas.

At lower altitudes, where water stress is more pronounced (Fig. 1), simulated changes in vegetation productivity and leaf area are also highly dependent on changes in water availability. According to the climate scenario used here, water stress increases in large parts of Europe (Fig. 2), leading to forest die-back and replacement with shrub vegetation in some Mediterranean areas, in particular when the physiological effects of increased CO_2 are not enabled (Appendix S1).

The effects of CO_2 on stomatal opening and g_c have been well researched. Reviewing the results from free air CO_2 enrichment experiments, Ainsworth & Long (2005) showed that g_c on average decreases by about 20% under elevated CO_2 (*c.* 550 p.p.m.v.). In a global model experiment, applying the CO_2 elevation in FACE studies to the potentially forested area on earth (Hickler *et al.*, 2008), LPJ-GUESS predicted a reduction in g_c of 21.7%, averaged

over all PFTs, suggesting that the modelled stomatal closing is realistic in general terms. The potential of this effect for altering the water balance of ecosystems has been demonstrated in a number of modelling studies (Gerten *et al.*, 2005; Betts *et al.*, 2007), but factors other than g_c are also important in controlling plant transpiration. For example, the leaf boundary layer resistance can crucially limit transpiration in canopies that are poorly coupled to the atmosphere (Wullschleger *et al.*, 2002), and there exists substantial variation between species. Currently available data from natural ecosystems (which are not affected by chamber artefacts), suggest that grasslands and crops show the largest reductions in stomatal conductance (–30 to –50%), broad-leaved forests have intermediate responses (*c.* –20%), and conifers show the smallest response, within the measurement uncertainty (< –10%). However, water savings at the ecosystem level in terms of reduced transpiration are surprisingly constant for a doubling of atmospheric CO_2 (*c.* 5%) because atmospheric coupling is strongest in conifers, followed by broad-leaved forests and grasslands with the weakest coupling (Körner *et al.*, 2007). As the stomatal response to elevated CO_2 is strongest under relatively wet conditions, much of the water saving might occur during the wet season (Körner *et al.*, 2007). LPJ-GUESS does not account for species-specific responses in stomatal conductance and canopy-specific strength of atmospheric coupling. The CO_2 response of transpiration has not been analysed here, but the effect on soil water (+2.9%; see Results) corresponds well with the available data. In summary, important uncertainties remain when projecting the effects of increasing CO_2 on water cycling, but the existing evidence suggests that the overall response in LPJ-GUESS is realistic.

Final considerations

The effects of changes in vegetation structure and functioning on water availability should be considered in species distribution modelling studies. Ecosystem models, such as LPJ-GUESS, have become common research tools, making it unnecessary to rely solely on simpler measures of water availability. Rickebusch *et al.* (2008) have replaced the proxies for water availability commonly used by bioclimatic envelope models with the soil water content presented here and show that considerable differences occur when projecting future ranges of 108 European tree species. In particular, using the 'wetter' fAWC as a water proxy resulted in significantly less habitat shrinkage for boreal-alpine and alpine species. As the water stress experienced by plants is not only a function of water availability but also of the atmospheric demand, using both soil water and variables such as PET may also be biologically meaningful (Stephenson, 1990, 1998).

The presented analyses are meant to inform scientists working with species distribution modelling about potential implications of their choice of water availability measures. However, the modelled changes in soil water should not be treated as predictions, for two reasons: first of all, we have not accounted for actual land use and land-use changes, which clearly affect hydrological cycling. At the scale of the simulations presented here, many different land-cover types occur in most grid cells. Our simulations

are representative of those areas that are 'semi-natural', such as forest reserves. The modelled physiological changes, such as increases in photosynthesis in the north under longer growing seasons and potential water savings under elevated CO_2, are likely to apply independently of land use, but may to a large extent be species specific. Second, we have only used one particular climate change scenario. Further scenarios would be necessary to fully cover the uncertainties in our projections.

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SUPPORTING INFORMATION

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

Appendix S1 Simulated present-day and future distribution of vegetation types: maps and methodology.

Appendix S2 Correlations between different measures of water availability for present-day climate.

Appendix S3 Correlations between projected changes in measures of water availability.

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