Past and Future Drivers of an Unmanaged Carbon Sink in European Temperate Forest

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ABSTRACT

Forests are major carbon stores on a global scale but there are significant uncertainties about changes in carbon flux through time and the relative contributions of drivers such as land use, climate and atmospheric CO_2. We used the dynamic vegetation model LPJ-GUESS to test the relative influence of CO_2 increase, temperature increase and management on carbon storage in living biomass in an unmanaged European temperate deciduous forest. The model agreed well with living biomass reconstructed from forest surveys and maximum biomass values from other studies. High-resolution climate data from both historical records and general circulation models were used to force the model and was manipulated for some simulations to allow relative contributions of individual drivers to be assessed. Release from management was the major driver of carbon storage for most of the historical period, whereas CO_2 took over as the most important driver in the last 20 years. Relatively, little of the observed historical increase in carbon stocks was attributable to increased temperature. Future simulations using IPCC RCP4.5 and RCP8.5 scenarios indicated that carbon stocks could increase by as much as 3 kg C m^{-2} by the end of the century, which is likely to be driven by CO_2 increase. This study suggests that unmanaged semi-natural woodland in Europe can be a major potential carbon sink that has been previously underestimated. Increasing the area of unmanaged forest would provide carbon sink services during recovery from timber extraction, while long-term protection would ensure carbon stocks are maintained.

Key words: forest management; carbon storage dynamics; dynamic vegetation model; LPJ-GUESS; climate change; atmospheric CO_2.

INTRODUCTION

Global forests provide a substantial and important carbon store but significant uncertainties exist about the drivers of changes in carbon flux through time (Erb and others 2013; Mackey and others 2013). Over the last 300 years, the US forests have switched from being a carbon source to a carbon sink (Birdsey and others 2006) and this is also likely to have occurred in China and Europe because of reforestation and reduction of intensive

land-use practices, which are returning carbon to forest ecosystems (Erb and others 2013; Mackey and others 2013). Indeed Mackey and others (2013) estimate that global terrestrial ecosystems currently act as a significant net carbon sink, due to recovery from past land use (especially deforestation and logging). Estimates for recent changes in carbon fluxes are available at global (Pan and others 2011) and regional (Birdsey and others 2006; Ciais and others 2008) scales, but uncertainty remains about the drivers of these changes, which may include reduced management, CO_2 fertilization, nitrogen availability and climatic influence on photosynthesis and respiration. Bellassen and others (2011) used a dynamic vegetation model to suggest that CO_2 fertilization and climate change were the dominant influences on carbon stocks in European forests between AD 1950 and 2000, whereas Erb and others (2013) stressed the role of management relaxation. The relationship between these drivers of carbon flux in terrestrial ecosystems is likely to have shifted through the recent past and will continue to do so in future.

Increases in forest carbon stocks in the recent past are commonly reported and have been estimated at 1.7 kg C m^{-2} in the last 50 years in Europe (Ciais and others 2008) and 0.5 kg C m^{-2} in the last 17 years in the United States (Pan and others 2011). This is most commonly attributed to increased forest density due to recovery from more intense management (Rautiainen and others 2011; Erb and others 2013), or changes in atmospheric composition or climate (for example, Bellassen and others 2011; Mackey and others 2013). A meta-analysis of free-air CO_2 enrichment (FACE) experiments revealed that elevated CO_2 resulted in larger plants, with greater allocation to wood and increased biomass production in trees (Ainsworth and Long 2005). The effect of climate warming is less clear, as carbon stocks may be increased in some regions through extended growing seasons due to increased temperature, but may also be reduced by negative effects on plant growth through drying or heat stress (Mackey and others 2013).

The capacity to store carbon in vegetation is ultimately limited, although the maximum will change with prevailing environmental conditions. Carbon carrying capacity at a landscape scale has been defined as the mass of carbon stored in an ecosystem under prevailing environmental conditions and natural disturbance regimes, but excluding anthropogenic disturbance (Keith and others 2010). Ciais and others (2008) suggested a potential maximum carbon stock of 17 kg C m^{-2} for broad-leaved forests (14–15 kg C m^{-2} for for-

ests in general) using managed forest data, although such inventory data may underestimate the true carbon carrying capacity significantly (Keith and others 2009). A review of global and European datasets revealed that most forests are below or close to this suggested maximum, but some forests already store considerably more (for example, Mountford and Peterken 2003). These may be primary forests which are under-represented in the data used by Ciais and others (2008), but it is possible that as a forest recovers from management, it may exceed its theoretical maximum until self-thinning processes restore equilibrium densities (Shugart 1998). Therefore, as much primary European forest is recovering from some form of timber extraction, these elevated levels may still subside to a long-term maximum.

Native temperate deciduous forests account for 36.7% of European forest cover and 12.8% (1.2×10^8 ha) of European land area (Schuck and others 2002). Most of this forest is managed or experiencing the effects of management legacy (for example, Erb and others 2013) and only 26% of Europe's forest is now primary forest (FAO 2010). Unmanaged forest has the potential to store more carbon as living biomass than forest experiencing current or recent timber extraction, although it is not clear by how much. Keith and others (2009) reported biomass data from mature and older forests to be 2–3 times the temperate biome default values (from forest inventory data) used to inform climate change mitigation policies (IPCC 2013). Better understanding of the role of management in determining carbon flux in forests, and how it relates to other drivers such as atmospheric CO_2 fertilization and climatic change is clearly crucial for guiding policy to optimize carbon storage.

Here, we use long-term monitoring data from a European, temperate, semi-natural, deciduous forest to reconstruct carbon storage in living biomass. This forest has been unmanaged since 1945 and as such represents an important contrast to studies of plantations and managed forests. We compared output from the dynamic vegetation model LPJ-GUESS with long-term monitoring data to establish reliability of simulated carbon stock estimates. We then used the model to explore the sensitivity of forest carbon stocks in this region to temperature, precipitation, CO_2 and management. Simulation results were compared to estimate the relative contribution of different variables to carbon fluxes during the last 65 years. Only living biomass (above- and below-ground) was considered; carbon stored in soils and dead biomass was omitted. The nitrogen cycle is not represented in

LPJ-GUESS, and therefore, N fertilization could not be considered.

MATERIALS AND METHODS

Site Description and Data Collection

Lady Park Wood is an ancient, semi-natural woodland in the UK (51°49′N, 2°39′W; 30–190 m elevation), which was coppiced for centuries but designated an unmanaged nature reserve in 1945. The main species present are beech (*Fagus sylvatica* L.), oak (*Quercus petraea* (Matt.) Liebl.), ash (*Fraxinus excelsior* L.), lime (*Tilia cordata* Mill., *T. platyphyllos* Scop.), wych elm (*Ulmus glabra* Huds.) and birch (*Betula pendula* Roth). The reserve covers 35.2 ha, of which 14 ha (old-growth stands) have experienced no management since about 1900 when approximately 50% of tree biomass was removed (Peterken and Jones 1987). We follow Peterken and Jones (1987, 1989) in the use of the term ''old-growth'' for describing mature stands within the wood. These stands are dominated by trees of ages that many authors have judged to be in the old-growth age for temperate broad-leaved deciduous forest, although providing a concise scientific definition of the term ''old-growth'' has been judged to be an impractical task (Wirth and others 2009). The oldest trees in Lady Park Wood are about 220 years and these stands have been well stocked with standing dead trees since 1976 when many were killed by drought (Cavin and others 2013). Canopy height and basal area have oscillated around a ceiling achieved by 1976 and the volume of coarse woody debris in the 1990's was similar to temperate deciduous 'virgin' forests and USA old-growth forests. The remaining 21 ha (young-growth stands) were virtually clear-felled in 1943 (Peterken and Jones 1989).

Estimates of carbon storage in living biomass from Lady Park Wood were used to ground truth LPJ-GUESS estimates. Transects were established in old and young-growth areas in 1944. Old-growth transects were recorded in 1945, 1955, 1977, 1983, 1986, 1992, 2000 and 2010 and young-growth transects in 1977, 1993 and 2002 (details in Peterken and Jones 1987, 1989). These long-term monitoring data (Mountford, E. unpub) provide location, species and diameter of all trees achieving at least 1.3 m height. Allometric regression equations were used to calculate living biomass in order to reconstruct long-term carbon dynamics. Species-specific equations were used where available and otherwise the equation for a similar species was substituted. Carbon content was assumed to have a mean of 48.8% (Thomas and Martin 2012). For more detail see supplementary material.

The LPJ-GUESS Model

LPJ-GUESS (Smith and others 2001) is a dynamic vegetation model that uses a gap modelling approach (Shugart 1984; Prentice and others 1993; Bugmann 2001). Various plant functional types (representing groups of species with similar functional traits) and species can be simulated (hereafter PFT refers to both PFTs and species) (Hickler and others 2004). Bioclimatic limits (Prentice and others 1992; Sykes and others 1996) are used to define the climate space in which each PFT may occur. Biophysical and physiological processes are represented mechanistically, using the formulations given in Sitch and others (2003) for LPJ-DGVM, which uses an area-averaged representation of vegetation structure. In contrast, LPJ-GUESS simulates vegetation as age cohorts of different species, competing for light and water on replicate patches (100 in the present study). The model is driven by short-wave radiation (photosynthetically active light), temperature, precipitation and CO_2 concentration of the air. Soil conditions modify the water uptake of the plant. CO_2 influences assimilation rate following the Farquhar and others (1980) approach.

Twenty-two PFTs and species were modelled including the major tree and shrub species plus a group comprising grasses and herbaceous plants, which compete with trees for resources. We used the full set of PFTs to test the capability of LPJ-GUESS to reproduce the current stage of the vegetation. Bioclimatic limits determine whether plants establish and whether they die in cold spells (for details and species-specific parameters see Hickler and others 2012). Each PFT also has a specific drought tolerance, characterised by its water uptake rate. Summergreen species require varying periods of chilling to induce budburst (Murray and others 1989). Cohort establishment and mortality are modelled as stochastic processes within each patch. In addition, stochastic patch-destroying disturbances, representing processes such as herbivory and storm damage, result in all vegetation in a patch being transferred to the patch's litter pool and occur with an annual probability of 1/500.

Model Forcing and Simulation Protocol

To equilibrate initial vegetation and carbon pools with climate at the beginning of the study period, the model was first ''spun-up'' for 1000 years using

climate data for the period 1901–1930 cycled repeatedly and the 1901 CO_2 value. The study period then ran from 1901 to 2005. Temperature, precipitation and short-wave radiation data for 1901–2005 were taken from the WATCH dataset (Weedon and others 2011). Both WFD (1901–1978) and WFDEI (1979–2005) were used to cover the study period and a bias correction was applied to the WFD data to create a continuous dataset. Locally measured daily temperature and precipitation data were also available from Ross on Wye (11 km from site) for years 1961–2005 (UK Meterological Office). These data were used in place of the WATCH dataset for the available years and the WATCH dataset was further bias corrected using these local data (see supplementary material for method). Missing values in the local station climate data were interpolated using a linear relationship ($r^2 = 0.94$, $P < 0.0001$) with data from Preston Wynne (34 km from site). Atmospheric CO_2 was taken from the RCP Concentration Calculation and Data Group (Meinshausen and others 2011). Simulations using modifications of these data are described below.

To project future carbon pools, temperature, precipitation and short-wave radiation for the period 2006–2100 were calculated to represent the IPCC representative concentration pathways (RCP) 4.5 and 8.5, which project an approximate 40% increase in atmospheric CO_2 from 2006 to 2100 or a 250% increase, respectively. These scenarios were chosen as they represent the two extremes of global temperature increase by 2100, within the range given by the IPCC AR5 report (IPCC 2013) for both stabilization scenarios (RCP4.5 and RCP6.0) and high greenhouse gas emission scenarios (RCP8.5). The RCP2.5 is considered highly unlikely and the derived climate data are not yet available. The two chosen scenarios are to some extent comparable to the AR4 SRES scenarios B1 and A2. Climate projections for the period were taken from CORDEX (Coordinated Regional Climate Downscaling; http://www.euro-cordex.net/) using data downscaled to high resolution (11′ longitude/latitude). We used downscaled climate data for the grid cell containing Lady Park Wood from the CMIP5 ensemble general circulation models (GCMs) HadGEM, MPI, IPSL and CNRM. These were the only models for which downscaled data at high resolution for RCPs 4.5 and 8.5 were available. Anomalies for each month in each future year were calculated as the difference between the future month mean and the climatology (monthly mean across all years 1970–2005) for each climate variable. Daily data for the relevant climate vari-

able from the period 1970–2005 were cycled through repeatedly to provide a baseline for future climate, maintaining intra-annual variation, and anomalies were applied to these data. A significant increasing trend was identified in the station temperature data, however, and this trend was removed before applying anomalies. For further details see supplementary material.

Comparison of Monitoring Data with Model Output

Vegetation dynamics in Lady Park Wood were simulated in LPJ-GUESS for the period 1901–2005; firstly without simulated clearance, to represent the carbon carrying capacity of the forest in a ''natural'' state with no history of anthropogenic disturbance or management. This hypothetical simulation provides a baseline against which carbon stocks under other real or modelled conditions can be compared and is referred to as ''no-clearance'' throughout. The clear-felling (100% biomass removal) that took place in the young-growth areas of Lady Park wood in 1943 and the partial felling (50%) of old-growth stands in 1901 were then simulated. These results were compared with observed old- and young-growth biomass data.

Relative Effects of Temperature, CO_2 and Management

Using the old-growth simulation as a baseline, simulations with no-clearance, with de-trended temperature throughout and de-trended CO_2 throughout were then compared. This allowed consideration of how different carbon storage would have been if each observed effect had not been present. As no trend in precipitation or radiation was identified in the weather data, the effects of these variables could not be examined, but they cannot have been drivers of the observed biomass increase.

Extreme Weather

Different climate variables are related strongly to each other; for example, years with higher than average summer temperatures are likely to have decreased precipitation. Hence, when investigating the effect of temperature, changing temperature alone in the driving data would be an oversimplification (but see supplementary material). The extreme climate experiments assessed the effect of climate factors by replicating years in which those factors were unusually pronounced (for example, dry years). Local weather data were ranked in terms of temperature or precipitation levels and the

Table 1. Summary of Weather Conditions During Top Ranking Years for Mean Temperature (March to September) and Precipitation (May to July)

Top 5	Mean temp Mar–Sep (°C)	Mean prec May–Jul (mm)	Years
Warmest	13.70	1.07	1989, 1990, 1995, 1997, 1999
Driest	12.98	0.89	1975, 1976, 1978, 1984, 1995
Coldest	11.57	1.83	1962, 1965, 1972, 1974, 1986
Wettest	12.18	2.60	1967, 1968, 1969, 1985, 1993

Climate data from these years were used to produce Figure 3.

top five warmest, coldest, wettest and driest years were extracted (Table 1) and cycled through repeatedly to simulate an extreme climate. By using real daily data from these top ranking years, the relationship between temperature, precipitation and radiation was preserved. Clearance was not simulated here in order to focus on the effects of climate.

Future Projections

The potential for carbon storage as biomass towards the end of this century was projected using climate data representing IPCC AR5 scenarios RCP4.5 and RCP8.5. The model was run to 2100, using the end of the no-clearance and young-growth simulations as starting points, the old-growth simulation was not used as its end point in 2000 was very similar to the no-clearance simulation.

RESULTS

Comparison to Data

Carbon stocks increased in old-growth unmanaged stands by 8.5 kg m^{-2} over 65 years and in young-growth stands by 9 kg m^{-2} over 57 years [Figure 1; see Hale (2015) for more details]. Simulations of the partial clearance in 1901 and clear-felling in 1943 agree relatively well with these data (mean difference in years with data points = −0.61 and 0.29 kg m^{-2}, respectively), with modelled values falling within the limits of the 95% confidence intervals of observed values in all cases except the two earliest old-growth observations (mean difference −2.23 kg m^{-2}). By the year 2005, simulated carbon mass in old-growth stands approaches the values of the no-clearance simulation, suggesting recovery from timber extraction is almost complete, in terms of biomass. The model correctly identified the major tree species (*Fagus*, *Quercus*, *Fraxinus*, *Tilia*,
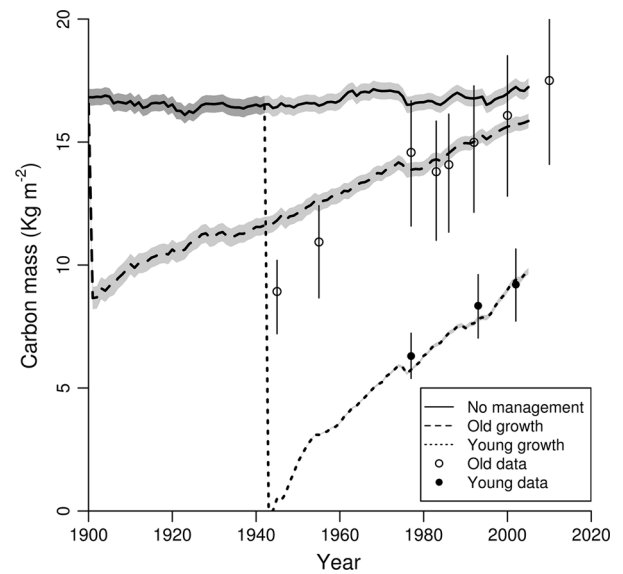

Figure 1. Observed biomass in old- (*open circles*) and young-growth stands (*filled circles*) at Lady Park Wood and LPJ-GUESS output representing carbon mass under various past management conditions (*lines* represent mean values): 50% clearance of all tree species in 1901 representing the old-growth stands (*dashed*); total clearance in 1943 representing young-growth stands (*dotted*); and no-clearance representing the potential carbon carrying capacity or 'natural' state with a mosaic of age cohorts and no anthropogenic disturbance (*solid*). *Shaded regions* represent the standard error of mean values. *Error bars* on data points are bootstrapped 95% confidence intervals.

Ulmus and *Betula*) but tended to overestimate *Quercus* abundance and underestimate *Fraxinus* and *Tilia*. This may indicate that some model parameterisations were sub-optimal for local conditions, although models can never perfectly recreate observed conditions due the random effects on vegetation establishment in multi species mixtures.

Relative Effects of Temperature, CO_2 and Management

The no-clearance simulation represents the carbon carrying capacity of Lady Park Wood if no management had ever been applied. Simulated carbon storage was more than 50% greater in the no-clearance than in the old-growth simulation in 1900, although the difference decreased through time as old-growth stands recovered. The size of this difference reveals that, for most of the study period, management legacy is the most important factor determining carbon stored in living biomass (Figure 2), and has a large but decreasing negati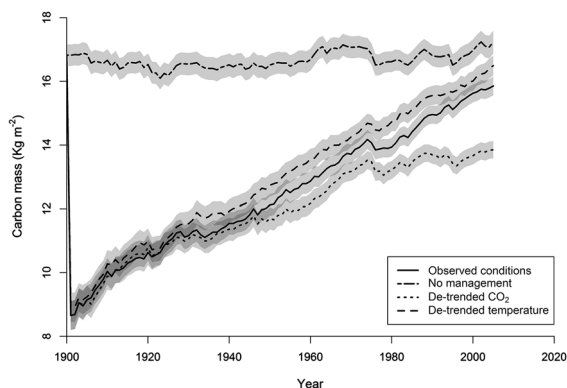ve effect on carbon mass as the forest recovers from past felling. Conversely, CO_2 has an increasingly large positive effect as atmospheric levels rise, indicated by reduced carbon mass when CO_2 is de-trended. Indeed, by the end of the period, the positive effect of CO_2 is larger than the negative effect of management legacy (Table 2). Temperature has a much smaller effect, which is negative overall. This suggests that the increase in forest biomass observed over the last century is more attributable to CO_2 fertilization than to warmer conditions in Lady Park Wood.

Effects of Extreme Climate Conditions

Figure 3 compares the extreme climate simulations to that without climate manipulation (all without clearance). Under dry conditions carbon stored as living biomass was reduced (mean difference -5.84 ± 0.31 kg C m^{-2} across years 1900–2000), whereas under wet conditions biomass production did a little better than under actual climate (1.30 ± 0.33 kg C m^{-2}). However, biomass production was also greatly suppressed under warm conditions (-2.62 ± 0.36 kg C m^{-2}) and increased in cold conditions (0.97 ± 0.45 kg C m^{-2}).

Future Carbon Storage

During the period 2006–2100, carbon stored as living biomass was projected to either maintain approximately 2005 levels or increase by up to 3 kg C m^{-2} in the simulations with no historical clearance. In the young-growth stands, carbon storage increased rapidly to approach simulated levels without historical clearance (17 kg C m^{-2} in 2000) and, in some cases, continued to rise by up to 4 kg C m^{-2} (Figure 4). There are some consistent differences between GCMs but the overall trends are very similar in most cases. Regardless of clearance history or GCM, the difference between the two RCPs is small.

Figure 2. LPJ-GUESS output showing the effect on stored carbon of removing single variables relative to observed conditions in old-growth stands (that is, 50% tree clearance in 1901, increasing temperature and CO_2; *solid line*). The effect of management was removed by running the model without simulated clearance (*long dashes*). CO_2 was de-trended by using 1901 levels throughout (*dotted line*). Temperature was de-trended using a linear regression (*short dashes*; see text). *Lines* represent means of 500 replicate patches and *shaded areas* represent standard error.

Table 2. Projected Carbon Mass Values in 1960, 1980 and 2000 (Mean ± SD)

Simulation	1960 Cmass	Δ Cmass	1980 Cmass	Δ Cmass	2000 Cmass	Δ Cmass
Observed temperature & CO_2 with 50% clearance in 1901	12.87 ± 7.18	0.00	13.93 ± 6.48	0.00	15.63 ± 6.36	0.00
De-trended CO_2	12.17 ± 7.00	−0.7	13.21 ± 6.31	−0.72	13.67 ± 6.10	**−1.96**
De-trended temperature	13.56 ± 7.30	0.69	14.73 ± 6.62	0.8	16.01 ± 6.78	0.33
No-clearance	16.68 ± 7.64	**3.81**	16.62 ± 7.27	**2.69**	16.97 ± 7.74	1.34

The simulation using observed conditions represents old-growth conditions as a baseline. ΔCmass shows the difference between each modified condition and that baseline. The biggest driver of C mass at each time point is highlighted in bold text.
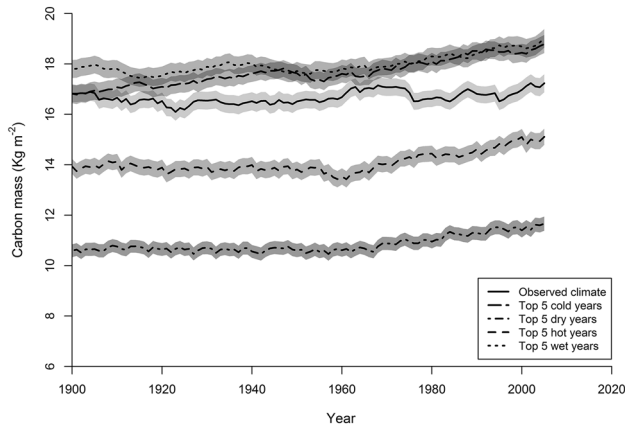
Figure 3. Effects of extreme weather conditions on stored carbon simulated by LPJ-GUESS using local weather data from the most extreme 5 years in terms of high /low temperature and high/ low rainfall. *Lines* represent means of 500 replicate patches and *shaded areas* represent standard error.
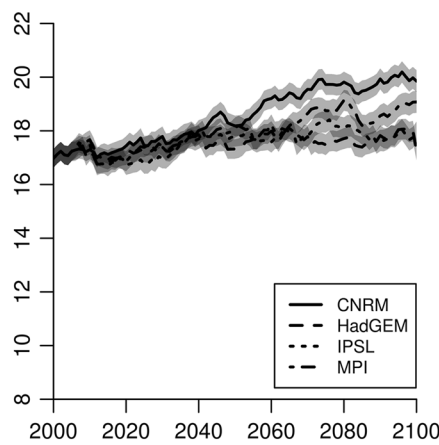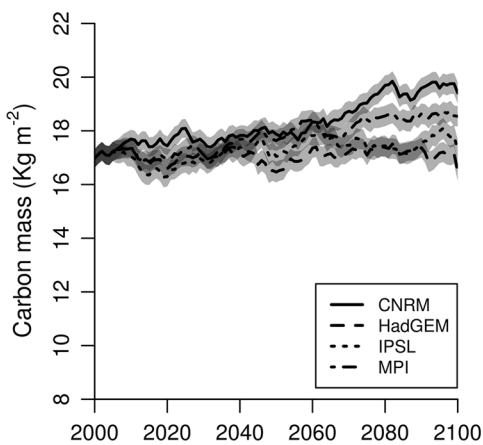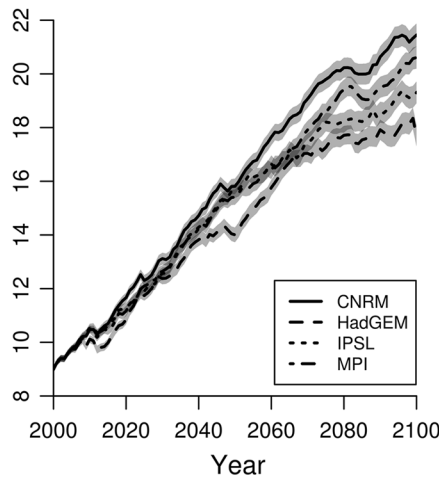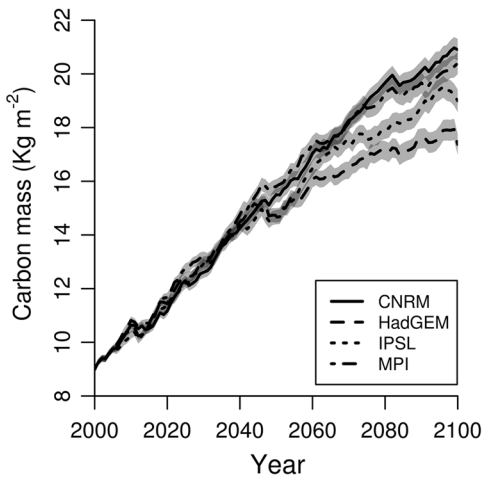

Figure 4. Future projections of carbon mass in Lady Park Wood using the RCP4.5 (*left*) and RCP 8.5 (*right*) climate models. The starting point for future projections was the no-clearance simulation (*top*) and new growth simulation (*bottom*). *Lines* represent means of 500 replicate patches and *shaded areas* represent standard error.

DISCUSSION

Monitoring data reveal that, since release from management, the old-growth stands in Lady Park Wood have more than doubled their carbon storage as living biomass (Figure 1). Furthermore, greater biomass appears to be possible and still rising (old-growth stands in 2010 = 18.11 kg C m^{-2}). This al-

ready exceeds the 17 kg C m^{-2} maximum potential biomass suggested by Ciais and others (2008) for European broad-leaved forest, although it may be within the range of natural variability. Previous estimates of current carbon sequestration have been based mostly on inventories of commercial forests in the European temperate zone and are

lower than the values we report from this unmanaged area, which may still be at the lower end of the UK range. In the New Forest (50°51.5′N and 1°32.5′W), for example, a value of 28 kg C m^{-2} has been recorded (Hale 2015). The potential range of carbon in above-ground living biomass for American, Chinese and Australasian temperate forest given by Keith and others (2009) (c. 15–38 kg C m^{-2}) therefore also seems accurate for European forest, even under sub-optimal conditions. The no-clearance simulations represent the potential carbon carrying capacity as living biomass in Lady Park Wood if no management had ever been applied. At around 17 kg C m^{-2}, it is similar to the suggested max of 17 kg C m^{-2} for broad-leaved forest (Ciais and others 2008). Future projections in the no-clearance stands showed either stability at 2005 levels or an increase towards the end of the century of up to 3 kg C m^{-2} (Figure 4). However, the time scale is relatively short for forest dynamics and longer projections would be required to determine where carbon levels might stabilize in the long-term.

Management had the greatest effect on carbon stocks throughout most of the study period (Table 2; Figure 2). However, towards the end of the study period, CO_2 has taken over as the bigger driver. This has a parallel with Erb and others' (2013) work in Austria, where a shift from management to 'climate and management' was identified as the major driver of mean annual increment during the latter part of the twentieth century, although they did not distinguish CO_2 from climate. Relatively little of the observed historical increase in carbon stocks was attributable to climatic change, once the effects of increasing CO_2 and management were removed.

Climate manipulation experiments demonstrated that increased temperature (and associated rainfall reduction) had negative effects on carbon storage even though warmer conditions have been proposed to stimulate net primary productivity at northern latitudes (for example, Zaehle and others 2007) and this can also be demonstrated by manipulating temperature or precipitation in isolation (see supplementary material). Although less precipitation will clearly cause water limitation, increased temperatures can also cause water stress by increasing demand for water. Furthermore, assimilation is inhibited in LPJ-GUESS by a negative effect of temperature on light-use efficiency above 5°C, which has been demonstrated experimentally (Farquhar and others 1980; Haxeltine and Prentice 1996). A negative effect of increased temperature might be rather unusual in a Euro-

pean context, since most temperate broad-leaved forests occur in areas with a continental climate, and therefore more pronounced temperature seasonality and longer winters. Under these conditions, an increase in temperature would extend the growing season, allowing more photosynthesis and therefore productivity. However, at Lady Park Wood the climate is oceanic, therefore the growing season could be only marginally extended as temperatures are generally above the photosynthesis threshold already. Any positive effect on winter net primary productivity would be outweighed by a decrease over summer, when increased temperature would increase water demand and reduce light-use efficiency. At other locations with a more continental climate a higher annual temperature may result in increased productivity.

Carbon mass in old-growth stands was approaching ''natural'' levels by 2005, which indicates an approximate 100-year recovery time from 50% clearance. Recovery from 100% clearance might be expected to take significantly longer, but Figure 4 shows projected recovery times of 110–140 years. Therefore, intensively managed forest stands may recover relatively quickly if released from management. Any increase in growth rate is likely to be driven by increased CO_2 levels rather than associated warming (Figure 2). In the simulations of ''natural'' forest without historical clearance, forecasts of carbon stocks for the next century based on the two RCPs are qualitatively similar over the first decades. In the latter period, all climate models show some increase under RCP8.5, of between 1 and 3 kg C m^{-2}, whereas for RCP4.5 some show a comparable increase, whereas others project a continuing stable state around 17 kg C m^{-2}.

LPJ-GUESS has been used in a large number of studies and its performance has been evaluated several times. Lehsten and others (2015, Appendix S4) reviewed evaluations of model performance and uncertainty of parameters. Numerous applications have added a feature to LPJ-GUESS in cases where the standard model was not sufficient to describe a certain phenomenon, for example LPJ-GUESS has been coupled to a climate model to look at feedbacks of vegetation on climate change (Wramneby and others 2010). Current developments include the incorporation of the N cycle and a representation of peatland processes, although these were not available for this study.

This study was confined to living biomass carbon stocks, which are closely related to soil and dead biomass carbon stocks. Currently in Lady Park Wood, 29% of carbon stocks are in the soil and 3%

in coarse woody debris within the old-growth stands and 46% and 5%, respectively, in the young-growth stands (Hale 2015). These values are rather low compared with other sites in the UK because of the thin soil cover on the steeply sloping site (Vanguelova and others 2013).

Previous European estimates of carbon storage as biomass have been far lower than the values we report from this unmanaged area, where both model and data approach the potential maximum stock estimated from old forest data and yield tables (Ciais and others 2008). However, this potential maximum is likely to be site dependent and is significantly exceeded in other old-growth deciduous forests in the UK (Hale 2015). Native temperate deciduous forests cover a significant amount of European land area (12.8% or 1.2×10^8 ha) (Schuck and others 2002) but are mostly managed for some level of timber extraction. Nabuurs and others (2013) reported that European forests are approaching equilibrium with the current level of management and thus the carbon sink effect is declining.

This study suggests that forests released from management can provide a major carbon sink during the recovery phase, as suggested by Erb and others (2013) and Mackey and others (2013). Consequently, the contribution of European native deciduous forests to recent carbon sequestration is likely to be significant when total ecosystem carbon is considered and this contribution has almost certainly been underestimated in the UK for the latest Global Forest Resources Assessment, where observations from plantations predominated (FAO 2010; Hale 2015). However, there are strict environmental limits on the carbon carrying capacity of a degraded forest and further limits on the degree to which that can be restored. The ultimate value of these areas for carbon mitigation therefore lies in their long-term preservation, rather than their current sink status (Mackey and others 2013). Therefore increasing the area of unmanaged semi-natural woodland in Europe will help to maximize the positive effect of CO_2 fertilization on their carbon sink status and mitigate any negative effect due to associated climate warming. Protecting these areas in the long-term will ensure carbon stocks are maintained and that a return to source behaviour does not occur.

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