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; Caïs 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
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, Penuelas & 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 & Penuelas 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), Tilia cordata and T. platyphyllos (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 altered 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 km² 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, Begeuria & 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 weighted 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 km² 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 CocoRecorder 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 for each tree using the 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...
BAI, basal area increment; $r$, 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 can-

Table 1. Descriptive statistics for the tree-ring chronologies

<table>
<thead>
<tr>
<th>Tree species</th>
<th>No. of trees</th>
<th>No. of cores</th>
<th>Mean series length (years)</th>
<th>Series duration</th>
<th>Mean BAI (mm²)</th>
<th>Mean Sensitivity $r$</th>
<th>EPS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fagus sylvatica</td>
<td>31</td>
<td>62</td>
<td>109.6</td>
<td>1929–1975</td>
<td>2973 ± 92</td>
<td>0.24</td>
<td>0.41</td>
</tr>
<tr>
<td>(severely drought damaged)</td>
<td>32</td>
<td>68</td>
<td>111.8</td>
<td>1976–2009</td>
<td>1902 ± 128</td>
<td>0.39</td>
<td>0.34</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>32</td>
<td>68</td>
<td>111.8</td>
<td>1832–2010</td>
<td>2905 ± 95</td>
<td>0.32</td>
<td>0.42</td>
</tr>
<tr>
<td>(minimally drought damaged)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pre-drought subset</td>
<td>1929–1975</td>
<td>3265 ± 97</td>
<td>0.22</td>
<td>0.49</td>
<td>0.97</td>
<td></td>
<td></td>
</tr>
<tr>
<td>post-drought subset</td>
<td>1976–2009</td>
<td>2407 ± 152</td>
<td>0.35</td>
<td>0.43</td>
<td>0.96</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quercus petraea</td>
<td>30</td>
<td>58</td>
<td>174.6</td>
<td>1770–2009</td>
<td>2530 ± 51</td>
<td>0.23</td>
<td>0.45</td>
</tr>
<tr>
<td>pre-drought subset</td>
<td>1929–1975</td>
<td>2428 ± 66</td>
<td>0.22</td>
<td>0.43</td>
<td>0.96</td>
<td></td>
<td></td>
</tr>
<tr>
<td>post-drought subset</td>
<td>1976–2009</td>
<td>2671 ± 80</td>
<td>0.21</td>
<td>0.38</td>
<td>0.95</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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 crite-

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

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.

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.

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: Temperature = 1073 + 1.096(year + (2.824 × 10⁻⁴) year²), (R² adj = 0.302, P < 0.001). 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 (R² = 0.10, P < 0.001), 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.

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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 (R² adj = 0.14, P < 0.001), SPI = (R² adj = 0.07, P < 0.001), Difference = 7.6–0.004 time (R² adj = 0.20, P < 0.001).

representing a prolonged period of moisture deficit. The long-term trend for SPEI is for increasing drought (SPEI ($t$) = 26.99–0.138$t$, where $t$ = time, $R^2$ = 0.14, $P < 0.001$) and also increasing, but more weakly, for SPI (SPI ($t$) = 19.34–0.099$t$, $R^2$ = 0.07, $P < 0.001$). 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 ($t$) = 7.65–0.004$t$, $R^2$ = 0.20, $P < 0.001$).

**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 $r$ (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* ($t$ = 8.67, $df$ = 50.77, $P < 0.0001$) with a large effect size ($d$ = 2.17, 95% CI 1.54/2.80), and also increased for the minimally damaged *F. sylvatica* ($t$ = 6.50, $df$ = 53.13, $P < 0.0001$) 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, $P$ = 0.059; 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, $P$ = 0.003; medium effect size: $d$ = 0.74, 95% CI 0.22/1.24). $G$ did not change in *Q. petraea* following the drought ($t$ = 0.23, $df$ = 56.96, $P$ = 0.82).

**BASEL 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 ($t$ = 3.278, $P$ = 0.0015) 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
growth of 2973 ± 92 mm² fell to a minimum value of 374 mm² in 1977 (12.6% of pre-drought mean growth). Non-linear growth modelling shows a recovery to an asymptotic level of 2218 ± 152 mm² after the drought (BAI(x) = d(1 - exp(−ζ)), where d = 2218, P < 0.001 and ζ = 5.10, P = 0.004). In comparison, for the minimally damaged F. sylvatica, pre-drought annual mean BAI of 3265 ± 97 mm² fell to a minimum value of 862 ± 2 mm² (26.4% of pre-drought mean growth) and recovered to 2527 ± 145 mm² (d = 2527, P < 0.001 and ζ = 1.99, P = 0.020). The higher parameter ‘ζ’ 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 mm² fell to a minimum value of 1845 mm² (76.0% of pre-drought mean growth), increasing immediately after the drought to 2897 ± 90 mm². The initial increase in BAI underwent a further rapid reduction to 2410 ± 98 mm² around an inflection point in 1994 (BAI(x) = c + (d - c)/((1 + exp(−ζ)) − (log(ζ)))/ζ), where b = −86.07 (P = 0.63), c = 2897.1 (P < 0.001), d = 2410.3 (P < 0.001) and ζ = 2.93 (P < 0.001). 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).

**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

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**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.

**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 non-linear modelling shown using solid lines.
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 (Peterson & 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 insulate 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 National Environment Research Council (NERC, grant NE-G002118). 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


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).