Functional Ecology

British Ecological Society

Functional Ecology 2013, **27**, 1424–1435 doi: 10.1111/1365-2435.12126

Extreme drought alters competitive dominance within and between tree species in a mixed forest stand

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Summary

1. The effect of extreme climate events on ecosystems is an important driver of biotic responses to climate change. For forests, extreme drought has been linked to negative effects such as large-scale mortality and reduced primary production. However, the response of plant communities to extreme drought events remains poorly understood.

2. We used mortality data from a long-term monitoring programme in the core of the focal species' ranges, in combination with annual growth data from tree-rings, to study the effect of, and recovery from, an extreme drought event. We examined both the intraspecific and interspecific drought response and explored how differential responses affect competitive dominance between the dominant species *Fagus sylvatica* and *Quercus petraea*.

3. Mortality for the most drought-susceptible species, *F. sylvatica*, occurred alongside a temporary reduction in competition-induced mortality of *Q. petraea*, resulting in the long-term alteration of the relative abundance of the two species.

4. Significant intraspecific variation occurred in post-drought recovery in surviving *F. sylvatica,* with two distinct cohorts identified. A prolonged recovery period was coupled with the failure to regain pre-drought growth levels in this species, whereas for *Q. petraea,* no severe drought impacts were observed. This species instead experienced competitive release of growth.

5. Our results demonstrate that ecosystem responses to extreme drought can involve rapid, nonlinear threshold processes during the recovery phase as well as the initial drought impact. These sudden changes can lead to the reordering of dominance between species within communities, which may persist if extreme events become more frequent.

Key-words: basal area increment, community, competition, dendrochronology, drought stress, *Fagus sylvatica* (European beech), *Quercus petraea* (sessile oak), stress, tree mortality

Introduction

Contemporary climate change is characterized by increased temperatures and altered precipitation patterns, alongside a rise in both the frequency and intensity of extreme climatic events such as droughts, floods and storms (Schar *et al.* 2004; Della-Marta *et al.* 2007; IPCC 2007). These changing environmental conditions are affecting ecosystems world-wide, with a slight reduction in the global net primary production of all terrestrial vegetation observed for 2000–2009, attributed largely to regional droughts combined with drying in the southern hemisphere (Zhao & Running 2010). These global responses mask considerable variation across different regions and ecosystems.

Research on biotic responses to climate change has largely focused on assessing the response to gradual changes in mean conditions. However, the effect of extreme events is increasingly being recognized as a key driving force in the response of organisms, species and communities to climate change (Gutschick & BassiriRad 2003; Jentsch, Kreyling & Beierkuhnlein 2007; Smith 2011). Studies of the effect of drought have linked extreme events to increased risk of mortality, reduction in growth of ecosystem dominant species, reduction in ecosystem primary productivity and alteration of eco-hydrological regimes (Breshears *et al.* 2005; Ciais *et al.* 2005; Bigler *et al.* 2006; Gitlin *et al.* 2006; Adams *et al.* 2012). Furthermore, whilst the response to extreme events differs amongst species, species-specific impacts can cascade to ecosystem-level effects if dominant or competitor

*Correspondence author. E-mail: a.s.jump@stir.ac.uk species subjected to extreme events suffer differential mortality (Thibault & Brown 2008).

Given their importance for global carbon and hydrological cycles, and their role in providing and modifying habitat for a wide variety of associated organisms, shifts in species composition of forest trees may have far reaching consequences (Dixon *et al.* 1994; Soja *et al.* 2007; Bonan 2008). It is essential, therefore, to understand how extreme climatic events can affect growth and competition between co-occurring tree species. Recent studies have linked changes in the availability of moisture to increased levels of tree mortality in temperate and boreal forests (Hogg, Brandt & Michaelian 2008; van Mantgem *et al.* 2009; Michaelian *et al.* 2010; Peng *et al.* 2011). However, the long-term effects of extreme drought and the recovery of surviving trees are poorly documented (Martínez-Vilalta, Lloret & Breshears 2011).

The maintenance of species diversity has been suggested as a means to promote ecosystem resilience in the face of environmental change, through response diversity (Elmqvist *et al.* 2003). Where multiple species perform the same ecosystem function yet display a heterogeneous response to environmental change, biodiversity might provide insurance against ecosystem regime shift, where the ecosystem shifts to a less productive or otherwise less desired state (Folke *et al.* 2004). Monoculture systems, by contrast, can be particularly vulnerable to rapid ecosystem collapse and regime shift once thresholds in environmental conditions are breached (Scheffer & Carpenter 2003). This is particularly true for forests, where the longevity of individual trees means that establishment may have taken place under climate conditions which now occur rarely, or have even ceased to exist at that location (Petit & Hampe 2006). However, the response of a single species to environmental change can be expected to display a degree of heterogeneity, as intraspecific competition within any population can be mediated by fine-scale environmental site characteristics and variation in drought response traits (Choler, Michalet & Callaway 2001; Bolnick *et al.* 2011). Common garden studies have demonstrated considerable intraspecific variation in drought traits and responses for seedlings and saplings of provenances taken from different areas of a species' range (Peuke *et al.* 2002; Meier & Leuschner 2008; Rose *et al.* 2009; Robson *et al.* 2012). Recent work using molecular markers has demonstrated that altered climatic conditions can apply a selective pressure within natural populations, resulting in changing genotypic frequencies over time (Jump *et al.* 2006; Bilela *et al.* 2012). Whilst the fine-scale spatial patterns of drought response within a species are often patchy, eliciting details of this at the stand scale is challenging (Allen *et al.* 2010; Martínez-Vilalta, Lloret & Breshears 2011). With changing environmental conditions, a competitive advantage for a dominant species may weaken, with increasing frequency and strength of drought conditions acting as a stabilizing mechanism favouring coexistence with otherwise less competitive species (Terradas, Peñuelas & Lloret 2009). Once a threshold of drought intensity and frequency has been reached, the competitive advantage could switch to the historically less competitive but more drought tolerant species. Understanding the effect of predicted climatic change on widespread dominant species is, therefore, particularly important to inform on potential future responses at the community level.

European beech (*Fagus sylvatica L.*) is one of Europe's most significant late successional tree species which is an important component of around 17 million hectares of European forest (Petit & Hampe 2006). This species dominates temperate forests over large areas of Europe, but is considered to be particularly drought sensitive and is predicted to be outcompeted by more drought tolerant species in many regions as the climate warms (Broadmeadow, Ray & Samuel 2005; Czucz, Galhidy & Matyas 2011; Hlasny *et al.* 2011). Dendroecological studies from the equatorial edge of the species' range have shown a reduction in growth as a response to elevated drought stress associated with climate change, which is expected to result in a reduction in available habitat area in this mountainous part of the species' range (Jump, Hunt & Peñuelas 2006; Piovesan *et al.* 2008). However, growth decline has recently been reported in some regions within the range core of *F. sylvatica* and linked to increased drought stress (Bontemps, Hervé & Dhôte 2010; Charru *et al.* 2010).

Although usually dominant, *F. sylvatica* frequently coexists with competitor species in mesic, multi-species forests, with one common co-dominant being sessile oak (*Quercus petraea*). Many studies have demonstrated the superior below- and above-ground competitive ability of *F. sylvatica* over oak (*Quercus* sp.) in mature mixed species forests (von Lüpke 1998; Leuschner *et al.* 2001; Hein & Dhôte 2006). By contrast, greater rooting depth, lower fine root sensitivity to drought, differing hydraulic architecture and lower susceptibility to cavitation of *Q. petraea* all contribute to overall greater drought tolerance (Aranda, Gil & Pardos 2000, 2005; Leuschner *et al.* 2004). Thus, modelling studies forecast an increase in the spatial segregation of *F. sylvatica* with competitor species such as *Q. petraea* under climate change scenarios, with a reduction in habitat suitability and biomass yield of *F. sylvatica* (Broadmeadow, Ray & Samuel 2005; Meier *et al.* 2011). Ultimately, therefore, differing ecological and physiological characteristics between *F. sylvatica* and its competitors will combine to determine their responses to altered water availability, with the expectation that the competitive ability of *F. sylvatica* may be reduced in many regions throughout its range if droughts become more frequent and more severe.

Consequently, we sought to determine the extent to which extreme drought led to changes in the growth and mortality of adult *F. sylvatica* and the competitor species, *Q. petraea* and how these changes modulate inter- and intraspecific competitive interactions between these species. We focus on the following key issues: (i) How do surviving *F. sylvatica* and *Q. petraea* cohorts differ in growth pre and post-drought? (ii) How long do the different cohorts and species take to recover from the effects of an extreme drought, and do they return to previous levels of growth? (iii) Given expected differences in drought susceptibility and competitive ability between these species, how have their competitive interactions been altered by drought and what are the implications for future forest composition?

To address these questions, we used tree condition and mortality data derived from a long-term monitoring site where individual tree growth and condition have been assessed since 1945, in combination with new dendroecological data (Peterken & Jones 1987, 1989). At this site, an extreme drought in 1976 led to divergent responses of condition and mortality within and between co-occurring species (Peterken & Mountford 1996), thereby enabling us to explore the intra- and interspecific responses to drought and post-drought recovery.

Materials and methods

STUDY SITE

Lady Park Wood National Nature Reserve (southwest UK, 51° 49′N, 2°39′W) is a 35·2 hectare, ancient, mixed species, deciduous forest that has been managed as a minimum intervention forest reserve for ecological research since 1944 (Peterken & Jones 1989; Peterken & Mountford 1996). The most abundant canopy dominant tree species are as follows: *F. sylvatica, Q. petraea*, *Fraxinus excelsior L.* (common ash), *Tillia cordata* and *T. platyphylos* (small-leaved lime and large-leaved lime respectively). The site is in a steep sided valley, where the River Wye has cut through the underlying carboniferous limestone. Thin well-drained acidic brown earth and skeletal, organic loam rendzina soils cover much of the upper slopes where the old growth predominates (Peterken & Jones 1987). The regional climate is temperate, with 803 mm of precipitation annually and a mean temperature of 9·3 °C (using the baseline period 1961–1990). Because *F. sylvatica* extends from southern Fennoscandia in the north to the Mediterranean region in the south, and from the edge of Western Europe to the Carpathian Mountains in the east, our study site is within the core of the species climatic distribution (see Fig. S1, Supporting information), although human intervention has significantly advanced its postglacial geographical distribution in more northern parts of the United Kingdom (Birks 1989).

CLIMATE DATA & DROUGHT INDICES

Climate data for the site were obtained from the Met Office UK 5 km^2 gridded data set, covering the period 1914–2006 (Perry & Hollis 2005). Using this data set, annual values were calculated for mean temperature and total precipitation for 1914–2006, and regression analyses performed to identify any temporal trends (see Fig. S2, Supporting information).

Droughts were identified using the Standardized Precipitation-Evapotranspiration Index (SPEI). This method has the advantage over alternatives, such as the Palmer Drought Severity Index, of enabling the calculation of drought utilizing a time-scale relevant to the study system in question (Vicente-Serrano, Beguería & López-Moreno 2010). In combination with the Standardized Precipitation Index (SPI), the SPEI enables an evaluation of the degree to which climate warming contributes to drought. SPEI uses monthly precipitation and potential evapotranspiration (PET) as input data, whilst SPI uses only precipitation data. PET was calculated using the Thornthwaite method, using monthly mean temperature and a correction coefficient derived from latitude (Thornthwaite 1948). SPEI and SPI were calculated at 12-month time-scales, with monthly index values derived from climate data over the previous 12 months, and using log-logistic distributed indices with parameters fitted using unbiased probability weighed moments. This time-scale represents current and partial previous year conditions for tree growth. The difference between the two indices was calculated (SPEI−SPI), representing the contribution of PET to drought (Vicente-Serrano *et al.* 2011). Linear regressions were performed on SPEI, SPI and the difference, to identify any temporal trends. SPI and SPEI were compared by calculating Pearson's r correlation coefficients between monthly values.

The Thornthwaite method for calculating PET used above has recently received criticism for causing assessments of drought to be overestimated (Sheffield, Wood & Roderick 2012). The Met Office UK 5 km^2 gridded data set includes data for mean monthly cloud cover and wind speed for the period 1969–2004 (Perry & Hollis 2005), enabling PET to be calculated by other methods. To validate drought indices calculated over the longer 1914–2006 period using the Thornthwaite method, we additionally calculated SPEI for this shorter time period, using PET derived from the Penman–Monteith equation (Allen *et al.* 1994). Correlation analysis and linear regression were then used to compare it with SPEI calculated using the Thornthwaite method, and to identify any trend.

TREE-RING SAMPLING

Previous research at this site assigned individual *F. sylvatica* drought survivors into two classifications according to the level of drought damage sustained in 1976 (Peterken & Mountford 1996). Severely damaged individuals had suffered extensive canopy dieback, bark necrosis, trunk scarring and limb loss. Minimally damaged individuals escaped with only minor canopy dieback. These two classes, along with the individuals that perished, were intermixed throughout the old growth stand. We were particularly interested in assessing pre-drought growth differences between these damage classes and their post-drought recovery rate, to identify if growth- or size-related factors might predispose individuals to drought-induced growth decline.

Three sets of mature, canopy dominant or co-dominant trees were identified using existing site stem maps for the site in combination with examination of individuals in the field. These three sets were as follows: severely damaged *F. sylvatica* ($n = 32$), minimally damaged *F. sylvatica* ($n = 33$) and *Q. petraea* ($n = 30$), as described in Table 1. In 2010, two or three cores were taken per tree at 1·3 m using a 4·3 mm increment borer, with samples then stored and air-dried in paper straws. The dried samples were mounted, sanded and scanned at 1600 dpi, then measured with an accuracy of 0·001 mm using CooRecorder v7.4. (Larsson 2003b). Samples were cross-dated using CDendro v7.4 and COFECHA (Holmes 1983; Larsson 2003a). A mean ring width value was calculated per tree using the total number of cores available for each tree. In total, 188 cores from 93 trees were included in the final 3 series for analysis.

PERMANENT TRANSECT INVENTORY

A series of permanent transects were established on the site in 1945, covering 0·9 ha of the 14 ha of old growth forest (Peterken & Jones 1987). These were 20 m wide transects running downslope and recorded in 1945, 1955, 1977, 1983, 1986, 1992, 2000 and 2010, thus providing a 65-year record of tree growth, mortality and recruitment for all individual trees and shrubs present

Table 1. Descriptive statistics for the tree-ring chronologies

	No. of trees	No. of cores	Mean series length (years)	Series duration	Mean BAI (mm^2)	Mean Sensitivity	$\bar{r}$	EPS
Fagus sylvatica (severely drought damaged)	31	62	109·6	1856–2009	2523 ± 94	0·29	0·35	0·94
pre-drought subset				1929–1975	2973 ± 92	0·24	0·41	0·96
post-drought subset				1976–2009	1902 ± 128	0·39	0·34	0·94
Fagus sylvatica (minimally drought damaged)	32	68	111·8	1832–2010	2905 ± 95	0·32	0·42	0·96
pre-drought subset				1929–1975	3265 ± 97	0·22	0·49	0·97
post-drought subset				1976–2009	2407 ± 152	0·35	0·43	0·96
Quercus petraea	30	58	174·6	1770–2009	2530 ± 51	0·23	0·45	0·96
pre-drought subset				1929–1975	2428 ± 66	0·22	0·43	0·96
post-drought subset				1976–2009	2671 ± 80	0·21	0·38	0·95

BAI, basal area increment; $\bar{r}$, mean inter-series correlation; EPS, expressed population signal.

(Peterken & Mountford 1996). Each tree or shrub attaining a height of 1·3 m was mapped, and circumference at breast height recorded. Records were also made of canopy position, crown size, crown dieback and notes of the condition of individual stems. For each case of tree death, the primary cause of death was attributed based on survey assessment and classified as either drought (i.e. severe drought damaged as described above, followed by death), competitive exclusion (overtopping by neighbouring trees, followed by decline and death) or other factors. Mortality of canopy *F. sylvatica* ($n = 102$) and *Q. petraea* ($n = 34$) was examined from 1955–2010 using records from the permanent transects. 1955 was used as a baseline date, as no canopy trees of either species died during the period 1945–1955.

DATA ANALYSIS

Chronology building, and all further data analysis, was performed in R using the packages dplR and bootRes (Bunn 2008; R Development Core Team 2012; Zang & Biondi 2012). The ring width series were detrended using a smoothing spline function with a rigidity of 2/3 of the series length. For one core from the minimally damaged series, the spline function was inappropriate and so a modified negative exponential function was used. Chronologies were then built using the detrended ring widths, taking average ring width index values and using Tukey's biweight robust mean. The resulting chronologies used to identify years in which strong growth reductions occurred, and the severity of the reductions. The suitability of the chronologies for cross-dating was assessed using mean sensitivity (MS), a measure of the year-to-year variability of tree growth (Biondi & Qeadan 2008a). The signal strength of the chronologies was evaluated using the mean inter-series correlation ($\bar{r}$) and the expressed population signal (EPS), a measure of how well a chronology captures the signal of a hypothetical perfect chronology (Fritts 1976). As not all cores reached the centre of the tree, series length is used as an approximation of tree age.

Basal area increment (BAI) is well established in forest ecology as measure of tree growth which can be used to study the vigour of individual trees and populations (Biondi 1999; Bigler & Bugmann 2003; Biondi & Qeadan 2008b). BAI tends to increase sharply in juvenile trees before reducing in gradient when the tree reaches maturity; however, it does not display the same age-related trends as raw ring widths and is expected not to decline markedly during the mature phase of a tree's growth unless the tree is severely stressed (Pedersen 1998). Here, BAI was calculated using raw, non-detrended ring widths and radii ($\text{BAI} = \pi(R_n^2 - R_{n-1}^2)$ where R is the radius of the tree and n is the tree-ring year). BAI was then plotted using a 9-year running mean to facilitate the visual identification of the long-term growth trend (Jump, Hunt & Peñuelas 2006). The inflection point at which post-release growth started to plateau was identified as being the beginning of the mature phase of growth, mature growth being 1929–2009 for the severely damaged *F. sylvatica,* 1927–2009 for the minimally damaged *F. sylvatica*, and 1883–2009 for *Q. petraea*. The same 1929–2009 mature phase of growth was subsequently used for all three BAI series, to allow the comparison of the series over the same period. All further BAI analysis used the raw BAI data, not the running means. The three mature growth series were then split into pre-drought (1929–1975) and post-drought (1976–2009) subsets.

To compare pre-drought growth rates for the *F. sylvatica* cohorts, pre-drought BAI for each tree was pre-whitened by fitting an autoregressive model, selected using Akaike's information criterion (AIC) and combined into pre-drought chronologies. Pre-drought growth was then compared by pooling the severely and minimally damaged BAI chronologies, with dummy variables assigned according to cohort of tree. Linear regression was then performed on the pooled data, with the statistical significance of the dummy variable used to assess differences in pre-drought growth between the cohorts (Draper & Smith 1998).

Post-drought growth for all *F. sylvatica* and *Q. petraea* cohorts was assessed using linear and nonlinear growth models (Paine *et al.* 2012) fitted to mean BAI chronologies, and with the most appropriate models chosen by evaluation of AIC. The best performing models selected for post-drought BAI were: two-parameter asymptotic regression models for both *F. sylvatica* series, and a four-parameter log-logistic model for *Q. petraea*. Subsequently, post-drought BAI was standardized by dividing individual year growth values by the mean pre-drought annual BAI, thus transforming BAI into a dimensionless and comparable index, and then plotted to illustrate relative recovery.

To assess whether the 1976 growth response was extreme from an organismal, rather than simply an anthropogenic point of view, BAI for the severely damaged *F. sylvatica* was compared with SPEI. Growing season mean SPEI was calculated for the period April to September, giving a value for the drought stress during the growing season which was then transformed using the formula log(−SPEI+1), to obtain a normally distributed data set. BAI and growing season mean SPEI for the period 1929–1975 were then converted to z-scores and plotted with normal probability contours added as data ellipses around the scatterplot. The 1976 value was then added for comparison with the probability contours of the 1929–1975 data.

Trees stressed by environmental factors (such as aridity) will generally produce rings with higher year-to-year variability than less stressed individuals (Fritts 1976). Therefore, inter-year growth variability can be used as an indicator of plant stress. Gini coefficient (G) is a common measure of data heterogeneity and has been proposed as being particularly appropriate for the analysis of tree-ring data (Biondi & Qeadan 2008a). Therefore, G was calculated for the pre (1929–1975)- and post (1976–2009)-drought portions of the mature phase of tree growth for all groups. G for the minimally damaged *F. sylvatica* was transformed using $\frac{1}{G^{0.5}}$ to obtain normally distributed data. G was then compared within and between groups using t-tests and paired t-tests (utilizing the same transformation for comparison with the minimally damaged data). Given recent efforts to integrate the use of effect size statistics in the biological sciences as a way of evaluating the biological importance of the factor under investigation (Nakagawa & Cuthill 2007), standardized mean difference (Cohen's d, the difference between the two means divided by the standard deviation) was calculated to evaluate effect size and reported using established values of effect size, that is, small ($0{\cdot}2 < d < 0{\cdot}5$), medium ($0{\cdot}5 < d < 0{\cdot}8$) and large ($d > 0{\cdot}8$) (Cohen 1988).

The relationship between tree growth and climate was examined using response function analysis, a variant of multiple regression analysis which uses monthly climate predictor variables, orthogonalized as principal components, to elicit the climate drivers of growth (Zang & Biondi 2012). In this analysis, a series of coefficients were calculated, relating the ring width indices from the de-trended chronologies to monthly climate variables covering from the beginning of the previous year's growing season until the end of the current year's growing season (Cook & Kairiukstis 1990; Biondi & Waikul 2004). Monthly precipitation and temperature values from the 1914–2006 climate data set described above were used, with a 17-month window from May of the previous year until September of the current year. A total of 1000 bootstrap replicates were used (Biondi 1997), and significance calculated at the 95% level. The analysis was repeated using Pearson's product moment correlation functions.

Results

CLIMATE AND DROUGHT INDICES

Temperature has increased over time, with the rate of increase accelerating from the mid 1960's onwards (see Fig. S2, Supporting information). Temperature increased by 1·02 °C over the 40 years 1966–2006, according to the relationship: $\text{Temperature} = 1073 - 1.096\text{year} + (2.824\times 10^{-4})\text{year}^2$, ($R^2$ adj = 0·302, $P < 0{\cdot}001$). Precipitation declined over the study period, but has remained stable since the 1960′s. Mean precipitation for the period 1996–2006 was 853 mm ± 20·4. Comparison of SPEI calculated using the Penman–Monteith and Thornthwaite methods showed that both methods produced similar results (Pearson's r correlation coefficient = 0·987). Linear regression of SPEI (Thornthwaite) $-SPEI(Penman)$ revealed a small but statistically significant positive trend ($R^2 = 0{\cdot}10$, $P < 0{\cdot}001$), that is, SPEI (Penman) gave results showing a stronger drought trend. Consequently, the more conservative approach using calculation of SPEI based on PET calculated by the Thornthwaite method over the longer time-scale (1914–2006) is used in all further analyses.

The drought indices SPEI and SPI show that the 1976 drought was the most exceptional drought during the period 1914–2006 (Fig. 1). Using the minimum recorded index value as a measure of peak drought intensity, the 1976 drought exceeded the second most intense drought (in 1921) by 30·8%. The minimum SPEI value recorded during the drought was −3·08. Index values were almost constantly negative throughout the period 1970–1976,

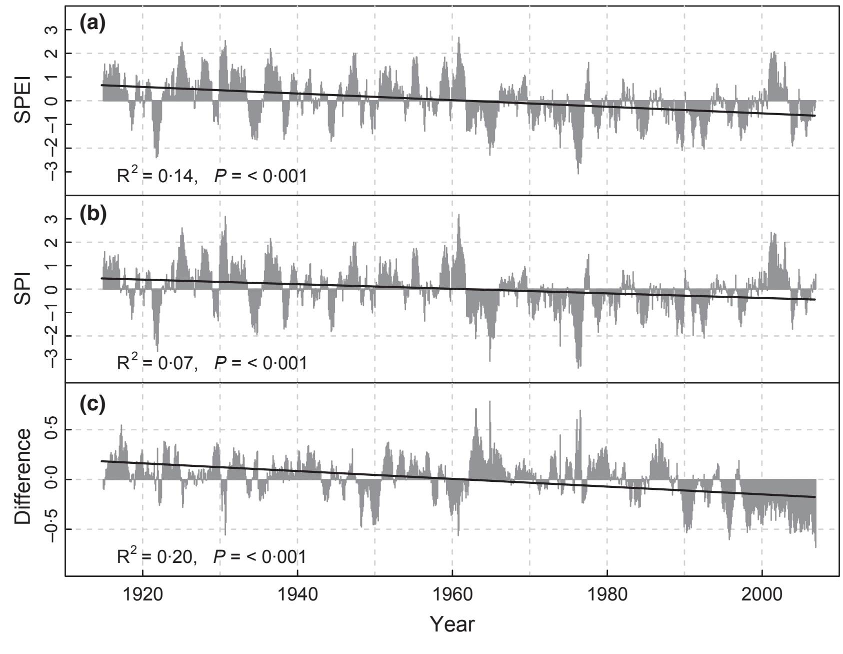

Fig. 1. Drought indices for the study site, calculated using 5 km² gridded climate data. The indices shown are as follows: (a) Standardized Precipitation-Evapotranspiration Index (SPEI), (b) Standardized Precipitation Index (SPI) and (c) Difference (SPEI – SPI). Monthly values are plotted, calculated over a 12-month time-scale. Index values are z-scores. Linear regressions are shown: SPEI = 27−0·01 time (R^2 adj = 0·14, $P < 0{\cdot}001$), SPI = (R^2 adj = 0·07, $P < 0{\cdot}001$), Difference = 7·6−0·004 time (R^2 adj = 0·20, $P < 0{\cdot}001$).

representing a prolonged period of moisture deficit. The long-term trend for SPEI is for increasing drought (SPEI $(t) = 26{\cdot}99 - 0{\cdot}138t$, where t = time, $R^2 = 0{\cdot}14$, $P < 0{\cdot}001$) and also increasing, but more weakly, for SPI (SPI $(t) = 19{\cdot}34 - 0{\cdot}099t$, $R^2 = 0{\cdot}07$, $P < 0{\cdot}001$). The two indices are highly similar with a Pearson's r correlation coefficient of 0·97. However, despite this strong similarity, the difference plot reveals a deepening contribution of PET (and therefore of climate warming) to drought stress (Difference $(\mathrm{t}) = 7{\cdot}65 - 0{\cdot}004t$, $\mathrm{R}^2 = 0{\cdot}20$, $P < 0{\cdot}001$).

CLIMATE GROWTH RELATIONSHIPS

Response function analysis shows that for both *F. sylvatica* damage classes, warm springs and wet summers in the current year favour growth. There is a negative effect of high temperatures in the previous summer for the minimally damaged group (see Fig. S3, Supporting information). However, whilst the same negative effect is present for the severely damaged group, it is weaker and narrowly fails to achieve statistical significance. *Q. petraea* has no statistically significant relationships between climate and growth in any month demonstrating that, at this site, the growth of *F. sylvatica* is more sensitive to climatic variation than that of *Q. petraea*. These results were corroborated by similar output from correlation function analysis.

MORTALITY

On the permanent transects, of 102 initial live, mature and canopy dominant *F. sylvatica* recorded in 1955, 28 had died by 2010, with 24 of those occurring between 1977 and 2010. In Fig. 2, tree mortality is broken down over time by cause of death, revealing a strong pulse of mortality in *F. sylvatica* following the 1976 drought. *Q. petraea* mortality, by contrast, was predominantly due to competition, that is, through exclusion by overtopping from neighbours. No *Q. petraea* death occurred during the period 1977–1992 immediately following the drought, whereas 17% of *F. sylvatica* died. Other causes of death for both species reported were as follows: windthrow (n = 3) and squirrel debarking (n = 1).

RING WIDTH INDEX CHRONOLOGIES

Summary statistics for the three chronologies are given in Table 1. *Q. petraea* (175 years mean series length) were older than *F. sylvatica* (110 and 112 years mean series length for the severely and minimally damaged respectively). Mean sensitivity was in the region of 0·22–0·37 for all series, within the range of 0·1–0·4 judged to be suitable for cross-dating (Fritts 1976). Lower $\bar{r}$ (inter-series correlation) was recorded for all three chronologies after the drought compared with before, that is, the growth response to climate was more variable between trees in each chronology after the drought. EPS was consistently high, with a minimum value of 0·94 being comfortably above the threshold minimum of 0·85 (Wigley, Briffa & Jones 1984; Cook & Kairiukstis 1990). Fig. S4 (Supporting information) shows de-trended and standardized chronologies.

GROWTH VARIABILITY

Analysis of growth variability using Gini coefficient for the series, show that G increased post-drought for the severely damaged *F. sylvatica* ($t = 8{\cdot}67$, df = 50·77, $P < 0{\cdot}0001$) with a large effect size (d = 2·17, 95% CI 1·54/2·80), and also increased for the minimally damaged *F. sylvatica* ($t = 6{\cdot}50$, df = 53·13, $P < 0{\cdot}0001$) again with a large effect size (d = 1·41, 95% CI 0·86/1·96) (Fig. 3). There was no significant difference between the severely damaged and minimally damaged trees before the 1976 drought ($W = 634$, $P = 0{\cdot}059$; small effect size: d = 0·45, 95% CI −0·05/0·95). Post-drought, G was higher in the severely damaged compared with the minimally damaged trees ($W = 714$, $P = 0{\cdot}003$; medium effect size: d = 0·74, 95% CI 0·22/1·24). G did not change in *Q. petraea* following the drought ($t = 0{\cdot}23$, df = 56·96, $P = 0{\cdot}82$).

BASAL AREA INCREMENT

The BAI series of the three tree cohorts are shown in Fig. 4. The difference in pre-drought BAI (1929–1975) between the two *F. sylvatica* groups, analysed using dummy variables regression, was 358 mm^2 ± 109, which was statistically significant ($t = 3{\cdot}278$, $P = 0{\cdot}0015$) but with a small effect size (d = 0·44, 95% CI −0·06/0·95). For the severely damaged *F. sylvatica*, 1929–1975 mean annual

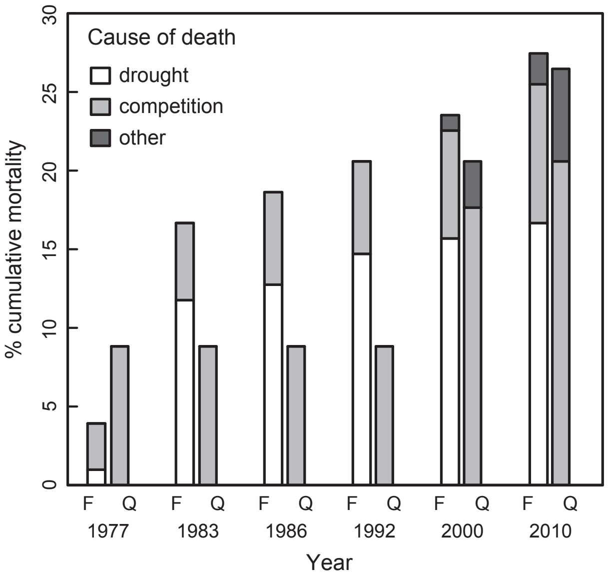

Fig. 2. Mortality of canopy trees assessed in survey years on the permanent transects from 1977–2010, with cause of death apportioned. On the x-axis, *F* = *F. sylvatica* and *Q* = *Q. petraea*. Of an original 102 living *F. sylvatica* sample, 28 died. Of an original 34 living *Q. petraea* sample, 9 died.

growth of 2973 ± 92 mm^2 fell to a minimum value of 374 mm^2 in 1977 (12·6% of pre-drought mean growth). Nonlinear growth modelling shows a recovery to an asymptotic level of 2218 ± 152 mm^2 after the drought ($\mathrm{BAI}(x) = d(1 - \exp(-\frac{x}{e}))$, where d = 2218, $P < 0{\cdot}001$ and e = 5·10, $P = 0{\cdot}004$). In comparison, for the minimally damaged *F. sylvatica*, pre-drought annual mean BAI of 3265 ± 97 mm^2 fell to a minimum value of 862^2 mm (26·4% of pre-drought mean growth) and recovered to 2527 ± 145 mm^2 (d = 2527, $P < 0{\cdot}001$ and e = 1·99, $P = 0{\cdot}020$). The higher parameter 'e' for the severely damaged *F. sylvatica* represents a lower slope gradient and therefore a slower recovery rate. Therefore, the minimally damaged trees had higher BAI rates than the severely damaged trees both before and after the drought, and both groups had a clear step change reduction in BAI after the drought. For *Q. petraea*, pre-drought annual mean growth of 2428 ± 66 mm^2 fell to a minimum value of 1845 mm^2 (76·0% of pre-drought mean growth), increasing immediately after the drought to 2897 ± 90 mm^2. The initial increase in BAI underwent a further rapid reduction to 2410 ± 98 mm^2 around an inflection point in 1994 ($\mathrm{BAI}(x) = c + \left(\frac{d-c}{(1+\exp(b(\log(x))-(log(e))))}\right)$, where b = −86·07 ($P = 0{\cdot}63$), c = 2897·1 ($P < 0{\cdot}001$), d = 2410·3 ($P < 0{\cdot}001$) and e = 2·93 ($P < 0{\cdot}001$)). Focusing on the post-drought trends, the standardized BAI recovery (Fig. 5) shows that the partial recovery for both *F. sylvatica* groups reached their asymptote at around 75% of pre-drought BAI. Whilst the initial increase in growth for *Q. petraea* was temporary, overall pre-drought BAI levels were maintained for this species. The inflection point of the step reduction in *Q. petraea* growth occurs at 1994 – the same point in time as the severely damaged *F. sylvatica* BAI approaches its asymptote (with the minimally damaged having recovered around a decade earlier), and also at the same time as a strong surge in *F. sylvatica* growth. The extremeness of the 1976 BAI response to drought is further demonstrated by the comparison of BAI for the severely damaged *F. sylvatica* to growing season mean SPEI where the 1976 response lies at around the 99·7% normal probability contour for the pre-drought data (see Fig. 6).

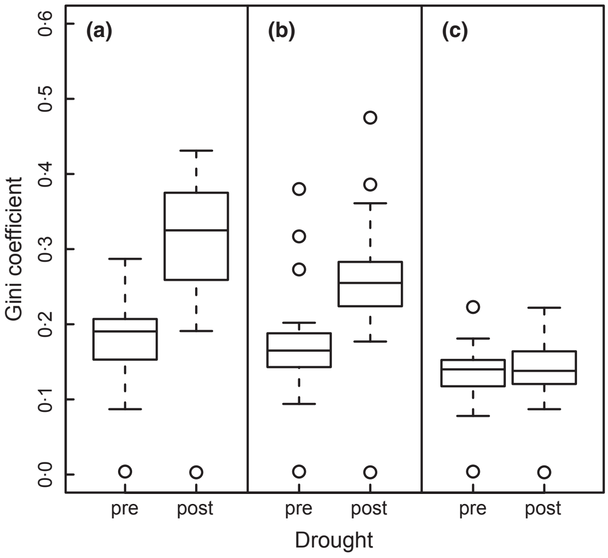

Fig. 3. Gini coefficients for the three tree cohorts, pre (1929–1975)- and post-drought (1976–2009). The 3 cohorts are as follows: (a) severely damaged *F. sylvatica*, (b) minimally damaged *F. sylvatica*, (c) *Q. petraea*.

Discussion

This study highlights key effects of an extreme drought on the subsequent recovery of a mixed species forest; 1) intra- and interspecific variability in the response of the focal species; 2) long-term failure of the dominant species to regain pre-drought growth rates; 3) a divergent response of a normally less competitive co-dominant, with no decrease in long-term growth following an initial competitive

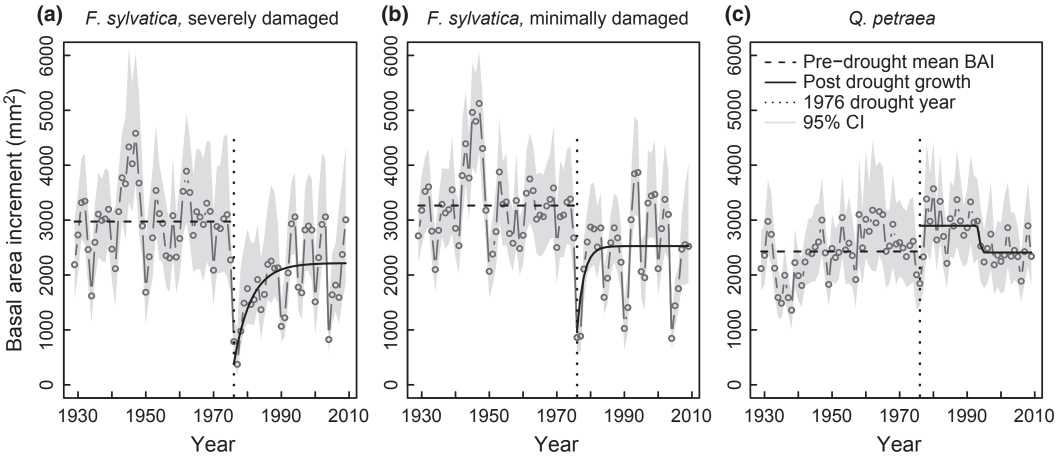

Fig. 4. Mean basal area increment of the three tree cohorts. Yearly values are represented by open circles, with 95% confidence intervals shaded in grey. Mean growth pre-drought (1929–1975) is shown by the dashed lines, and post-drought (1976–2009) growth derived using nonlinear modelling shown using solid lines.

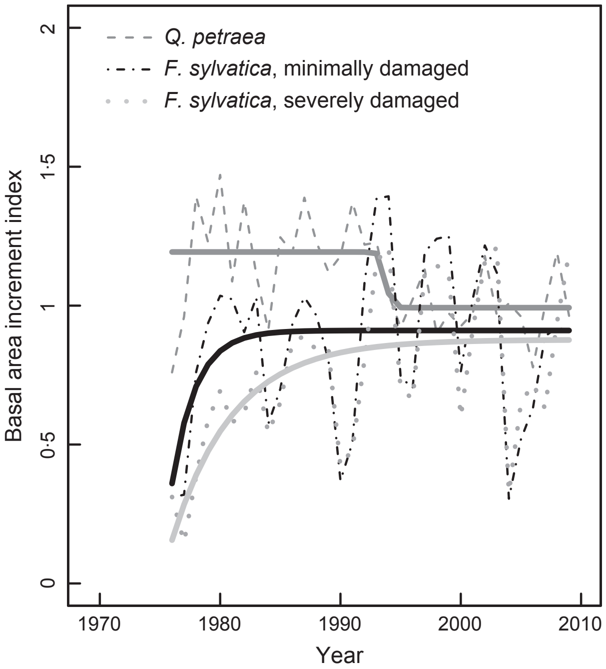

Fig. 5. Basal area increment index for the post-drought period (1976–2009), for the three tree cohorts. Index values were calculated by dividing annual radial growth by the mean value for the pre-drought period (1929–1976). Nonlinear post-drought growth models are shown as solid lines.

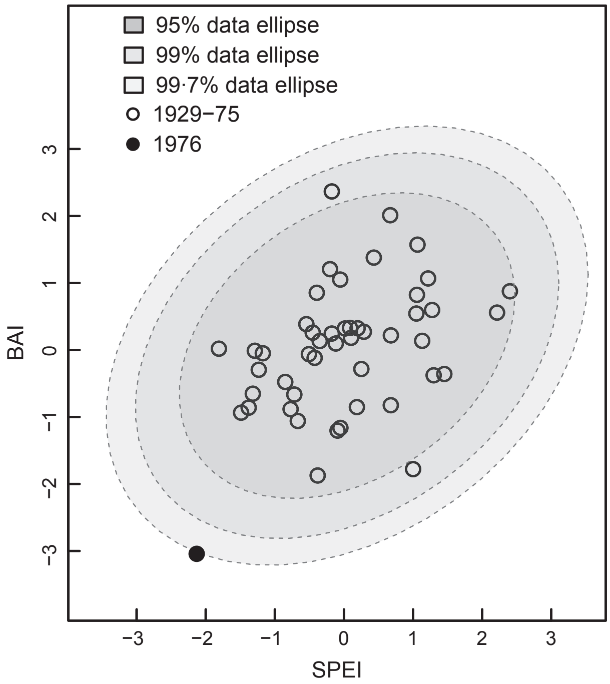

Fig. 6. Comparison of basal area increment to SPEI, for the severely damaged *F. sylvatica* cohort. Annual mean values were converted to z-scores and plotted with normal probability contours added as data ellipses. Open circles represent the years 1929–1975, and the filled circle represents the drought year 1976.

release; 4) a long-term effect on relative abundance, due to differential sensitivity to drought and reduced competition-induced mortality of the two focal species.

In assessing the impact of an extreme climatic event (ECE) as defined by Smith (2011), it is essential that both the climate driver and the ecological response are extreme. The drought investigated here can be considered extreme as a climatic event – it was the most severe drought episode of the period studied, exceeding the 2nd most severe by around 30% in peak intensity. Furthermore, from an ecological perspective, the drought affected *F. sylvatica* through a growth and mortality response unmatched by the prior variation (see Figs 2 and 4). For *Q. petraea*, no such extreme response occurred. Our study relates to the 'hierarchical-response framework' (HRF) conceptual framework for evaluating ecosystem responses to climate events (Smith, Knapp & Collins 2009), by demonstrating that this ecosystem responded to a large-scale resource alteration with a persistent shift in species abundance, described according to the HRF as species reordering. As predicted, the mechanisms specified in the framework have occurred simultaneously, with species reordering occurring alongside responses at the individual species level.

The growth analysis reported here demonstrates substantial intraspecific variation in the response and recovery of *F. sylvatica*. Furthermore, divergent interspecific responses resulted in stepwise changes in competitive interactions in response to extreme drought. For all *F. sylvatica,* radial growth dropped in response to drought, with a prolonged recovery period culminating in stable growth at around 75% of pre-drought levels. It is this failure to recover fully, combined with the differential effect on the species' abundance through mortality, which marks the effect of drought as an ECE. Furthermore, the comparison of normalized BAI with SPEI (Fig. 6) shows that the response to ECE is not simply a linear extension of previous behaviour, but has involved the breach of drought tolerance thresholds.

There is no evidence for pre-conditioning by the ECE for a further extreme response to subsequent droughts, as recovery from subsequent droughts was rapid (Fig. 4). *F. sylvatica* cohorts differed in growth before the drought, with the severely damaged trees having lower growth (low effect size: d = 0·44). This slightly lower growth may have predisposed these trees to greater drought response later, consistent with previous research showing higher drought mortality for poorly growing canopy trees (Peterken & Mountford 1996; Bigler *et al.* 2007; Das *et al.* 2007). Despite the small difference in growth prior to the ECE, the *F. sylvatica* cohorts diverge in response with the most severely damaged cohort taking longer to recover, in addition to greater interannual growth variability. This lagged recovery is a crucial feature of the ECE response at ecosystem level, as is the fact that recovery falls short of pre-ECE radial growth rates (Fig. 5). Intraspecific differences in drought resistance traits have been reported between tree populations (Mitton, Grant & Yoshino 1998;

Kavanagh *et al.* 1999) and shown to be related to genetic variation. The population studied here showed intraspecific variation amongst individuals that were physically intermixed and with only small differences in growth before the ECE. This raises the possibility that this population-level intraspecific response diversity could be related to genotypic differences in susceptibility and merits further investigation.

The ECE impact described above was not universal across both species studied: *Q. petraea* increased its growth rate by approximately 20% in the period immediately following the drought. Climate growth analysis show considerable differences in climate sensitivity between the species (see Fig. S3, Supporting information) and, therefore, drought could be expected to affect *Q. petraea* less, as has previously been shown for these species (Michelot *et al.* 2012). The increase in growth seen post-drought for this species is most likely due to competitive release as a result of drought-induced mortality and canopy damage, potentially acting in combination with reduction in carbohydrate reserves, and drought-induced damage to the root systems of previously dominant *F. sylvatica* individuals (Lloret, Siscart & Dalmases 2004; McDowell 2011). Furthermore, in contrast to the response of *F. sylvatica*, *Q. petraea* did not increase its growth variability post-drought. *Q. petraea* became the more productive species in terms of absolute radial growth immediately following the ECE. However, this effect was transient. In synchrony with the recovery of radial growth to near asymptotic levels for the severely damaged, and with good growth in 1994 for all *F. sylvatica*, a rapid reversal of *Q. petraea* growth back to pre-drought levels occurs (Fig. 5). The timing of this shift in growth is consistent with the resumption of competition-induced mortality for *Q. petraea* (Fig. 2). As the drop to pre-drought growth for *Q. petraea* occurs in synchrony with the delayed recovery of the severely damaged *F. sylvatica*, it suggests a direct consequence of poor resilience of the dominant species on its competitor's growth rate.

Abrupt and nonlinear ecosystem responses have previously been observed for some short-lived organisms, with population size and biomass productivity responding to abrupt changes in climate drivers (Bestelmeyer *et al.* 2011). Here, we demonstrate that the effects of extreme drought can cascade beyond the reduction in growth of a dominant species, resulting in the temporary release from suppression of a co-dominant competitor followed by a nonlinear threshold response upon recovery of the dominant species. These switches in ecosystem state are both sudden, threshold processes and, although stable growth is regained, it is to a lower level than that prior to the ECE for the dominant species (Fig. 5).

Climatic limitations on growth have combined with intraspecific competition to drive the dynamics of this mixed species forest ecosystem. Other recent studies have also shown a greater climate sensitivity of *F. sylvatica* over *Quercus spp.* and a decline in competitiveness of *F. sylvatica* (Scharnweber *et al.* 2011; Bontemps *et al.* 2012). Our study builds on these findings by combining growth modelling and long-term mortality data to demonstrate the lagged pulse of *F. sylvatica* mortality following extreme drought. Consequently, competition-induced mortality relaxes for the competitor species, alongside an increase in growth rate. Differential mortality rates as a result of drought have previously been shown to affect the species composition of forest ecosystems (Mueller *et al.* 2005). Resumption of competition-induced mortality for *Q. petraea* is tied to partial recovery of the dominant *F. sylvatica*, alongside a resumption of pre-ECE growth rates for *Q. petraea*. This adds significant detail to our understanding of the mechanisms at work within mixed species forests as a result of extreme drought stress. We have shown that in this mixed species system, an ECE has been a significant factor in maintaining species diversity, by promoting (at least temporarily) the normally less competitive, though more stress tolerant, species. Such species richness can insure against negative effects of climate change, as the long-term resilience of forest ecosystems is increased when key species display a diversity of response to climate stress (Elmqvist *et al.* 2003; Bodin & Wiman 2007). Regional scale networks of paleo-ecological records have provided evidence that communities can respond rapidly to ECE, with site-specific factors contributing to a temporal mosaic of responses to the climate driver (Williams, Blois & Shuman 2011). Thin, freely draining soils at the study site potentially make this site an early indicator of a drought response which could become more widespread as climate change intensifies. Further work should seek to elucidate the current extent of regional drought response, alongside examination of the thresholds that lead to the extreme response shown here.

Over the long term, the continued presence of a species within a community depends not only on the growth rates of adults and their mortality, but also on reproduction and subsequent establishment (Hurtt & Pacala 1995). In the absence of critical thresholds for rapid species loss being reached, the species composition of forests can be expected to be resilient to change given the longevity of organisms such as trees (Chapin *et al.* 2004). Therefore, the changes that we report here may not herald a sudden shift in community composition as the climate warms, because adult longevity is likely to combine with recruitment in favourable years (Lloret *et al.* 2012). Furthermore, the presence of both intraspecific and interspecific variation in drought susceptibility is likely to significantly buffer against rapid changes at the ecosystem level, ensuring that temperate forest remains, even though the abundance of the dominant species is likely to vary over time in response to climatic variation (Elmqvist *et al.* 2003; Folke *et al.* 2004). Critically, our results demonstrate that responses to extreme climatic events are nonlinear threshold processes that can result in sudden changes in growth and competition within natural populations and that the recovery of the dominant species can itself trigger threshold effects in its competitors.

Acknowledgements

This research was partially funded through the ERA-Net BiodivERsA project Beech Forests for the Future by the UK Natural Environment Research Council (NERC, grant NE/G002118/1). We thank anonymous reviewers for comments on an earlier version of this manuscript. Special thanks go to Andrew Hackett-Pain for assistance with fieldwork, to James Weir for assistance with laboratory work and to Bill Jamieson for assistance with the creation of graphics. We thank Natural England, particularly Terry Claxton, and the Forestry Commission for allowing access to the study site.

References

Adams, H.D., Luce, C.H., Breshears, D.D., Allen, C.D., Weiler, M., Hale, V.C., Smith, A.M.S. & Huxman, T.E. (2012) Ecohydrological consequences of drought- and infestation- triggered tree die-off: insights and hypotheses. *Ecohydrology*, **5**, 145–159.

Allen, R., Smith, M., Perrier, A. & Pereira, L. (1994) An update for the definition of reference evapotraspiration. *ICID Bulletin of the International Commission on Irrigation and Drainage*, **43**, 1–34.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzales, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N.S. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.

Aranda, I., Gil, L. & Pardos, J.A. (2000) Water relations and gas exchange in *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. *Trees*, **14**, 344–352.

Aranda, I., Gil, L. & Pardos, J.A. (2005) Seasonal changes in apparent hydraulic conductance and their implications for water use of European beech (*Fagus sylvatica* L.) and sessile oak [*Quercus petraea* (Matt.) Liebl] in South Europe. *Plant Ecology*, **179**, 155–167.

Bestelmeyer, B.T., Ellison, A.M., Fraser, W.R., Gorman, K.B., Holbrook, S.J., Laney, C.M., Ohman, M.D., Peters, D.P.C., Pillsbury, F.C., Rasswieler, A., Schmitt, R.J. & Sharma, S. (2011) Analysis of abrupt transitions in ecological systems. *Ecosphere*, **2**, 1–26.

Bigler, C. & Bugmann, H. (2003) Growth-dependent tree mortality models based on tree rings. *Canadian Journal of Forest Research*, **33**, 210–221.

Bigler, C., Bräker, O., Bugmann, H., Dobbertin, M. & Rigling, A. (2006) Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems*, **9**, 330–343.

Bigler, C., Gavin, D.G., Gunning, C. & Veblen, T.T. (2007) Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos*, **116**, 1983–1994.

Bilela, S., Dounavi, A., Fussi, B., Konnert, M., Holst, J., Mayer, H., Rennenberg, H. & Simon, J. (2012) Natural regeneration of *Fagus sylvatica* L. adapts with maturation to warmer and drier microclimatic conditions. *Forest Ecology and Management*, **275**, 60–67.

Biondi, F. (1997) Evolutionary and moving response functions in dendroclimatology. *Dendrochronologia*, **15**, 139–150.

Biondi, F. (1999) Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. *Ecological Applications*, **9**, 216–227.

Biondi, F. & Qeadan, F. (2008a) Inequality in paleorecords. *Ecology*, **89**, 1056–1067.

Biondi, F. & Qeadan, F. (2008b) A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research*, **64**, 81–96.

Biondi, F. & Waikul, K. (2004) DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences*, **30**, 303–311.

Birks, H.J.B. (1989) Holocene isochrone maps and patterns of tree-spreading in the British isles. *Journal of Biogeography*, **16**, 503–540.

Bodin, P. & Wiman, B.L.B. (2007) The usefulness of stability concepts in forest management when coping with increasing climate uncertainties. *Forest Ecology and Management*, **242**, 541–552.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D.A. (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, **26**, 183–192.

Bonan, G.B. (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, **320**, 1444–1449.

Bontemps, J.D., Hervé, J.C. & Dhôte, J.F. (2010) Dominant radial and height growth reveal comparable historical variations for common beech in north-eastern France. *Forest Ecology and Management*, **259**, 1455–1463.

Bontemps, J.-D., Herve, J.-C., Duplat, P. & Dhôte, J.-F. (2012) Shifts in the height-related competitiveness of tree species following recent climate warming and implications for tree community composition: the case of common beech and sessile oak as predominant broadleaved species in Europe. *Oikos*, **121**, 1287–1299.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B. & Meyer, C.W. (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 15144–15148.

Broadmeadow, M.S.J., Ray, D. & Samuel, C.J.A. (2005) Climate change and the future for broadleaved tree species in Britain. *Forestry*, **78**, 145–161.

Bunn, A.G. (2008) A dendrochronology program library in R (dplR). *Dendrochronologia*, **26**, 115–124.

Chapin, F.S., Callaghan, T.V., Bergeron, Y., Fukuda, M., Johnstone, J.F., Juday, G. & Zimov, S.A. (2004) Global change and the boreal forest: thresholds, shifting states or gradual change?. *AMBIO: A Journal of the Human Environment*, **33**, 361–365.

Charru, M., Seynave, I., Morneau, F. & Bontemps, J.D. (2010) Recent changes in forest productivity: an analysis of national forest inventory data for common beech (*Fagus sylvatica* L.) in north-eastern France. *Forest Ecology and Management*, **260**, 864–874.

Choler, P., Michalet, R. & Callaway, R.M. (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology*, **82**, 3295–3308.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grunwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T. & Valentini, R. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.

Cohen, J. (1988) *Statistical Power Analysis for the Behavioral Sciences*. Erlbaum, Hillsdale, NJ.

Cook, E.R. & Kairiukstis, L.A. (1990) *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht.

Czucz, B., Galhidy, L. & Matyas, C. (2011) Present and forecasted xeric climatic limits of beech and sessile oak distribution at low altitudes in Central Europe. *Annals of Forest Science*, **68**, 99–108.

Das, A.J., Battles, J.J., Stephenson, N.L. & Van Mantgem, P.J. (2007) The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada. *Canadian Journal of Forest Research*, **37**, 580–597.

Della-Marta, P.M., Haylock, M.R., Luterbacher, J. & Wanner, H. (2007) Doubled length of western European summer heat waves since 1880. *Journal of Geophysical Research-Atmospheres*, **112**, D15103.

Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexier, M.C. & Wisniewski, J. (1994) Carbon pools and flux of global forest ecosystems. *Science*, **263**, 185–190.

Draper, N.R. & Smith, H. (1998) *Applied Regression Analysis*, 3rd edn. Wiley-Blackwell, Chichester.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, **1**, 488–494.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 557–581.

Fritts, H.C. (1976) *Tree Rings and Climate*. Academic Press, London.

Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Muñoz, A., Bailey, J.K. & Whitham, T.G. (2006) Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology*, **20**, 1477–1486.

Gutschick, V.P. & BassiriRad, H. (2003) Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytologist*, **160**, 21–42.

Hein, S. & Dhôte, J.-F. (2006) Effect of species composition, stand density and site index on the basal area increment of oak trees (*Quercus* sp.) in mixed stands with beech (*Fagus sylvatica* L.) in northern France. *Annals of Forest Science*, **63**, 457–467.

Hlasny, T., Barcza, Z., Fabrika, M., Balazs, B., Churkina, G., Pajtik, J., Sedmak, R. & Turcani, M. (2011) Climate change impacts on growth and carbon balance of forests in Central Europe. *Climate Research*, **47**, 219–236.

Hogg, E.H., Brandt, J.P. & Michaelian, M. (2008) Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research*, **38**, 1373–1384.

Holmes, R.L. (1983) Computer assisted quality control in tree ring dating and measurement. *Tree-Ring Bulletin*, **43**, 69–78.

Hurtt, G.C. & Pacala, S.W. (1995) The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, **176**, 1–12.

IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

Jentsch, A., Kreyling, J. & Beierkuhnlein, C. (2007) A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*, **5**, 365–374.

Jump, A.S., Hunt, J.M. & Peñuelas, J. (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163–2174.

Jump, A.S., Hunt, J.M., Martinez-Izquierdo, J.A. & Peñuelas, J. (2006) Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. *Molecular Ecology*, **15**, 3469–3480.

Kavanagh, K.L., Bond, B.J., Aitken, S.N., Gartner, B.L. & Knowe, S. (1999) Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. *Tree Physiology*, **19**, 31–37.

Larsson, L.-A. (2003a) CDendro: Cybis Dendro dating program. Available at http://www.cybis.se.

Larsson, L.-A. (2003b) CooRecorder: image co-ordinate recording program. Available at http://www.cybis.se.

Leuschner, C., Hertel, D., Coners, H. & Büttner, V. (2001) Root competition between beech and oak: a hypothesis. *Oecologia*, **126**, 276–284.

Leuschner, C., Hertel, D., Schmid, I., Koch, O., Muhs, A. & Hölscher, D. (2004) Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. *Plant and Soil*, **258**, 43–56.

Lloret, F., Siscart, D. & Dalmases, C. (2004) Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology*, **10**, 2092–2099.

Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J. & Valladares, F. (2012) Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology*, **18**, 797–805.

von Lüpke, B. (1998) Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. *Forest Ecology and Management*, **106**, 19–26.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. (2009) Widespread increase in tree mortality rates in the western United States. *Science*, **323**, 521–524.

Martínez-Vilalta, J., Lloret, F. & Breshears, D.D. (2011) Drought-induced forest decline: causes, scope and implications. *Biology Letters*, **8**, 689–691.

McDowell, N.G. (2011) Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology*, **155**, 1051–1059.

Meier, I.C. & Leuschner, C. (2008) Genotypic variation and phenotypic plasticity in the drought response of fine roots of European beech. *Tree Physiology*, **28**, 297–209.

Meier, E.S., Edwards, T.C. Jr, Kienast, F., Dobbertin, M. & Zimmermann, N.E. (2011) Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. *Journal of Biogeography*, **38**, 371–382.

Michaelian, M., Hogg, E.H., Hall, R.J. & Arsenault, E. (2010) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*, **17**, 2084–2094.

Michelot, A., Bréda, N., Damesin, C. & Dufrêne, E. (2012) Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *Forest Ecology and Management*, **265**, 161–171.

Mitton, J.B., Grant, M.C. & Yoshino, A.M. (1998) Variation in allozymes and stomatal size in pinyon (*Pinus edulis, Pinaceae*), associated with soil moisture. *American Journal of Botany*, **85**, 1262–1265.

Mueller, R.C., Scudder, C.M., Porter, M.E., Talbot Trotter, R., Gehring, C.A. & Whitham, T.G. (2005) Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology*, **93**, 1085–1093.

Nakagawa, S. & Cuthill, I.C. (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, **82**, 591–605.

Paine, C.E.T., Marthews, T.R., Vogt, D.R., Purves, D., Rees, M., Hector, A. & Turnbull, L.A. (2012) How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. *Methods in Ecology and Evolution*, **3**, 245–256.

Pedersen, B.S. (1998) The role of stress in the mortality if midwestern oaks as indicated by growth prior to death. *Ecology*, **79**, 79–93.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X. & Zhou, X. (2011) A drought induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change*, **1**, 467–471.

Perry, M. & Hollis, D. (2005) The generation of monthly gridded datasets for a range of climatic variables over the UK. *International Journal of Climatology*, **25**, 1041–1054.

Peterken, G.F. & Jones, E.W. (1987) Forty years of Change in Lady Park Wood the old-growth stands. *Journal of Ecology*, **75**, 477–512.

Peterken, G.F. & Jones, E.W. (1989) Forty years of change in Lady Park Wood UK the young-growth stands. *Journal of Ecology*, **77**, 401–429.

Peterken, G.F. & Mountford, E.P. (1996) Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. *Forestry*, **69**, 125–136.

Petit, R.J. & Hampe, A. (2006) Some evolutionary consequences of being a tree. *Annual Review of Ecology Evolution and Systematics*, **37**, 187–214.

Peuke, A.D., Schraml, C., Hartung, W. & Rennenberg, H. (2002) Identification of drought-sensitive ecotypes by physiological parameters. *New Phytologist*, **154**, 373–387.

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. *Global Change Biology*, **14**, 1265–1281.

R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-900007-900050, URL http://www.R-project.org.

Robson, T.M., Sanchez-Gomez, D., Cano, F.J. & Aranda, I. (2012) Variation in functional leaf traits among beech provenances during a Spanish summer reflects the differences in their origin. *Tree Genetics & Genomes*, **8**, 1111–1121.

Rose, L., Leuschner, C., Kockermann, B. & Buschmann, H. (2009) Are marginal beech (*F. sylvatica* L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research*, **128**, 335–343.

Schar, C., Vidale, P.L., Luthi, D., Frei, C., Haberli, C., Liniger, M.A. & Appenzeller, C. (2004) The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–336.

Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schroder, C. & Wilmking, M. (2011) Drought matters - Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *Forest Ecology and Management*, **262**, 947–961.

Scheffer, M. & Carpenter, S.R. (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution*, **18**, 648–656.

Sheffield, J., Wood, E.F. & Roderick, M.L. (2012) Little change in global drought over the past 60 years. *Nature*, **491**, 435–438.

Smith, M.D. (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *Journal of Ecology*, **99**, 656–663.

Smith, M.D., Knapp, A.K. & Collins, S.L. (2009) A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, **90**, 3279–3289.

Soja, A.J., Tchebakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., Chapin , F.S.III & Stackhouse, P.W. Jr (2007) Climate-induced boreal forest change: predictions versus current observations. *Global and Planetary Change*, **56**, 274–296.

Terradas, J., Peñuelas, J. & Lloret, F. (2009) The fluctuation niche in plants. *International Journal of Ecology*, **2009**, doi: 10.1155/2009/959702.

Thibault, K.M. & Brown, J.H. (2008) Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences*, **105**, 3410–3415.

Thornthwaite, C.W. (1948) An approach toward a rational classification of climate. *Geographical Review*, **38**, 55–94.

Vicente-Serrano, S.M., Beguería, S. & López-Moreno, J.I. (2010) A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of Climate*, **23**, 1696–1718.

Vicente-Serrano, S., López-Moreno, J., Drumond, A., Gimeno, L., Nieto, R., Morán-Tejeda, E., Lorenzo-Lacruz, J., Beguería, S. & Zabalza, J. (2011) Effects of warming processes on droughts and water resources in the NW Iberian Peninsula (1930–2006). *Climate Research*, **48**, 203–212.

Wigley, T.M.L., Briffa, K.R. & Jones, P.D. (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, **23**, 201–213.

Williams, J.W., Blois, J.L. & Shuman, B.N. (2011) Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. *Journal of Ecology*, **99**, 664–677.

Zang, C. & Biondi, F. (2012) Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. *Dendrochronologi*, **31**, 68–74.

Zhao, M. & Running, S.W. (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science*, **329**, 940–943.

Received 22 November 2012; accepted 1 May 2013
Handling Editor: David Whitehead

Supporting Information

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

Fig. S1. Location of the study site in relation to the geographical range of *F. sylvatica* within the British Isles.

Fig. S2. Temperature and precipitation for the study site, using 5 km2 gridded climate data for the period 1914–2006 (Perry & Hollis 2005).

Fig. S3. Climate growth analysis for the three cohorts of trees, showing the relationship between annual radial growth and climate factors in the previous and current year over the period 1914–2006.

Fig. S4. Detrended ring width indices for the three cohorts of trees, with 99% bootstrapped confidence intervals (using 1000 bootstrap replicates).