Vol. 66: 25–36, 2015
doi: 10.3354/cr01323

CLIMATE RESEARCH
Clim Res

Published October 6

Modeling distribution of Mediterranean beech forests and soil carbon stock under climate change scenarios

Michele Innangi[1], Francesco d'Alessandro[1], Antonietta Fioretto[1], Mirko Di Febbraro[2,*]

[1]Department of Environmental, Biological and Pharmaceutical Sciences and Technologies, Second University of Naples, Via Vivaldi 43, 81100, Caserta, Italy

[2]Department of Biosciences and Territory, University of Molise, Contrada Fonte Lappone, 86090, Pesche (Isernia), Italy

ABSTRACT: Climate change is forecasted to alter forest species distributions and the organic carbon cycle, particularly in the Mediterranean region. In this context, one of the most important carbon reservoirs, both in terms of living biomass and soil organic matter, is represented by beech forests, which are highly vulnerable to global warming. Accordingly, we investigated how the effects of climate change predicted for 2070 could affect both beech distribution and soil carbon stocks in Italy. In order to achieve this goal, we predicted beech distribution using state of the art ecological niche modeling, projecting its potential range under climate change scenarios. Moreover, a field survey was carried out to quantify the proportion of organic carbon in the first 5 cm of soil, which are the most sensitive to climate effects. The latter results were used to explore the relationship between organic carbon and ecogeographical variables, projecting this relationship onto the predicted beech distribution. Our outcomes showed a substantial reduction in beech distribution, especially at its southern range limits, along with a remarkable shift towards higher elevations and latitudes. The organic carbon in beech forests was significantly related to temperature seasonality and elevation, showing a decrease between 64.5 and 98.8% under different IPCC scenarios.

KEY WORDS: Elevation · *Fagus sylvatica* · Italian Apennines · Soil organic carbon · Range shifts · Species distribution models

1. INTRODUCTION

Forests cover about 30% of the Earth's surface, providing ecosystem services whose importance has been recognized for a long time (FAO 2010). Among them, some of the most important include the major role of forests in the global carbon cycle and their key significance as reservoirs of biological diversity. By exchanging carbon with the atmosphere through photosynthesis and respiration, forests sequester a very high amount of carbon in their biomass and in soil organic matter (IPCC 2013). Moreover, forests represent the major reservoir of the world's terrestrial biodiversity, hosting likely more than 50% of all known land species (SCBD 2001). In temperate boreal countries, much of the previously forested land has recovered, counterbalancing CO_2 emissions (Dixon et al. 1994, Thuille et al. 2000, Masera et al. 2003). Nevertheless, ongoing global climatic change could overwhelm these mitigations by means of a substantial transformation in the suitability and range shift of the current forest species (Lindner et al. 2010, Chen et al. 2011).

Forest soil carbon accumulation depends on the balance between plant production and plant residue mineralization. The loss of carbon from the soil is determined by the flow of CO_2 produced by auto-

*Corresponding author: mirkodifebbraro@gmail.com

trophic and heterotrophic respiration. Like primary productivity, decomposition is also controlled by climate as well as by biotic factors, such as soil biota and litter quality. As a result, global change can profoundly affect both processes, especially the balance between them (Berg & McClaugherty 2014). An increase in atmospheric CO_2 could, on the one hand, enhance net primary production (Zak et al. 2011). On the other hand, a temperature increase could accelerate edaphic processes, especially biological ones, increasing litter degradation and nutrient cycling, with a further escalation of greenhouse gases (Hyvönen et al. 2007, Cotrufo et al. 2013). Thus, assessing climate change impact on carbon stocking in forest ecosystems is of crucial interest, both at regional and global scales.

This is particularly true for the Mediterranean region, as it is highly susceptible to climate warming (Giorgi & Lionello 2008). For instance, in terms of the carbon cycle, climate change could switch the role of forest soil from a sink to a source of CO_2 to the atmosphere (Belay-Tedla et al. 2009, Briones et al. 2010, Meier & Leuschner 2010). At the same time, there could be a substantial change in the ranges of forest species, with the forecasted global warming and fire increase that could trigger irrecoverable biodiversity losses and shifts in vegetational composition within a few decades or centuries at most (Lindner et al. 2010).

One of the forest species that is most threatened by climate change is the European beech *Fagus sylvatica* L. (Tognetti et al. 1995, Sabaté et al. 2002, Jump et al. 2006, Peñuelas et al. 2007, Kramer et al. 2010). Within the Mediterranean context, the beech is mostly associated with mountain ecosystems (von Wühlisch 2008). In Italy, for instance, this species normally grows between altitudes of 800 and 1800 m along the Apennines (Pignatti 1982), covering 9.4% of the country's total forest area (Nocentini 2009), with a carbon sequestration rate of up to 6.0 Mg C ha^{-1} yr^{-1}, similar to tropical forests (Valentini et al. 2000).

Although decomposition processes and carbon stocks in beech forests have been extensively studied in central Europe, (e.g. Albers et al. 2004, D'Annunzio et al. 2008, Hedde et al. 2008, Mueller et al. 2009, Guckland et al. 2009, Meier & Leuschner 2010), few studies have been conducted in the Mediterranean region (Alianiello et al. 2002, Cecchini et al. 2002, Scarfò & Mercurio 2009, Piovesan et al. 2010, Innangi et al. 2015). When it comes to addressing impacts of climate change on forest or agricultural ecosystems at different spatial scales, the vast majority of studies have dealt with either the effects on carbon stocks (e.g. Kasurinen et al. 2007, Hyvönen et al. 2007, Lugato & Berti 2008, Scarfò & Mercurio 2009, Albert & Schmidt 2010, Chiesi et al. 2010, Álvaro-Fuentes et al. 2012, Francaviglia et al. 2012, Muñoz-Rojas et al. 2015) or species distribution (e.g. McKenney et al. 2007, Kramer et al. 2010, Tang & Beckage 2010, Chen et al. 2011, Anaya-Romero et al. 2015). Nevertheless, there is a substantial lack of integrated approaches dealing with both aspects simultaneously. Accordingly, modeling the effects of climate change on both forest species distribution and carbon stock, at the same time, is of great interest. In order to achieve this goal, we propose a modelling approach integrating species distribution models, an important and widely used tool for several issues in conservation biology, climate change research and invasion biology (Maiorano et al. 2011, Di Febbraro et al. 2013, Yannic et al. 2013), and a spatially-explicit estimate of carbon stock and its relationship with ecogeographical predictors in Italian beech forests.

In detail, our objectives were to: (1) model the current and future beech distribution in Italy; (2) estimate organic carbon for the first 5 cm of soil by means of a field survey; (3) investigate the relationship between organic carbon and ecogeographical predictors; and (4) combine the results of the previous points to obtain a forecast of organic carbon in beech forest soil under different climate change scenarios.

2. MATERIALS AND METHODS

2.1. Ecological niche model

We modeled the potential distribution of beech in Italy starting from the present location of beech forests along the Apennines chain. The areas of beech-dominated forests were derived from the CORINE Land Cover 2006 IV level provided by the Italian Ministry of the Environment and Protection of Land and Sea (www.pcn.minambiente.it/), which has a spatial resolution of 250 m. The obtained map was then resampled to a resolution of 1 km. Following Yannic et al. (2013), we used the resulting map as a mask for placing beech occurrences, which were subsequently used for the training of the ecological niche model (ENM). We randomly placed a number of occurrences equal to 10% of the total amount of cells in the mask. The selection procedure was repeated 10 times to obtain 10 replicated datasets of 985 occurrences.

As an initial set of environmental predictors, we considered the 19 bioclimatic variables and the digital elevation model (DEM) derived from the WORLD-

CLIM database (Hijmans et al. 2005). The following additional variables were derived from the DEM: slope, aspect, and topographic roughness (M. Wilson et al. 2007). All predictors have a spatial resolution of 30 arc seconds (ca. 1 km). The package 'raster' (Hijmans 2015) in the R environment (R Development Core Team 2012) was used to handle the cartographical data. The ENM was projected over the future climate model outputs relative to the year 2070 provided by the Intergovernmental Panel on Climate Change (IPCC) and available on the WORLDCLIM website (www.worldclim.org). In particular, we used the output from the CSIRO climate change model run by MK35 and considered the 4 representative concentration pathways (RCPs) described in the IPCC Fifth Assessment report (IPCC 2013) as alternative climate change scenarios. These 4 scenarios (RCP2.6, RCP4.5, RCP6, and RCP8.5) are identified by their approximate total radiative forcing in the year 2100 relative to 1750 (IPCC 2013).

We predicted the beech distribution using an ensemble forecasting approach, as implemented in the R package 'biomod2' (Thuiller et al. 2009). We considered the following 7 modeling techniques: generalized linear models (GLMs), generalized additive models (GAMs), classification tree analysis (CTA), generalized boosted models (GBMs), random forests (RFs), multivariate adaptive regression spline (MARS), and maximum entropy models (MAXENT), covering all of the main modeling classes implemented in biomod2 (for further details, see Thuiller et al. 2009). Each of the 10 replicated occurrence datasets was randomly split into a 70% sample, used for the calibration of the model, and the remaining 30%, used to evaluate model performance. A set of 10000 background points was randomly placed in Italy to characterize the environment of the area and to represent pseudo-absences. Predictive performance of the model was assessed by measuring the area under the receiver operating characteristic curve (AUC) (Hanley & McNeil 1982) and the true skill statistic (TSS) (Allouche et al. 2006). This data-splitting procedure was repeated 10 times, obtaining 100 final occurrence datasets, and the evaluation values were averaged.

The ensemble forecasting approach was used to perform a variable selection procedure based on the pairwise correlation and described in the Supplement at www.int-res.com/articles/suppl/c066p025_supp.pdf. The final set of environmental predictors resulting from the variable selection procedure included: (1) isothermality; (2) temperature seasonality; (3) mean temperature of the wettest quarter; (4) mean temperature of the driest quarter; (5) mean temperature of the warmest quarter; (6) precipitation of the coldest quarter; (7) aspect, and (8) topographic roughness.

Model projections over current and future climates were carried out for the entire Italian peninsula. To avoid using poorly calibrated models, only projections from models with AUC $\geq$ 0.8 and TSS $\geq$ 0.6 were considered in all subsequent analyses. Model averaging was performed by weighting the individual model projections respectively by their AUC or TSS scores and averaging the result, as this method is particularly robust (Marmion et al. 2009). The final consensus models for the present and future scenarios were transformed into presence–absence values using a threshold maximizing the sum of sensitivity (the percentage of presence correctly predicted) and specificity (the percentage of absence correctly predicted) (Fielding & Bell 1997). The final 5 sets (1 for the present and 4 for the future climate change scenarios) of 10 binarized outputs were then respectively summed. All cells with presence predicted by at least 7 of the 10 outputs were retained in the final binary maps. Eventually, the predicted beech distribution for the present was clipped to the boundaries of the current beech forests in Italy (also including beech forests of the Alps) derived from the CORINE Land Cover 2006 IV level, in order to distinguish between actual and potential current beech distributions. The obtained maps have also been used to estimate the stable areas where beech will maintain its presence without distribution shifts in any scenario.

2.2. Soil sampling and chemical measurements

Following other studies (Peñuelas et al. 2007, Hilli et al. 2008, Piovesan et al. 2010), a total of 15 locations were sampled in the central-southern part of the Italian Apennines. The northernmost location is Pradaccio (44° N), in Emilia-Romagna, while the southernmost is Nebrodi (38° N), on the island of Sicily, close to the southernmost tip of beech distribution (Fig. 1). Sampling was carried out between late March and late June of 2012–2013, as these times of the year are those most frequently chosen for topsoil analyses in beech forests (Meier & Leuschner 2010, Langenbruch et al. 2012, Papa et al. 2014). All sampled stands are located between elevations of 1000 and 1600 m a.s.l., with the exception of 2 locations (Umbra and Vulture), which occur below 800 m a.s.l. Thus, the latter are considered heterotopic stands (Pignatti 1994). For further information about the sampling sites, refer to Table S1 in the Supplement.

For each location, 6 random replicates where chosen at a fixed distance of approximately 16 m from each other, in an area of 1 ha. Soil was sampled with steel core samplers to obtain cores of 5 cm length with the 0 cm level beginning exactly when no more forest floor was recognizable. This method was used in order to standardize the results and because the topsoil contains the highest concentration of organic carbon (Virzo De Santo et al. 1976, Jobbágy & Jackson 2000, Alianiello et al. 2002, Papa et al. 2014). Moreover, the effects of climate change, like droughts or fires, which are predicted to become particularly severe in the Mediterranean, affect mostly the top layers of the soil (Certini 2005, Lindner et al. 2010).

Several variables were evaluated from soil cores, namely pH, the ratio between the mass of dry soil and the core volume (i.e. bulk density), soil organic matter, organic carbon, and organic carbon stock. Organic matter and carbon were expressed as a proportion to the overall weight of dry soil (i.e. g g^{-1}) while carbon stock was expressed as Mg ha^{-1}. For further details, refer to the Supplement.

2.3. Organic matter and ecogeographical predictors

The relationship between the proportion of organic matter sampled over the Apennine beech forests and climatic and topographic predictors was investigated through a GLM (Dobson 2001) with a binomial distribution of errors and a logit link function. The initial set of environmental predictors included the same variables used in the ENM. Following Zuur et al. (2010), the correlation between the predictors was checked through a variance inflation factor (VIF) analysis, recursively dropping every predictor with a VIF >3. The resulting variables were further subselected through Akaike's information criterion (Akaike 1974). As a result, the procedure retained only temperature seasonality. We tested the relationship between the organic matter and this predictor but decided to also include elevation based on its effect on the duration of the vegetative period for beeches and, consequently, organic matter accumulation (Bayat et al. 2012, Berg & McClaugherty 2014, Innangi 2014). After checking for the non-significant

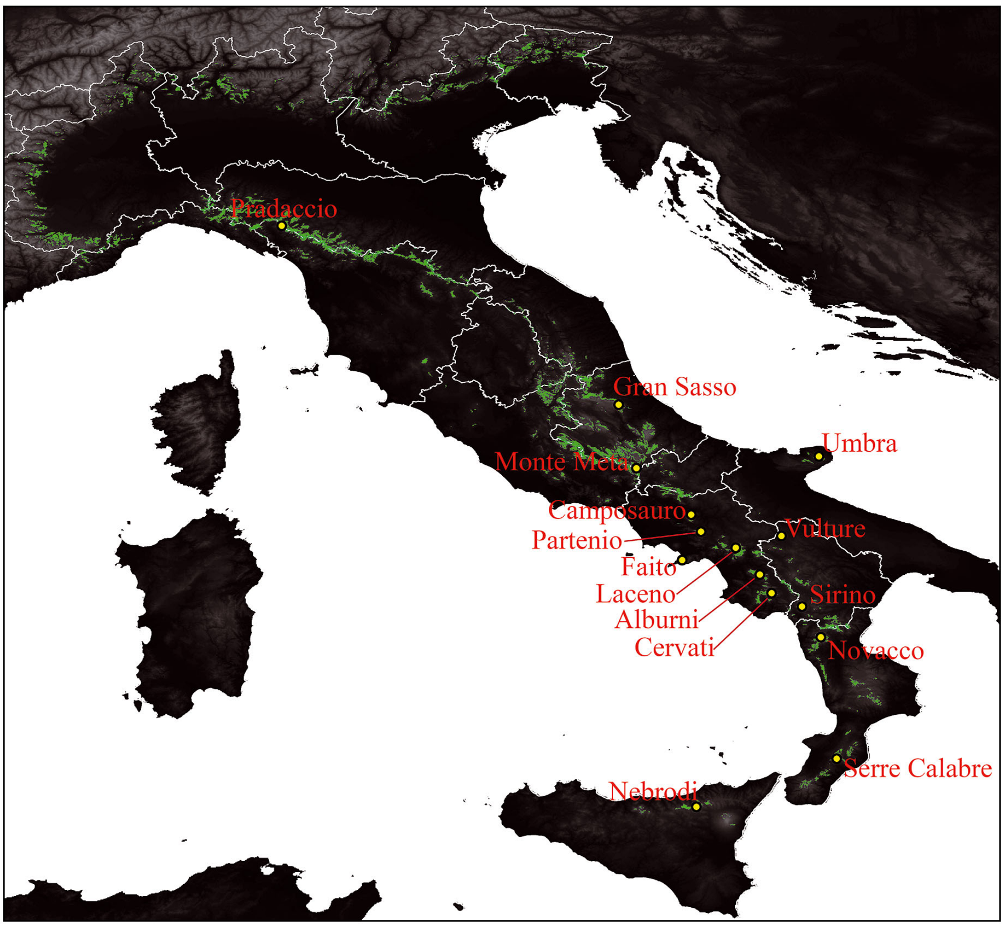

Fig. 1. Sampled locations (yellow dots) throughout the range of European beech *Fagus sylvatica* in Italy (green areas)

correlation between temperature seasonality and elevation (VIF <1.5; Spearman rho = 0.257, p = 0.353), we tested their relationship with organic matter, including quadratic and cubic terms. The goodness of fit of each model was assessed by the explained variance, calculated as the ratio of the difference between null and residual deviance to null deviance (Zuur et al. 2009), and by Nagelkerke's adjusted R-squared (Nagelkerke 1991). The presence of non-linear patterns in the model residuals was tested by fitting a GAM (Green & Silverman 1993) between the model residuals and the 2 covariates, respectively (Zuur et al. 2009). The R packages 'MASS' (Venables & Ripley 2002), 'MuMIn' (Barto 2015), 'fmsb' (Nakazawa 2014), and 'mgcv' (Wood 2011) were used to perform the analyses.

The relationship between organic matter and temperature seasonality and elevation was then projected over the Italian peninsula for the current time and for the 2070 climate change scenarios. The proportion of organic matter, expressed as g of organic matter per g of dry soil, was converted to amount of organic carbon per hectare (Mg ha^{-1}) applying a conversion as explained in the Supplement.

Afterwards, the resulting maps were clipped to the boundaries of the potential, current, and future beech distribution predicted by the ENM, providing the estimated distribution and carbon stock in Italian beech forests for the present time and for the future under climate change scenarios.

To account for the extrapolation effect implied by the projections of both the species distribution model and the estimate of organic carbon in the climate change scenarios, we calculated the multivariate environmental similarity surface index (Elith et al. 2010), estimating similarities between the ecogeographical predictors used in the training and the future projections (Figs. S1 & S2 in the Supplement).

3. RESULTS

ENM showed an excellent predictive performance with a mean (±SD) AUC = 0.970 ± 0.001 and a mean (±SD) TSS = 0.838 ± 0.008. The actual distribution of Italian beech forests was accurately predicted along the Apennines and the Alps, with a slight underprediction of beech forests located in the easternmost districts of the Alps (Fig. 2). Moreover, the actual distribution of beech was noticeably smaller than the potential one. All maps showing the actual, potential, and future forecasted distribution of beech in Italy are shown in Fig. S3 in the Supplement.

The results from the field soil sampling showed a mean proportion of organic carbon in the first 5 cm of soil of 0.13 ± 0.01 g g^{-1}, with a maximum of 0.21 ± 0.04 g g^{-1} in the northernmost site (Pradaccio) and a minimum of 0.08 ± 0.01 g g^{-1} at Partenio. Regarding the organic carbon stock, the mean values were 30.33 ± 1.34 Mg ha^{-1}, with a maximum of 48.62 ± 12.05 Mg ha^{-1} for Laceno and a minimum of 17.03 ± 2.05 Mg ha^{-1} for Umbra. Further details can be found in Table S1.

Table 1 reports estimates and significance levels of the coefficients of the relationship between the proportion of organic matter vs. temperature seasonality and elevation. Estimation of coefficients for linear and cubic terms for elevation yielded significant results, whereas only the linear term for temperature seasonality was significant. The relationship including only the linear term for temperature seasonality and linear, quadratic, and cubic terms for elevation was used in all subsequent analyses and reported an adjusted R-squared of 0.771 and 79.17% of explained variance. In detail, the organic matter showed a moderate, inverse relationship with temperature seasonality, whereas a non-linear relationship can be seen with elevation, with optimum values between 1250 and 1450 m (Table 1; Fig. S4a,b). The relationship accurately predicted the organic matter content in the heterotopic stands as well, which are the 2 leftmost points in Fig. S4b, although with an inverted trend compared to the other data. No data points are associated with the minimum in the curve depicting the relationship between the organic matter proportion and elevation (Fig. S4). No significant non-linear patterns in residuals were detected (Table S2).

The predicted changes in beech distribution and carbon stock under the different climate change scenarios can be seen in Fig. 3, highlighting the persistence of beech forests in the Alps and a few isolated high-mountain enclaves in the central Apennines predicted in 2070 under the most severe climate change scenario (Fig. 3d). These trends are accompanied by a noticeable shift of the distribution toward higher latitude and elevation (Fig. 4b,c), along with a sharp decrease in the extent of the beech distribution in 2070 and, consequently, in the amount of organic carbon (Fig. 4a,d), with the effect getting more severe among the 4 climate change scenarios. A very small extent of beech forests (ca. 100 000 ha) remained stable in all scenarios (Fig. 4d). These stable forests have mid to low organic carbon content and are located mostly at the northern edge of the Italian beech distribution, at mid to high elevations (Fig. 4a–c). The overall organic carbon stock, computed by summing all cells predicted by the model for each sce-

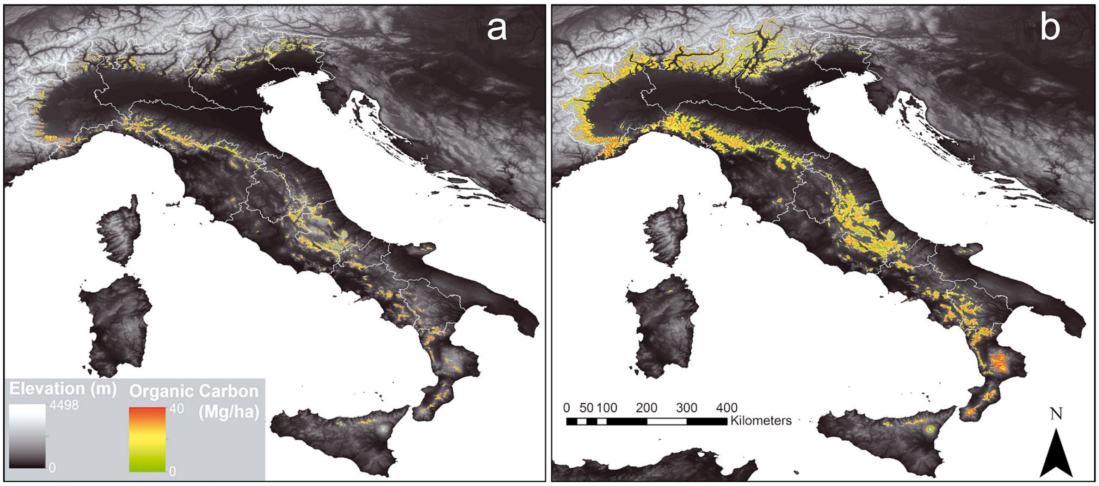

Fig. 2. Current (a) actual and (b) potential European beech *Fagus sylvatica* distribution in Italy and carbon stock estimates. Carbon stocks were estimated exclusively within the predicted beech distribution resulting from the ecological niche model

Table 1. Estimates and significance levels of the coefficients of the relationship between proportion of organic matter vs. temperature seasonality and elevation. ns: not significant, *$p \le 0.05$; **$p \le 0.01$; ***$p \le 0.001$

Relationship	Coefficient estimate	p
Organic matter ~ Intercept +	22.393	ns
Temperature Seasonality	−0.0005	ns
Organic matter ~ Intercept +	−1.370	***
Temperature Seasonality +	−0.730	**
Temperature Seasonality^2 +	−0.221	ns
Temperature Seasonality^3 +	−0.169	ns
Elevation +	0.606	*
Elevation^2 +	0.111	ns
Elevation^3	−0.920	***
Organic matter ~ Intercept +	4.838	*
Temperature Seasonality +	−0.001	**
Elevation +	0.528	*
Elevation^2 +	0.067	ns
Elevation^3	0.896	***

nario, are shown in Table S3. The effect of climate change on the current potential carbon stock showed a reduction of 64.5, 78.6, 84.7, and 98.8% for the 4 future climate scenarios, respectively, whereas the current carbon stock for the present distribution of beech in Italy is estimated to be approximately 31×10^6 Mg.

4. DISCUSSION

Our study highlights the effects of climate change on both distribution and carbon stock in Mediterranean beech forests.

Our results show a remarkable difference between actual and potential beech distributions in Italy. This can be explained by the intensive human impact on beech forests, especially in the Mediterranean area (Coppini & Hermanin 2007). Nevertheless, the potential for expansion of beech forests in Italy is confirmed by the fact that, following a decrease in human impacts on these forests in the last 60 yr (Ciancio et al. 2006), beech area has expanded by ca. 300 000 ha according to National Inventories conducted in 1985 and 2005 (Coppini & Hermanin 2007, Nocentini 2009). Moreover, some differences between actual and potential distribution may be the result of other variables that can affect beech distribution (e.g. soil type, flooding, groundwater level) (Ellenberg 2009), which were not taken into account by the ENM. Also for carbon stocks, our results are in line with analogous studies in central Europe (Schulp & Nabuurs 2008, Langenbruch et al. 2012). For Italy, according to the National Inventory of Forests and Forest Carbon Sinks, carbon stock estimates for the soil organic horizon provided a figure of approximately 10×10^6 Mg (Gasparini & Tabacchi 2011). Our estimate for the actual beech distribution was almost 3 times higher, although some substantial methodological differences must be taken into account. The estimates provided by the National Inventory are based on a depth of organic horizons that may vary between a few millimetres to more than 30 cm (Gasparini & Tabacchi 2011). Conversely, we estimated the amount of soil organic carbon considering a constant depth of 5 cm. This approach appeared appropriate, as national inventories and assessments of trends in soil carbon content are affected by a considerable degree of

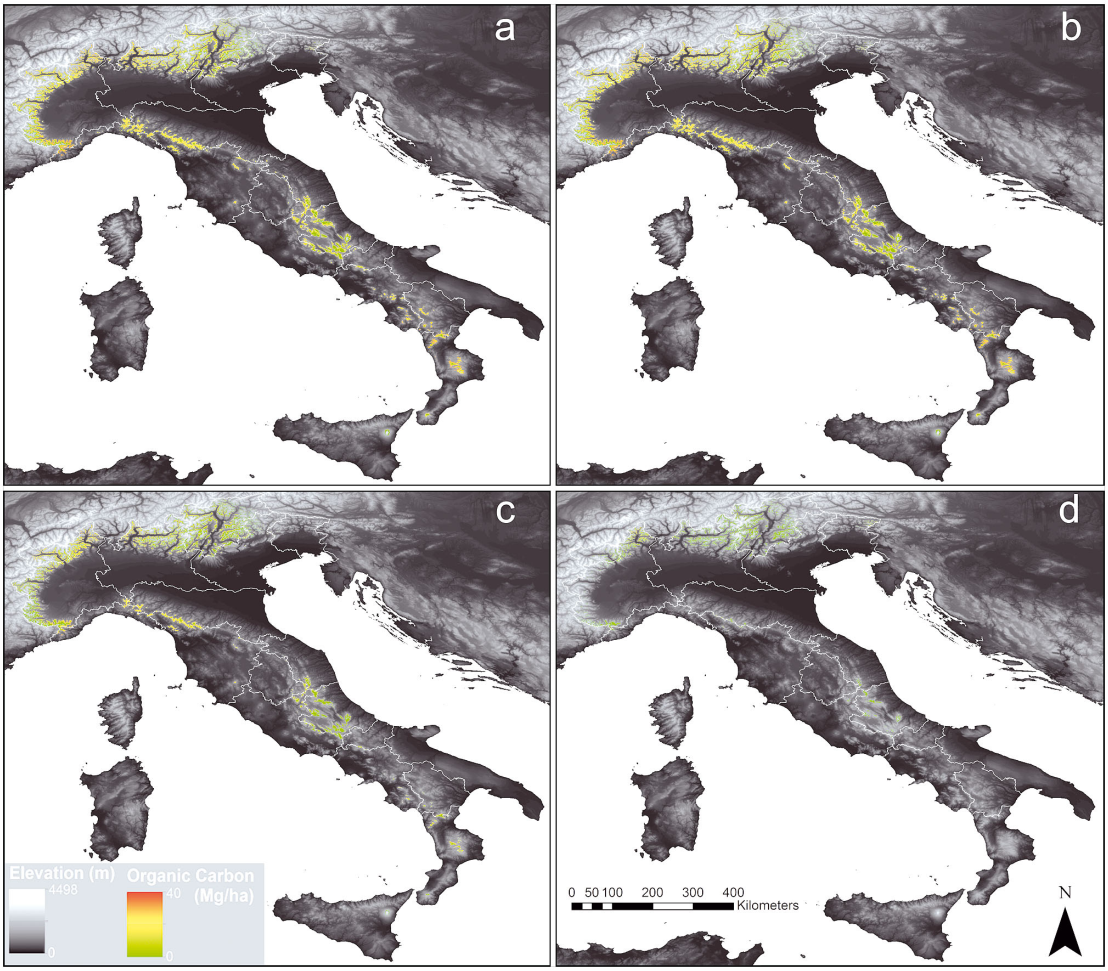

Fig. 3. Future potential European beech *Fagus sylvatica* distribution and carbon stock estimates for Italy. Panels represent different climate change scenarios: (a) RCP2.6, (b) RCP4.5, (c) RCP6, and (d) RCP8.5. Carbon stocks were estimated exclusively within the predicted beech distribution resulting from the ecological niche model

uncertainty due to inadequate methods (Houghton 2003, Schulp et al. 2013).

The proportion of organic carbon was significantly related to 2 ecogeographical predictors, namely temperature seasonality and elevation. The effect of the first variable can be explained by the fact that beech does not tolerate climates with excessive continentality (i.e. strong temperature differences between the coldest and warmest months; Czerepko 2004), resulting in a decrease in productivity. In addition, temperature seasonality may play a role in slowing down decomposition and, thus, carbon accumulation in the soil (Breymeyer & Laskowski 1999). Concerning elevation, a non-linear relationship with the length of the beech growing season has been found for central Italy, with an optimum at elevations of 1300–1500 m (Bayat et al. 2012), where beech is thought to have its highest productivity. This range of elevations was also the best with regard to the proportion of organic matter. Accumulation of organic carbon in soils is positively correlated with precipitation and negatively correlated with temperature (Jobbágy & Jackson 2000, Dai & Huang 2006, Meier & Leuschner 2010). For the Apennines, temperatures decrease with elevation (Körner 2007), but precipitation also has a strong, direct relationship with elevation (Piovesan et al. 2008). Consequently, elevation functions as a proxy of temperature and precipitation in the Apennines, affecting beech productivity and carbon accumulation simultaneously. This relationship holds for those heterotopic stands which, even though they are located at elevations unusual for beech forests, have special climatic features that compensate for the elevation effect. This also explains why there are no data points associated with the minimum of the non-linear relationship between organic matter and ele-

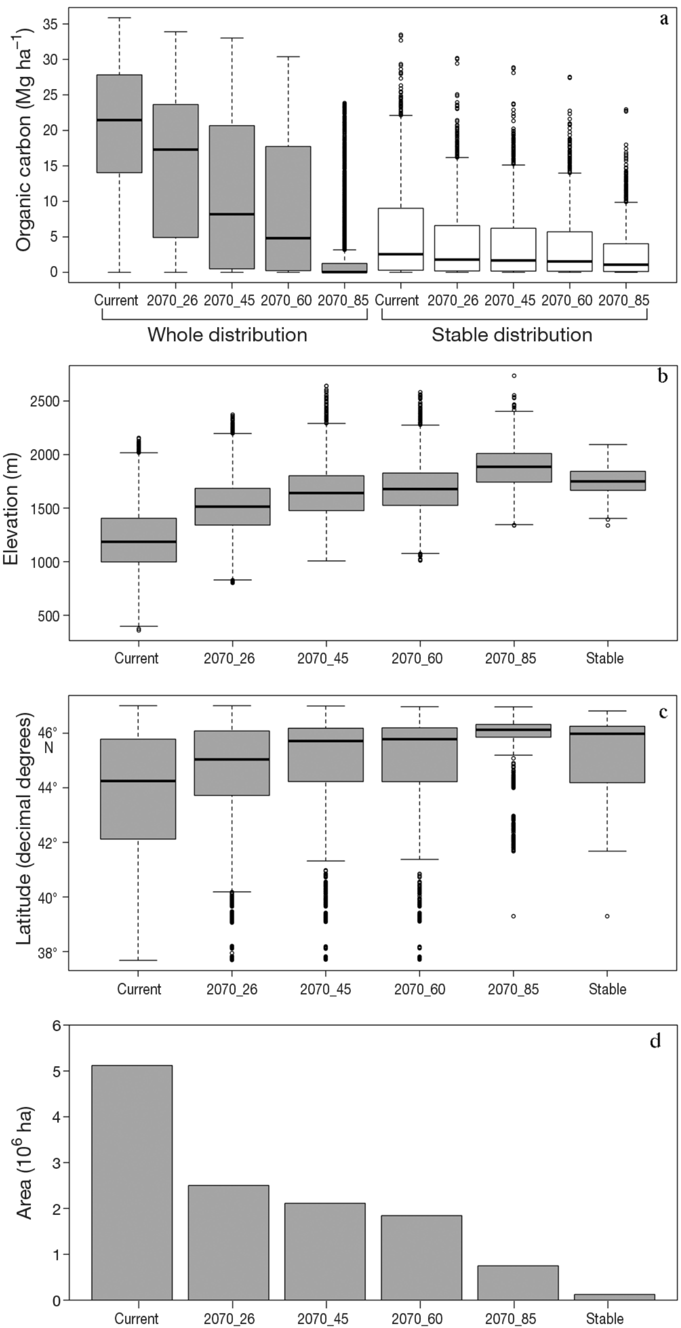

Fig. 4. Values of (a) carbon stock, (b) elevation ranges, (c) latitudinal ranges, and (d) extent of European beech *Fagus sylvatica* distribution in Italy for all scenarios and for stable beech forests. RCP2.6, RCP4.5, RCP6, and RCP8.5 represent different climate change scenarios. In the box plots, the central line represents the median, while the box comprises the interquartile range (IQR). The upper whisker represents the 3rd quartile + 1.5 IQR while the lower whisker is 1st quartile – 1.5 IQR

vation, as there are almost no beech forests in the elevation range of 750–900 m a.s.l. (Pignatti 1994). Eventually, both temperature seasonality and elevation participate in the balance between beech productivity and rate of decomposition of its litter which, ultimately, accumulates in the soil as organic carbon (Chiesi et al. 2010, Berg & McClaugherty 2014).

Our forecasts for 2070 highlight the effects of climate change on both beech distribution and carbon stock. The effects appeared to be mostly at the expense of beech distribution rather than organic carbon itself, yet a substantial impact was also evident on the organic carbon alone, as it also decreases in those beech forests predicted to be persistent in all scenarios (Fig. 4a,d).

Kramer et al. (2010) predicted a northward shift of the southern limit of the distribution of beech in 2050, with most of the current habitats, which could become unsuitable, located in the Mediterranean. Although our forecasts of beech distribution in 2070 did not account for the role of extreme weather events, whose frequency is predicted to increase under climate change scenarios (Lindner et al. 2010), they confirm this trend. Furthermore, our results provide an even more serve picture, with beech losing up to ca. 80 % of its potential distribution under the most severe scenario, especially in southern Italy where it could totally disappear. Simultaneously, our predictions showed a trend for beech to climb to higher elevations in response to climate change, which is a well-documented pattern for several taxonomic groups (e.g. Hickling et al. 2006, Wilson et al. 2007b, Kelly & Goulden 2008, Lenoir et al. 2008). This trend has already been observed in Spain in the last 50 yr, where a temperature increase of 1.4°C (with stable annual precipitation) resulted in progressive replacement of beech by holm oak *Quercus ilex* in the higher elevations of the Pyrenees (Peñuelas & Boada 2003). According to our outcomes, this altitudinal shift could cause local extinctions, especially in the southern parts of the Apennines, which do not offer sufficient refuge for beech because of the lack of mountain peaks that are high enough. Drought is also a major risk factor for Mediterranean forests, as it could cause long-term stress, reducing the productivity of beech forests at the southern range limit (Jump et al. 2006). Moreover, prolonged droughts and hot spells will further aggravate forest fire risks (Lindner et al. 2010).

Climate change scenarios provided a forecasted increase in annual mean temperatures (4–5°C in summer and 2–3°C in winter) in the Mediterranean zone (Lindner et al. 2010), implying a larger temperature seasonality. As already discussed, temperature seasonality can be seen as a predictor affecting both beech productivity and decomposition rate.

Accordingly, our results highlighted a marked effect of climate change on organic carbon accumulation in the topsoil. Even though there is no consensus about the relevance and the effects of the temperature-related impacts on soil carbon accumulation (Davidson & Janssens 2006), a fast, short-term effect of higher temperatures could decrease net primary production and also imply a loss of soil carbon through increased soil respiration (Hyvönen et al. 2007). In particular, this is true for the first 5 cm of soil (Briones et al. 2010).

The present study provided a new approach to simultaneously model beech distribution and its soil organic carbon stock under a changing climate. Among the caveats of our research, given the large area over which we extended our predictions, the sampling size of the field survey may not have been extensive enough, as it did not cover the entire extent of beech in Italy. However, to verify the spatial and temporal transferability of our estimates, specific analyses were performed establishing the reliability of our predictions (Figs. S1 & S2). A negligible extrapolation effect for beech distribution projections was evidenced, whereas for organic carbon estimates, this effect progressed from low to moderate. In addition, modeling techniques to estimate carbon stocks, incorporating a more complex array of predictors, are available in the literature (e.g. Lugato & Berti 2008, Francaviglia et al. 2012, Muñoz-Rojas et al. 2015). We are aware that such process-based approaches may be more thorough in describing the complexity of carbon dynamics. Nevertheless, a statistical estimate of carbon stocks based on ecogeographical variables, even if less accurate, appeared to be the most appropriate for the geographical and temporal scales used in the present study.

Among the other shortcomings, our study did not provide evidence of how much carbon could be stored in other forest associations, such as oak species or other more thermophilous woody plants (Peñuelas & Boada 2003), which could replace beech forests following climate change. However, when compared to other non-coniferous forest associations, beech forests have the largest soil carbon stock (e.g. Gasparini & Tabacchi 2011, Vesterdal et al. 2013). Thus, the replacement of beech by other forests is likely to result in a net loss of carbon from the soil. Moreover, our estimates of soil carbon content of new areas potentially colonized by beech cannot take into account the amount of carbon formerly stored in the soil before the colonization. Additionally, since some forests will colonize new areas, our study did not take into account whether litter productivity and decomposition dynamics of new forests in 2070 would be the same as in long-established forests such as those we sampled. Finally, the future projected estimates for carbon stocks did not directly take into account rainfall regimes, which may be altered as a consequence of climate change (Jump et al. 2006) and have an effect on soil dynamics (Meier & Leuschner 2010). However, precipitation was included as a predictor in modeling beech distribution, thus indirectly acknowledging its impact on carbon stocks.

Notwithstanding the limits of our research suggesting the need to improve and expand the proposed approach, the current results show that an important species might be strongly affected by climate change in the Mediterranean, with a severe reduction in its distribution, especially at its southern range limit, and a substantial loss of organic carbon stored in the topsoil of beech forests.

Acknowledgements. The authors would like to acknowledge the editor Tim Sparks and 2 anonymous referees who improved the manuscript. Mr. Agostino Bortone is also acknowledged for his substantial contribution to field work.

LITERATURE CITED

Akaike H (1974) A new look at the statistical model identification. Autom Control IEEE Trans 19:716–723

Albers D, Migge S, Schaefer M, Scheu S (2004) Decomposition of beech leaves (*Fagus sylvatica*) and spruce needles (*Picea abies*) in pure and mixed stands of beech and spruce. Soil Biol Biochem 36:155–164

Albert M, Schmidt M (2010) Climate-sensitive modelling of site–productivity relationships for Norway spruce (*Picea abies* (L.) Karst.) and common beech (*Fagus sylvatica* L.). For Ecol Manag 259:739–749

Alianiello F, Biondi FA, Ferrari C, Mecella G, Nisini L (2002) Forest soil conditions in the CONECOFOR Permanent Monitoring Plots and in the Level I Network in Italy. J Limnol 61:25–35

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232

Álvaro-Fuentes J, Easter M, Paustian K (2012) Climate change effects on organic carbon storage in agricultural soils of northeastern Spain. Agric Ecosyst Environ 155: 87–94

Anaya-Romero M, Abd-Elmabod SK, Muñoz-Rojas M, Castellano G and others (2015) Evaluating soil threats under climate change scenarios in the Andalusia region, southern Spain. Land Degrad Dev 26:441–449

Barto K (2015) MuMIn: multi model inference. http://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf

Bayat AT, van Gils H, Weir M (2012) Carbon stock of European beech forest; a case at M. Pizzalto, Italy. APCBEE Procedia 1:159–168

Belay-Tedla A, Zhou X, Su B, Wan S, Luo Y (2009) Labile, recalcitrant, and microbial carbon and nitrogen pools of a tallgrass prairie soil in the US Great Plains subjected to experimental warming and clipping. Soil Biol Biochem 41:110–116

Berg B, McClaugherty C (2014) Plant litter: decomposition, humus formation, carbon sequestration, 3rd edn. Springer Verlag, Berlin

Breymeyer AI, Laskowski R (1999) Ecosystem process studies along a climatic transect at 52–53° N (12–32° E): pine litter decomposition. Geogr Pol 72:45–64

Briones M, Garnett M, Ineson P (2010) Soil biology and warming play a key role in the release of 'old C' from organic soils. Soil Biol Biochem 42:960–967

Cecchini G, Carnicelli S, Mirabella A, Mantelli F, Sanesi G (2002) Soil conditions under a *Fagus sylvatica* CONECOFOR stand in central Italy: an integrated assessment through combined solid phase and solution studies. J Limnol 61:36–45

Certini G (2005) Effects of fire on properties of forest soils: a review. Oecologia 143:1–10

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026

Chiesi M, Moriondo M, Maselli F, Gardin L, Fibbi L, Bindi M, Running SW (2010) Simulation of Mediterranean forest carbon pools under expected environmental scenarios. Can J Res 40:850–860

Ciancio O, Corona P, Lamonaca A, Portoghesi L, Travaglini D (2006) Conversion of clearcut beech coppices into high forests with continuous cover: a case study in central Italy. For Ecol Manag 224:235–240

Coppini M, Hermanin L (2007) Restoration of selective beech coppices: a case study in the Apennines (Italy). For Ecol Manag 249:18–27

Cotrufo MF, Wallenstein MD, Boot CM, Denef K, Paul E (2013) The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Glob Change Biol 19:988–995

Czerepko J (2004) Development of vegetation in managed Scots pine (*Pinus sylvestris* L.) stands in an oak-lime-hornbeam forest habitat. For Ecol Manag 202:119–130

D'Annunzio R, Zeller B, Nicolas M, Dhôte JF, Saint-André L (2008) Decomposition of European beech (*Fagus sylvatica*) litter: combining quality theory and ^{15}N labelling experiments. Soil Biol Biochem 40:322–333

Dai W, Huang Y (2006) Relation of soil organic matter concentration to climate and altitude in zonal soils of China. Catena 65:87–94

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173

Di Febbraro M, Lurz PWW, Genovesi P, Maiorano L, Girardello M, Bertolino S (2013) The use of climatic niches in screening procedures for introduced species to evaluate risk of spread: a case with the American eastern grey squirrel. PLoS ONE 8:e66559

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. Science 263:185–190

Dobson AJ (2001) An introduction to generalized linear models. Chapman & Hall/CRC, Boca Raton, FL

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342

Ellenberg H (2009) Vegetation ecology of central Europe. Cambridge University Press, Cambridge

FAO (Food and Agriculture Organization of the United Nations) (2010) Global forest resources assessment 2010. FAO, Rome

Fielding A, Bell J (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49

Francaviglia R, Coleman K, Whitmore AP, Doro L, Urracci G, Rubino M, Ledda L (2012) Changes in soil organic carbon and climate change—application of the RothC model in agro-silvo-pastoral Mediterranean systems. Agric Syst 112:48–54

Gasparini P, Tabacchi G (2011) L'inventario nazionale delle foreste e dei serbatoi forestali di carbonio INFC 2005. Edagricole-Il sole 24 Ore, Bologna

Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. Global Planet Change 63: 90–104

Green PJ, Silverman BW (1993) Nonparametric regression and generalized linear models: a roughness penalty approach. Chapman & Hall/CRC, Boca Raton, FL

Guckland A, Jacob M, Flessa H, Thomas FM, Leuschner C (2009) Acidity, nutrient stocks, and organic-matter content in soils of a temperate deciduous forest with different abundance of European beech (*Fagus sylvatica* L.). J Plant Nutr Soil Sci 172:500–511

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29–36

Hedde M, Aubert M, Decaëns T, Bureau F (2008) Dynamics of soil carbon in a beechwood chronosequence forest. For Ecol Manag 255:193–202

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Glob Change Biol 12:450–455

Hijmans RJ (20154) raster: Geographic Data Analysis and Modeling. R package version 2.3-40. http://CRAN.R-project.org/package=raster

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Hilli S, Stark S, Derome J (2008) Carbon quality and stocks in organic horizons in boreal forest soils. Ecosystems 11: 270–282

Houghton RA (2003) Why are estimates of the terrestrial carbon balance so different? Glob Change Biol 9:500–509

Hyvönen R, Agren GI, Linder S, Persson T and others (2007) The likely impact of elevated [CO_2], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. New Phytol 173:463–480

Innangi M (2014) The beech, *Fagus sylvatica* L. (Fagaceae) in the Italian Apennines: an ecology approach to understand organic matter quantity and quality in leaf litter and soil. PhD dissertation, University of Naples

Innangi M, Schenk MK, d'Alessandro F, Pinto S, Menta C, Papa S, Fioretto A (2015) Field and microcosms decomposition dynamics of European beech leaf litter: influence of climate, plant material and soil with focus on N and Mn. Appl Soil Ecol 93:88–97

IPCC (Intergovernmental Panel on Climate Change) (2013) Climate change 2013: the physical science basis. Cambridge University Press, Cambridge

Jobbágy E, Jackson R (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol Appl 10:423–436

Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. Glob Change Biol 12:2163–2174

Kasurinen A, Peltonen PA, Holopainen JK, Vapaavuori E, Holopainen T (2007) Leaf litter under changing climate: Will increasing levels of CO_2 and O_3 affect decomposition and nutrient cycling processes? Dyn Soil Dyn Plant 1:58–67

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proc Natl Acad Sci USA 105:11823–11826

Körner C (2007) The use of 'altitude' in ecological research. Trends Ecol Evol 22:569–574

Kramer K, Degen B, Buschbom J, Hickler T, Thuiller W, Sykes MT, de Winter W (2010) Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change — range, abundance, genetic diversity and adaptive response. For Ecol Manag 259:2213–2222

Langenbruch C, Helfrich M, Flessa H (2012) Effects of beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*) and lime (*Tilia* spec.) on soil chemical properties in a mixed deciduous forest. Plant Soil 352:389–403

Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320: 1768–1771

Lindner M, Maroschek M, Netherer S, Kremer A and others (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For Ecol Manag 259:698–709

Lugato E, Berti A (2008) Potential carbon sequestration in a cultivated soil under different climate change scenarios: a modelling approach for evaluating promising management practices in north-east Italy. Agric Ecosyst Environ 128:97–103

Maiorano L, Falcucci A, Zimmermann NE, Psomas A and others (2011) The future of terrestrial mammals in the Mediterranean basin under climate change. Philos Trans R Soc Lond B Biol Sci 366:2681–2692

Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in predictive species distribution modelling. Divers Distrib 15:59–69

Masera OR, Garza-Caligaris JF, Kanninen M, Karjalainen T and others (2003) Modeling carbon sequestration in afforestation, agroforestry and forest management projects: the CO2FIX V.2 approach. Ecol Model 164:177–199

McKenney D, Pedlar J, Lawrance K, Campbell K, Hutchinson M (2007) Potential impacts of climate change on the distribution of North American trees. Bioscience 57: 939–948

Meier IC, Leuschner C (2010) Variation of soil and biomass carbon pools in beech forests across a precipitation gradient. Glob Change Biol 16:1035–1045

Mueller CW, Brüggemann N, Pritsch K, Stoelken G, Gayler S, Winkler JB, Kögel-Knabner I (2009) Initial differentiation of vertical soil organic matter distribution and composition under juvenile beech (*Fagus sylvatica* L.) trees. Plant Soil 323:111–123

Muñoz-Rojas M, Doro L, Ledda L, Francaviglia R (2015) Application of CarboSOIL model to predict the effects of climate change on soil organic carbon stocks in agro-silvo-pastoral Mediterranean management systems. Agric Ecosyst Environ 202:8–16

Nagelkerke N (1991) A note on a general definition of the coefficient of determination. Biometrika 78:691–692

Nakazawa M (2014) fmsb: Functions for medical statistics book with some demographic data. Available at http://CRAN.R-project.org/package=fmsb

Nocentini S (2009) The sound bases of systemic silviculture. Forest@ 6:337–346

Papa S, Pellegrino A, Bartoli G, Ruosi R, Rianna S, Fuggi A, Fioretto A (2014) Soil organic matter, nutrient distribution, fungal and microbial biomass and enzyme activities in a forest beech stand on the Apennines of southern Italy. Plant Biosyst 148:1187–1198

Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). Glob Change Biol 9:131–140

Peñuelas J, Ogaya R, Boada M, Jump AS (2007) Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). Ecography 30:829–837

Pignatti S (1982) Flora d'Italia. Edagricole, Florence

Pignatti S (1994) Ecologia del Paesaggio. UTET, Bologna

Piovesan G, Biondi F, Di Filippo A, Alessandrini A, Maugeri M (2008) Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. Glob Change Biol 14:1265–1281

Piovesan G, Alessandrini A, Baliva M, Chiti T and others (2010) Structural patterns, growth processes, carbon stocks in an Italian network of old-growth beech forests. Ital J For Mt Environ 65:557–590

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Sabaté S, Gracia C, Sànchez A (2002) Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean. For Ecol Manag 162:23–37

Scarfò F, Mercurio R (2009) Carbon credit accounting: the model CO2FIX v. 3.1 applied to a beech stand under forest management in southern Italy. Forest@ 6:215–228

SCBD (Secretariat of the Convention on Biological Diversity) (2001) The value of forest ecosystems. CBD Tech Ser 4. SCBD, Montreal

Schulp CJE, Nabuurs GJ (2008) Effect of tree species on carbon stocks in forest floor and mineral soil and implications for soil carbon inventories. For Ecol Manag 256: 482–490

Schulp CJE, Verburg PH, Kuikman PJ, Nabuurs GJ, Olivier JGJ, de Vries W, Veldkamp T (2013) Improving national-scale carbon stock inventories using knowledge on land use history. Environ Manag 51:709–723

Tang G, Beckage B (2010) Projecting the distribution of forests in New England in response to climate change. Divers Distrib 16:144–158

Thuille A, Buchmann N, Schulze ED (2000) Carbon stocks and soil respiration rates during deforestation, grassland use and subsequent Norway spruce afforestation in the Southern Alps, Italy. Tree Physiol 20:849–857

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

Tognetti R, Johnson J, Michelozzi M (1995) The response of European beech (*Fagus sylvatica* L.) seedlings from two Italian populations to drought and recovery. Trees (Berl) 9:348–354

Valentini R, Matteucci G, Dolman AJ, Schulze ED and others (2000) Respiration as the main determinant of carbon balance in European forests. Nature 404:861–865

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Available at http://www.planta.cn/forum/files_planta/modern_applied_statistics_with_s_192.pdf
Vesterdal L, Clarke N, Sigurdsson BD, Gundersen P (2013) Do tree species influence soil carbon stocks in temperate and boreal forests? For Ecol Manag 309:4–18
Virzo De Santo A, Alfani A, Sapio S (1976) Soil metabolism in beech forests of Monte Taburno (Campania Apennines). Oikos 27:144–152
von Wühlisch G (2008) European beech (*Fagus sylvatica*). In: EUFORGEN technical guidelines for genetic conservation and use. Biodiversity International, Rome, p 1–6
Wilson MFJ, O'Connell B, Brown C, Guinan JC, Grehan AJ (2007) Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Mar Geod 30:3–35
Wilson RJ, Gutiérrez J, Gutiérrez D, Montserrat VJ (2007) An elevational shift in butterfly species richness and composition accompanying recent climate change. Glob Change Biol 13:1873–1887
Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R Stat Soc Ser B Stat Methodol 73:3–36
Yannic G, Pellissier L, Ortego J, Lecomte N and others (2013) Genetic diversity in caribou linked to past and future climate change. Nat Clim Change 4:132–137
Zak DR, Pregitzer KS, Kubiske ME, Burton AJ (2011) Forest productivity under elevated CO_2 and O_2: positive feedbacks to soil N cycling sustain decade-long net primary productivity enhancement by CO_2. Ecol Lett 14:1220–1226
Zuur AF, Ieno EN, Walker N, Saveliev A, Smith G (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY
Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

Editorial responsibility: Tim Sparks, Cambridge, UK

Submitted: February 16, 2015; Accepted: June 25, 2015
Proofs received from author(s): August 24, 2015