**Title: Stand dieback and collapse in a temperate forest and its impact on forest structure and biodiversity**

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**Abstract**

Concern is increasing about large-scale dieback that is occurring in many forest ecosystems, as a result of novel pressures such as climate change and its interactive effects on drought and the spread of novel pathogens and invertebrate species. However, understanding of the processes of forest dieback and its potential impacts is limited, partly owing to the lack of long-term monitoring data for forest stands in which dieback has occurred. Here we present monitoring data collected for 50 years along two transects in a temperate forest ecosystem, in which the canopy dominant beech (*Fagus sylvatica* L.) has demonstrated significant dieback. Results highlighted that a decline in both basal area (BA) and stem density in individual subplots frequently displayed non-linear trajectories, although the overall pattern of decline of both was best described by linear models. We hypothesise that this high mortality may be due to the interactive effects of on-going climate change and novel pathogenic fungi. Curvilinear responses to BA loss were observed in tree community change; in species richness of the ground flora; and in the percentage cover of grass, providing evidence of thresholds associated with stand dieback. Evidence also suggested that the ability of BA to recover following decline demonstrated a threshold response; where BA declined by more than 25%, it tended not to recover. Critical values of BA for a change in ground flora species richness and grass cover were around 40% decline from initial values. These thresholds are considered in relation to the concept of regime shifts in forest ecosystems, and the potential implications for forest management and conservation are explored. While managers might consider accepting forest dieback as part of an adaptive response of the system to novel environmental conditions, this would likely be associated with significant change in biodiversity.

**Introduction**

There is growing concern that on-going climate change may result in large-scale forest dieback as a result of increased drought and heat stress. Such impacts have now been recorded in all wooded continents across a wide range of different climates (Allen et al., 2010; Scholes et al., 2014). Examples of this include increases in tree mortality over the past 50 years in the western USA and boreal Canada, apparently as a result of regional warming and water deficit (Peng et al., 2011; van Mantgem et al., 2009) leading to alteration of forest community composition (Mcintyre et al., 2014) and reductions in carbon storage (Ma et al., 2012). Similarly, changing climatic conditions have allowed spread of bark and pine beetles, resulting in epidemics in the previously unaffected areas of the western USA and Canada (Kurz et al., 2008; Raffa et al., 2008).Though invertebrate herbivores play an important role in ecosystem functioning, when these species’s ranges expand beyond their native range this can result in widespread damage. Drought may also interact with damage caused by invertebrates to cause large-scale tree mortality, as in the southwestern USA when the combination of drought and bark beetle infestation lead to death of 90% of trees in some forests (Breshears et al., 2005). Major diseases have also recently caused extensive tree mortality, including pine wilt in Asia, Dutch elm disease in Europe and North America, ash dieback in Europe (Pautasso et al., 2013) and *Phytophthora* spp. in Australia (Boyd et al., 2013). It is likely that the rate of spread of these diseases will increase with greater globalisation and climatic change (Boyd et al., 2013).

Despite such trends, the ecological implications of dieback or collapse of forest ecosystems are poorly understood. A recent IPCC assessment noted that increased tree mortality and associated forest dieback is projected to occur in many regions over the 21st century, and that this is likely to pose risks for carbon storage, biodiversity, wood production, amenity and economic activity (Scholes et al., 2014). However, the magnitude of such risks has not been evaluated in detail (Bellassen and Luyssaert, 2014; Boyd et al., 2013). The long-term impacts of dieback will depend critically on the ability of forest ecosystems to recover from disturbance. Of particular concern are rapid transitions or “regime shifts”, which have been documented in a number of different ecosystem types following major disturbance events (Scheffer and Carpenter, 2003; Scheffer et al., 2001, 2012).

Regime shifts are thought to occur when the controlling variables in a system (including feedbacks) result in the alteration of the system structure and dynamics (Walker et al., 2004). A number of studies have provided evidence of regime shifts that have occurred in forest ecosystems, such as the impact of spruce budworm on boreal forests in North America (Holling, 1978) and transitions from forest to savannah as a result of changes in fire regimes (Hirota et al., 2011; Staver et al., 2011). Once a regime shift has occurred, because an ecological threshold has been crossed, recovery to the original ecosystem state may be difficult (Petraitis, 2013). While the underlying theory of regime shifts or abrupt transitions is well established (Bestelmeyer et al., 2011; Scheffer and Carpenter, 2003; Scheffer et al., 2001, 2012), their existence in forest ecosystems remains the subject of debate, reflecting the lack of robust evidence (Petraitis, 2013). Theories relating to regime shifts and thresholds in ecosystems suggest that declines are likely to be non-linear, and may be characterised by feedbacks between different pressures (Scheffer et al., 2001, 2012). Understanding the pattern of such responses is of critical importance to ecosystem resilience which is increasingly being incorporated into environmental policy, and are consequently becoming the explicit focus of forest management (Newton and Cantarello, 2015). From a management and policy perspective, there is also a need to understand the conditions under which ecological thresholds are likely to be crossed, which ecosystems are particularly at risk, and the potential consequences both for biodiversity and the associated provision of ecosystem services (Groffman et al., 2006).

Key questions connected to forest dieback or collapse relate to the trajectory of decline in forest structure and its potential relationship with forest biodiversity, to determine whether such relationships are characterised by threshold responses, and whether regime shifts have occurred (Groffman et al., 2006; Thrush et al., 2009). Theories relating to regime shifts and thresholds in ecosystems suggest that declines are likely to be non-linear, and may be characterised by feedbacks between different pressures (Scheffer et al., 2001, 2012). Understanding the pattern of such responses is of critical importance to concepts such as ecosystem resilience and resistance, which are increasingly being incorporated into environmental policy, and are consequently becoming the explicit focus of forest management (Newton and Cantarello, 2015). From a management and policy perspective, there is also a need to understand the conditions under which ecological thresholds are likely to be crossed, which ecosystems are particularly at risk, and the potential consequences both for biodiversity and the associated provision of ecosystem services (Groffman et al., 2006).

Here we examine a long-term data set, collected in a temperate forest ecosystem that has undergone partial stand dieback in recent decades. In this location in southern England, monitoring data have been collected repeatedly over a period of 50 years. Changes from 1964-2001 were presented by Mountford et al. (1999) and Mountford and Peterken (2003), who revealed that major tree mortality had occurred since measurements were initiated, resulting in localised stand collapse and apparent transition to communities dominated by grass or bracken-. This mortality appears to be associated with a regional-scale decline in beech health, potentially associated with climate change (Newton, 2011; Power et al., 1995). Here we build on these data through an additional survey undertaken in 2014, and for the first time explore the entire data set from the perspective of analysing ecosystem thresholds and regime shifts. Specifically, in this paper we aim to: (1) describe the pattern of stand dieback in the woodland over the past five decades, (2) identify the ecological processes that might be driving the changes, (3) identify the consequences of these changes for forest structure and plant biodiversity.

**Methods**

**Site history and characteristics**

The site used in this study, Denny Wood, is located in the New Forest National Park in Southern England (Lat: 50o 51.5’ N and 1o 32.5’ W). It has a temperate oceanic climate: mean annual precipitation between 1957 and 2014 ± SD at the Hurn weather monitoring station approximately 23km from Denny Wood was 832 ± 150mm and mean annual temperature was 10.17 ± 0.64°C (www.metoffice.gov.uk/public/weather/climate-historic/ - accessed 16/04/2015).

Detailed site descriptions are provided Mountford et al. (1999) and Mountford and Peterken (2003) and are briefly summarized here. The site is situated on gentle slopes (1–3°), primarily on clay-rich brown earth soils (pH 4.5–5.0 at 10 cm depth) that are prone to winter waterlogging and summer drying, with localised areas of strongly acid (pH 3.5–4.5) podsols developed on sandier substrates. Woodland vegetation is dominated by beech (*Fagus sylvatica*)withfrequent pedunculate oak (*Quercus robur*) and occasional birch (*Betula pendula, B. pubescens*), and an understorey primarily composed of holly (*Ilex aquifolium*). In open areas, the ground vegetation is mostly comprised of *Agrostis*-dominated grassland or stands of bracken (*Pteridium aquilinum*); *Rubus fruticosus* agg., *Juncus effusus* and *Molinia caerulea* are also locally abundant.

The New Forest is characterised by high herbivore pressure owing to large populations of deer and free-roaming livestock (principally ponies and cattle), as a result of its long-term maintenance of a traditional commoning system (Newton, 2011; Newton et al., 2013). Although the area surveyed here has largely been untouched by silvicultural treatment, since 1870 it has been divided into two portions, one of which (Denny Inclosure) was enclosed by fencing to exclude livestock, but not deer. Although browsing pressure was higher in the unenclosed part of the site during the early 20th century, since the 1960s browsing pressure has increased in both areas, though with different main herbivores: ponies and deer in the unenclosed part; and deer in Denny Inclosure (Mountford and Peterken 2003).

**Data collection**

Measurements were conducted in two 20 m-wide transects, which were originally established in the 1950s. The first of these was established in Denny Inclosure and was 1 km in length, whereas a shorter transect of 320 m length was established in the unenclosed part of Denny Wood. The transects were subdivided into contiguous 20 x 20 m (0.04 ha) subplots, with the longer transect containing 46 subplots and the shorter transect 15. The enclosed transect was surveyed in 1964, 1984, 1988, 1996 and 2014, while the unenclosed transect was surveyed in 1964, 1999 and 2014. Details of earlier measurements are presented by Mountford et al. (1999) and Mountford and Peterken (2003); data for 2014 are presented here for the first time.

In each survey, the location and species of all tree stems >1.3 m in height were recorded, their diameter at breast height (DBH) measured using diameter tapes, and their status assessed as alive, alive but fallen, or dead. Trees with DBH <10 cm were classified as saplings and those with a DBH >10 cm classified as mature trees. Multi-stemmed trees were treated as separate individuals. To assess ground flora a 10 x 10 m plot was located in the central part of each 20 x 20 m subplot and the percentage cover of each plant species assessed visually. Ground flora data were recorded in 1964, 2001 and 2014 for Denny Inclosure and 2014 for the unenclosed transect. In 2014 tree seedling abundance was also recorded for Denny Inclosure within the same 10 x 10 m plots used to assess ground flora.

**Analyses**

Basal area (BA) for all tree species ≥10 cm DBH was calculated for each subplot following Cantarello and Newton (2008) using the formula:

The percentage change in basal area for all species since 1964 for each subplot was calculated using the formula:

where represents the BA of a subplot in 1964 and represents the BA of a subplot in any of the subsequent survey years. Using these data, at each survey date we classified subplots into groups according to whether basal area had either remained stable or increased, or whether it had declined, defining a decline as a ≥25% reduction in BA since 1964. For some analyses subplots were also divided into five groups on the basis of the degree of BA decline, namely (i) Increasing, or (ii) 0-25%, (iii) 25-50%, (iv) 50-75% or (v) 75-100% loss of BA compared to the 1964 value. These groups were used for plotting of maps to show the spatial distribution of BA losses.

To examine temporal changes in plant biodiversity we calculated the species richness of subplots for both ground flora and for tree species as well as metrics of community composition change. The quantitative Sørensen similarity Index is commonly used to assess change in community composition but its use to assess changes in tree communities is problematic. This is because when calculated using stem density as a measure of abundance the Index treats differently sized trees as equal, but when it is calculated using BA, differences in stem density are ignored. We therefore assessed tree community change using the Tanner Index, which is calculated as the mean of the quantitative Sørensen indices using basal area and stem density as defined by Chai et al. (2012) and using the equation:

where and are the total BA and stem density for each tree species present in plot in 1964 and and are the same measurements in plot for year. Thus the Tanner Index overcomes the limitations of the quantitative Sørensen Index by accounting for both stem density and BA (Chai et al., 2012).

Where response variables represented a proportion, such as percentage cover or the Tanner Index, we undertook the following transformation:

where is an individual variable value for plot for year and is the maximum value of the variable in the dataset. This transformation constrains model predictions between 1 and 0 as well as reducing the heteroschedasticity that is common when proportional data is incorrectly analysed (Warton and Hui, 2011). As recommended by Warton and Hui (2011), a small non-zero constant was added to all values so that logit transformed variables did not equal minus infinity.

Two approaches were adopted in our analysis of stand collapse. First, we divided the dataset into subplots that had collapsed (defined as ≥25% BA loss) at some point between 1964 and 2014 and those that had not, to examine the differences in changes in BA, stem density of saplings and trees >10 cm DBH, proportions of subplot BA represented by oak, and grass cover for the two groups in between 1964 and 2014. For stem density and grass cover we fitted linear mixed models with an interaction between year and collapse status (i.e. collapsed or not). Since stem density constitutes a count, Poisson generalised linear mixed models were used to satisfy model assumptions. For analyses of BA and stem density time was considered as a continuous variable since we were interested in the general trajectories of subplots. However for analyses of changes of stem density of different size classes and grass cover it was considered as categorical because we were primarily concerned with whether subplots had changed between 1964 and 2014. In addition there were only three ground flora surveys limiting the usefulness of regression.

In our second set of analyses, we examined variation over a gradient of change in the basal area. The relationships between the collapse gradient and species richness, ground flora Sørensen similarity, tree community Tanner similarity and community weighted trait values were each assessed using linear mixed models. For each of these models, linear, squared and cubed terms describing the shape of the relationship with the collapse gradient were tested to identify any potential non-linearity. For assessments of grass cover, ground flora richness and community composition because one ground flora survey was undertaken in 2001 when no surveys of the tree community were undertaken values of BA from the 1996/9 surveys were used to estimate the gradient.

In both sets of analyses we used linear mixed models with subplot number as a random effect to account for repeated measures of the same subplots over time. Where the response variable constituted a count variable we used Poisson generalised linear mixed models to satisfy model assumptions. All analyses were performed in R 3.1.2 (R Development Core Team, 2011) with mixed models produced using the lme4 package (Bates et al., 2014) and figures produced using ggplot2 (Wickham, 2009). Model selection followed an information theoretic approach, with models ranked by AICc to determine parsimony (Burnham and Anderson, 2002). Where only one model had a ΔAICc≤7 this was selected as the best model since this indicates little support for alternative models (Burnham et al., 2011). Where there was more than one model with a ΔAICc≤7, model averaging was undertaken with AICc weights used to calculate coefficients and associated standard error and P values using the MuMIn package (Barton, 2014). R2 values for mixed models were calculated following Nakagawa and Schielzeth (2013) and Johnson (2014) using the R package MuMIn.

In addition to formal statistical analyses we produced summaries of subplot recovery by dividing subplots into groups based on their initial decline in BA. Following this we determined the number of subplots of each group that had increased or further declined in BA following this initial decline and calculated the mean percentage change in BA by 2014 for these groups. This allowed us to identify whether subplots tended to recover following a decline in BA and whether there was a threshold loss of BA below which recovery was unlikely.

To examine the spatial pattern of change in BA we produced maps showing the percentage BA decline of each subplot relative to 1964. To determine whether there was evidence of spatial autocorrelation in the severity of stand collapse Moran’s I correlation was calculated for pairwise comparisons of BA change between unenclosed and enclosed subplots separately using the R package ncf (Bjornstad, 2013). 1000 bootstrapped iterations were used to generate median values and 95% confidence intervals of Moran’s I values at lag distances of 20-1000 m, the minimum and maximum distance between subplots in the same transect. Where confidence intervals of the Moran’s I statistic overlapped zero, spatial autocorrelation was deemed to not be statistically significant.

We hypothesised that changes in the forest may be partly driven by mortality as a result of climate change over the past 50 years. To test this we used data on temperature and precipitation from the closest weather station, Hurn (www.metoffice.gov.uk/public/weather/climate-historic/ - accessed 16/04/2015). We used a subset of this data for the months April-September from 1960-2013. These months approximate the growing season for beech and oak and thus any climate anomalies during this period are likely to affect growth and mortality. We cannot link climatic change directly to mortality with our dataset since the resolution of data is not high enough and mortality caused by drought can occur many years after the event. As such we examined the temporal trends in mean growing season temperature and total rainfall using regression. In addition, we examined the occurance of precipitation and temperature anomalies, by calculating the mean and standard deviation of growing season temperature and plotting deviations of from this mean.

**Results**

**Pattern of collapse**

Subplots showed a median decline in BA of 33% from 1964-2014(Figure 1a). However, there were large variations in subplot changes in BA with some plots experiencing near 100% loss of BA and others increasing by >50% (Figure 1a). Declines in BA occurred in every survey period from 1964 to 2014. Between 1964 and 1984, 19 subplots declined in BA, between 1984 and 1988, 31 subplots declined in BA, and between 1996/9 and 2014, 13 subplots declined in BA. Of the subplots in the unenclosed transect 87% (14 out of 15) demonstrated BA loss over the entire survey period, while on the enclosed transect 48% (22 out of 46) showed declines.

Subplot stem density changes were best described by a regression model that included an interaction between survey year and whether subplots had collapsed at any point (Table S1). This model showed good fit (marginal R2=0.37); no other model had a ΔAICc ≤7 (Table S1). Subplots that collapsed and those that did not differ in their stem densities in 1964 (P=0.91), whereas both showed declines in stem density from 1964-2014. However, collapsed plots showed a more rapid decline in stem density than stable plots (slope=-0.029, SE=0.003, P<0.001, Figure 1b Table S2).

Similarly, the most parsimonious model for describing subplot density of trees >45 cm DBH included an interaction term between year and collapse status (Table S3). Density of trees >45 cm DBH subplots that subsequently collapsed and those that did not did not differ in 1964(P=0.057), but by 2014 collapsed plots had significantly lower stem densities (P<0.001). Mean (± SE) stem density of trees >45 cm DBH increased for stable plots from 68.75 (± 28.50) stems ha-1 in 1964 to 93.75 (± 29.50) in 2014 (P<0.001, Figure S1a, Table S4). Over the same time period the mean density of trees >45 cm DBH decreased in collapsed subplots from 84.5 (± 29.25) in 1964 to 37.75 (±31.25) trees ha-1 (P<0.001, Figure S1a,Table S4).

Trees with a DBH of 25-45 cm did not decrease in density for either stable (P=0.599) or collapsed plots (P=0.835). However, subplots that subsequently collapsed had a lower density of trees with a DBH of 25-45 cm in 1964 than did those that remained stable (P<0.001, Figure S1b, Table S6). Similarly, the density of trees with DBH of 15-25 cm was lower in subplots that subsequently collapsed in 1964 than those that remained stable (P<0.001, Figure S1c, Table S8), but there was no reduction in density by 2014 for collapsed or stable plots (P=0.426). Mean density of trees with a DBH of 10-15 cm declined between 1964 and 2014 for both collapsed and stable plots (P<0.001, Figure S1d, Table S10), but there were no significant differences between the two plot types in either 1964 (P=0.920) or 2014 (p=0.429).

Mean sapling density decreased for both collapsed and stable subplots between 1964 and 2014 (P<0.001, Figure S2, Tables S12 and S13), declining from 291 (± 28.75) to 70 (± 27.50) stems ha-1 in stable plots and from 321.25 (± 29.5) to 69.25 (± 26.75) stems ha-1 in collapsed plots. However there was no statistically significant difference between collapsed and stable plots in 1964 (P=0.289) or 2014 (P=0.620). Subplots that collapsed had a higher density of beech seedlings (139.4 ± 1.2 seedlings ha-1) when compared to stable subplots (77.78 ± 1.1 seedlings ha-1, P<0.001). Similarly holly seedlings were more abundant in collapsed subplots (3451.52 ± 18.39 seedlings ha-1) than in stable subplots (1903.70 ± 8.42 seedlings ha-1, P<0.001). However, oak seedling densities were higher in stable than in collapsed subplots (122.22 ± 2.15 and 96.97 ± 2.44 seedlings ha-1 respectively, P<0.001).

Visual inspection of a map of the subplots (Figure 3) suggested that collapse was first observed in 1984 in 19 subplots, and this then spread throughout both transects. By the 1996/9 surveys all but one of the unenclosed transect plots had suffered collapse (Figure 3d). Although subplots that were situated adjacent to collapsed plots appeared more likely to collapse, Moran’s I spatial correlograms indicated that spatial autocorrelation was not statistically significant at any pairwise distance between subplots that we examined (Figure S3).

**Causes of dieback**

The decline in BA for all subplots was 16.73 m2 ha-1, with 61% of this attributable to losses of beech BA and 34% to loss of oak BA. The combined mortality of beech and oak trees >45 cm in DBH was responsible for the majority of these declines, constituting 61% and 30% of total BA losses respectively. For other size classes, only oak 25-45 cm DBH contributed more than 5% of the declines in total BA loss.

We hypothesised that the loss of large trees in the woodland was partly due to changes in climate over the period 1964-2014. Growing season temperature increased from the 1960’s to 2014 at a rate of 0.02 ± 0.004°C year-1 (R2=0.28). However, precipitation showed no change over the period.

**Consequences of dieback**

In plots where BA declined by ≥ 25% it tended not to recover. While many subplots increased in BA following an initial loss, only in those that had initial declines of <25% did BA recover to values exhibited in 1964, with 43% of these subplots (3 of 7) achieving this degree of recovery by 2014. However, even for subplots that declined by < 25% of initial BA, the majority (4 of 7 subplots) failed to recover to BA values evident in 1964; in 2014, mean BA of these subplots was 11.8% (± 6.06) lower in 1964. While some subplots that showed initial losses of BA >25% also increased in BA following initial loss, 66% of subplots actually lost further BA by 2014.

Tree species richness showed a negative relationship with loss of BA (slope=-0.284 ± 0.108 SE, P=0.009, Table S14) but the most parsimonious models had very poor explanatory power (marginal R2=0.03-0.04, Table S13). Turnover in tree communities, as indicated by the Tanner Index, was strongly related to loss of BA (Figure 4). This relationship was best predicted by a model including both a linear and squared term for percentage basal area loss (R2=0.39, AICc=330.93), which provided a better fit than models of linear relationships (AICc= 406.00) or a null model (AICc=510.44, Table S15). The best model suggested a curvilinear response in tree community change with loss of BA, with losses of BA associated with large changes in community structure (Figure 4). Changes in tree community weighted Ellenberg values for light, nitrogen and moisture requirements showed little discernible trend with the decline in basal area, and in each case a null model was considered most parsimonious.

Changes in subplot grass cover were best described by a model with an interaction term between year and whether subplots collapsed during 1964-2014 (marginal R2=0.44, Table S17). In 1964, grass cover did not differ between subplots that subsequently collapsed and those that did not (P=0.64, Figure 5, Table S18), but by 1996 collapsed subplots showed four-fold higher grass cover (Stable: 5.2% (± 3.5), Collapsed: 22.8% (± 8.8), P=0.009). This difference had increased by 2014 (Stable: 3.8% (± 2.7), Collapsed: 26.7% (± 9.4), P<0.001, Figure 5). Changes in grass cover in subplots were strongly related to loss of BA, showing a non-linear relationship (Figure 6a). Model predictions suggested relatively little change in grass cover in subplots that increased in BA or showed losses <25%, while subplots that lost ≥25% of BA showed a rapid increase in grass cover with increasing loss of BA (Figure 6a). In contrast to grass, bracken (*Pteridium aquilinum)* cover showed no significant relationship with loss of subplot BA with a null model the most well supported (Tables S19 and S20, Figure S4).

Ground flora richness showed a positive non-linear relationship with BA loss (Tables S21 and S22). Model averaged predictions suggested little difference in ground flora richness for subplots that showed <40% loss of BA, with an increase in species richness for subplots with greater declines in BA (Figure 6b). Loss of basal area did not describe changes ground flora community composition well, with a null model best supported.

Community weighted Ellenberg values for ground flora light requirements increased with increasing loss of BA (P=0.030, Table S24), though the top ranked models showed relatively poor fit (marginal R2 = 0.10, Table S23). Neither community weighted Ellenburg values for nitrogen nor moisture requirements showed any significant trend with the gradient of BA loss and all models showed poor descriptive power with marginal R2<0.04 (Tables S25 and S26).

**Discussion**

Our study provides a number of insights into the changes that occurred in a temperate forest ecosystem undergoing stand dieback over several decades. This process of dieback largely resulted from death of large (>45 cm DBH) beech and oak trees. This was accompanied by a marked decline in density of saplings and small trees (10-15 cm DBH). As transects were surveyed at approximately decadal intervals it was difficult to identify precisely when mortality events occurred, but our results indicate that dieback occurred throughout the survey period, and importantly continued during the past decade. After a period of 50 years, some of the changes were very pronounced. Some areas of closed forest areas that were dominated by beech in 1964 became relatively open grassland with low tree density by 2014. This represents a substantial transition, both in terms of forest structure and composition.

**Possible causes of die-back**

Large beech trees have experienced high mortality rates in the New Forest in recent decades, although the precise causes remain uncertain (Newton, 2010; Tubbs, 2001). The principal cause of large beech mortality in Denny wood and the wider New Forest has previously been attributed to a major drought in 1976 (Manners and Edwards, 1986; Mountford and Peterken, 2003; Mountford et al., 1999). The same drought killed many large beech trees in Lady Park Wood in the west of the UK, and drought induced mortality continued for at least 15 years after the event (Peterken and Mountford, 1996).

Additional mortality in Denny Wood has been attributed to significant storms in 1987 and 1990, and in the case of smaller stemmed trees to debarking by grey squirrels (Mountford and Peterken, 2003; Mountford et al., 1999).

One striking feature of the current results is that mortality of beech is continuing. For example, between 1996/9 and 2014, 13 of 61 subplots declined in BA with mean decline of 32%. While this continued death may be partly attributable to the 1976 drought, weather events linked to climate change may also have contributed to this mortality. Our study showed that growing season temperatures have consistently increased in the area and that droughts have resulted in numerous serious water deficits since 1976. Indeed the drought recorded in 1995 was of comparable magnitude to that of 1976. While the lack of temporal resolution in our data prevents identification of direct linkages between drought and beech dieback in the New Forest, beech appears to be particularly sensitive to increased summer temperatures and water deficits, with dieback documented throughout its European range (Jump et al., 2006; Zimmermann et al., 2015). In our study site drought may have also promoted mortality of beech caused by *Phytophthora* fungi which have been recorded in the New Forest (Forestry Commission England, 2015) and have had apparently caused widespread mortality elsewhere in Europe and the USA (Jung, 2009; Jung et al., 2006).

The potential impacts of increases in the incidence of drought have recently been highlighted by Allen et al. (2010) and Scholes et al. (2014) who indicated that the effects of drought can range from local to regional die-off, and have occurred in diverse climates. However, many of the examples provided by Allen et al. (2010) and Scholes et al. (2014) are based on relatively short-term observations, with few studies analysing the process of forest dieback over multiple decades, as we have done in this study. Such long term datasets are vital for improving understanding of forest dynamics (Schimming et al., 2010), particularly following droughts which can cause mortality decades after the occurrence of drought stress (Bigler et al., 2007; Pedersen, 1998, 1999). However, the processes leading to drought-induced mortality of trees are poorly understood (Choat et al., 2012; McDowell et al., 2011; Sala et al., 2010) and as noted above, drought may be just one of several interacting factors responsible for the dieback observed here.

**Threshold responses and resilience**

Regardless of the causes of the stand dieback noted in our study, dieback was associated with a number of threshold responses. Thresholds occur when the response of an ecological variable to a particular process is not linear, but changes abruptly (Huggett, 2005; Toms and Lesperance, 2003). Curvilinear responses to BA loss were observed in tree community change, as represented by the Tanner Index; in species richness of the ground flora; and in the percentage cover of grass. In addition, evidence suggested that the ability of subplots to recover following BA decline also demonstrated a threshold response; where BA declined by more than 25%, it tended not to recover. Critical values of BA for a change in ground flora species richness and grass cover were around 40% decline from initial values.

Ecological thresholds have potentially dramatic effects on both biodiversity and ecosystem function if they are exceeded (Groffman et al., 2006). There is a critical need to identify when an ecosystem is approaching a threshold, so that appropriate interventions can be defined. Identification and characterisation of thresholds has proved challenging in terrestrial ecosystems, because of the relatively low rate of change (Groffman et al., 2006). Long-term monitoring data may have particular value in this context, as demonstrated here. Threshold responses may be interpreted as a switch from the dominance of negative feedbacks that regulate ecosystems to positive feedbacks leading to ecosystem degradation (Briske et al., 2006). These positive feedbacks may be the result of processes operating at different spatial and temporal scales (Reyer et al., 2015). In our study positive feedbacks between the regional impacts of drought and colonisation of fungi may have caused death of large trees. Thresholds in ground flora change were likely related to increasing light availability as canopy cover was lost. Any recovery via recruitment in our study area appears to have been impeded by high pony and deer density.

Much of the research on ecological thresholds has examined regime shifts in ecosystems, and the associated concept of multiple stable states (Briske et al., 2006; Groffman et al., 2006). In a system with multiple states, disturbance may result in the system crossing a threshold from one state to another, a process that is difficult to reverse (Folke et al., 2010). Potentially, the transitions recorded in Denny from beech-dominated closed forest stands to open, park-like areas dominated by grass cover could be considered a regime shift. However, we do not believe that the situation in our study meets the criteria set out for identification of a regime shift. The underlying theory of multiple stable states is based on the assumption that the system is initially at equilibrium, and that the disturbance causing the regime shift is a ‘pulse’ (i.e. short-term) disturbance rather than a ‘press’ (i.e. continuous) disturbance. It is clear that this condition is not fully met by Denny wood since the apparent causes of the transition to a non-forest state, drought and overgrazing by deer and ponies, represent pulse and press disturbances respectively. As such, the situation we present in this study might be better considered as providing evidence of “persistent alternative states” (Petraitis, 2013) rather than robust evidence of a regime shift.

**Conclusion**

Regardless of how it is defined, the transition observed here represents a significant challenge to forest management and conservation. The old-growth beech woodlands of the New Forest are of exceptional importance for biodiversity, providing habitat for highly diverse communities of lichens, fungi and invertebrates (Newton, 2010). The process of beech dieback observed in Denny Wood is widespread in the area (Tubbs, 2001), and is clearly on-going, and so the potential impacts on biodiversity and provision of ecosystem services could be very significant. As with other examples of forest dieback (Raffa et al., 2008; van Mantgem et al., 2009), the identification of appropriate management responses is a major problem. In the case of the New Forest, forest resilience could most readily be enhanced by protecting tree regeneration from the high herbivore pressure in the area, which limits recruitment of beech (Newton et al., 2013). Focussing on strengthening the “adaptive capacity” forest ecosystems by allowing forests to self-organize and adapt to novel environmental conditions may present an alternative to this approach (Messier et al., 2014). In the New Forest, the implication of this approach would be to accept the ecosystem change that is occurring, despite the potential negative impacts on biodiversity and ecosystem service provision. Whether the system has sufficient adaptive capacity to withstand the potential interactive effects of future climate change, spread of tree diseases, and on-going overgrazing is unknown, with major implications for the development of future management strategies. The new management strategy for the New Forest due to be drawn up in 2015 must take account of these issues.

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**References**

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. doi:10.1016/j.foreco.2009.09.001

Barton, K., 2014. MuMIn: Multi-model inference.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. ArXiv.

Bellassen, V., Luyssaert, S., 2014. Carbon sequestration: Managing forests in uncertain times. Nature 506, 153–155. doi:10.1038/506153a

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., Rassweiler, A., Schmitt, R.J., Sharma, S., 2011. Analysis of abrupt transitions in ecological systems. Ecosphere 2, art129. doi:10.1890/ES11-00216.1

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. doi:10.1111/j.2007.0030-1299.16034.x

Bjornstad, O.N., 2013. ncf: spatial nonparametric covariance functions. Version 1.1-5.

Boyd, I.L., Freer-Smith, P.H., Gilligan, C. a, Godfray, H.C.J., 2013. The consequence of tree pests and diseases for ecosystem services. Science 342, 1235773. doi:10.1126/science.1235773

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. Proc. Natl. Acad. Sci. U. S. A. 102, 15144–8. doi:10.1073/pnas.0505734102

Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2006. A Unified Framework for Assessment and Application of Ecological Thresholds. Rangel. Ecol. Manag. 59, 225–236. doi:10.2111/05-115R.1

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach, Ecological Modelling. doi:10.1016/j.ecolmodel.2003.11.004

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35.

Cantarello, E., Newton, A.C., 2008. Identifying cost-effective indicators to assess the conservation status of forested habitats in Natura 2000 sites. For. Ecol. Manage. 256, 815–826. doi:10.1016/j.foreco.2008.05.031

Chai, S.-L., Healey, J.R., Tanner, E.V.J., 2012. Evaluation of forest recovery over time and space using permanent plots monitored over 30 years in a Jamaican montane rain forest. PLoS One 7, e48859. doi:10.1371/journal.pone.0048859

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752–5. doi:10.1038/nature11688

Folke, C., Carpenter, S.R., Walker, B., Scheffer, M., Chapin, T., Rockström, J., 2010. Resilience thinking: Integrating resilience, adaptability and transformability. Ecol. Soc. 15. doi:10.1038/nnano.2011.191

Forestry Commission England, 2015. Phytophthora ramorum [WWW Document]. URL http://www.forestry.gov.uk/forestry/infd-8elbrv (accessed 5.12.15).

Goetsch, C., Wigg, J., Royo, A.A., Ristau, T., Carson, W.P., 2011. Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: results from a 60 year-old deer exclusion plot. J. Torrey Bot. Soc. 138, 220–224.

Groffman, P.M., Baron, J.S., Blett, T., Gold, A.J., Goodman, I., Gunderson, L.H., Levinson, B.M., Palmer, M.A., Paerl, H.W., Peterson, G.D., Poff, N.L., Rejeski, D.W., Reynolds, J.F., Turner, M.G., Weathers, K.C., Wiens, J., 2006. Ecological Thresholds: The Key to Successful Environmental Management or an Important Concept with No Practical Application? Ecosystems 9, 1–13. doi:10.1007/s10021-003-0142-z

Hirota, M., Holmgren, M., Van Nes, E.H., Scheffer, M., 2011. Global resilience of tropical forest and savanna to critical transitions. Science (80-. ). 334, 232–235. doi:10.1126/science.1210657

Holling, C.S., 1978. Adaptive environmental assessment and management.

Huggett, A.J., 2005. The concept and utility of “ecological thresholds” in biodiversity conservation. Biol. Conserv. 124, 301–310. doi:10.1016/j.biocon.2005.01.037

Johnson, P.C.D., 2014. Extension of Nakagawa & Schielzeth’s R 2 GLMM to random slopes models. Methods Ecol. Evol. n/a–n/a. doi:10.1111/2041-210X.12225

Jump, A.S., Hunt, J.M., Pen̈uelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of Fagus sylvatica. Glob. Chang. Biol. 12, 2163–2174. doi:10.1111/j.1365-2486.2006.01250.x

Jung, T., 2009. Beech decline in Central Europe driven by the interaction between Phytophthora infections and climatic extremes. For. Pathol. 39, 73–94. doi:10.1111/j.1439-0329.2008.00566.x

Jung, T., Hudler, G.W., Jensen-Tracey, S.L., Griffiths, H.M., Fleischmann, F., Osswald, W., 2006. Involvement of Phytophthora species in the decline of European beech in Europe and the USA. Mycologist 19, 159. doi:10.1017/S0269915X05004052

Kurz, W.A., Stinson, G., Rampley, G.J., Dymond, C.C., Neilson, E.T., 2008. Risk of natural disturbances makes future contribution of Canada’s forests to the global carbon cycle highly uncertain. Proc. Natl. Acad. Sci. U. S. A. 105, 1551–5. doi:10.1073/pnas.0708133105

Ma, Z., Peng, C., Zhu, Q., Chen, H., Yu, G., Li, W., Zhou, X., Wang, W., Zhang, W., 2012. Regional drought-induced reduction in the biomass carbon sink of Canada’s boreal forests. Proc. Natl. Acad. Sci. 109, 2423–2427. doi:10.1073/pnas.1111576109

Manners, J.G., Edwards, P.J., 1986. Death of old beech trees in the New Forest. Proc H F. Club Archaeol Soc 42, 155–156.

McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R. a, Raffa, K.F., Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends Ecol. Evol. 1–10. doi:10.1016/j.tree.2011.06.003

Mcintyre, P.J., Thorne, J.H., Dolanc, C.R., Flint, A.L., Flint, L.E., Kelly, M., Ackerly, D.D., 2014. Twentieth-century shifts in forest structure in California : Denser forests , smaller trees , and increased dominance of oaks 1–6. doi:10.1073/pnas.1410186112

Messier, C., Puettmann, K., Chazdon, R., Andersson, K., Angers, V., Brotons, L., Filotas, E., Tittler, R., Parrott, L., Levin, S., 2014. From management to stewardship: viewing forests as complex adaptive systems in an uncertain world. Conserv. Lett. 00, 1–10. doi:10.1111/conl.12156

Mountford, E.P., Peterken, G.F., 2003. Long-term change and implications for the management of wood-pastures: experience over 40 years from Denny Wood, New Forest. Forestry 76, 19–43. doi:10.1093/forestry/76.1.19

Mountford, E.P., Peterken, G.F., Edwards, P.J., Manners, J.G., 1999. Long-term change in growth, mortality and regeneration of trees in Denny Wood, an old-growth wood-pasture in the New Forest (UK). Perspect. Plant Ecol. Evol. Syst. 2, 223–272. doi:10.1078/1433-8319-00072

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R 2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. doi:10.1111/j.2041-210x.2012.00261.x

Newton, A.C., 2010. Biodiversity in the New Forest.

Newton, A.C., 2011. Social-ecological resilience and biodiversity conservation in a 900-yearold protected area. Ecol. Soc. 16. doi:http://dx.doi.org/10.5751/ES-04308-160413

Newton, A.C., Cantarello, E., 2015. Restoration of forest resilience: an achievable goal? New For. In review.

Newton, A.C., Cantarello, E., Tejedor, N., Myers, G., 2013. Dynamics and Conservation Management of a Wooded Landscape under High Herbivore Pressure. Int. J. Biodivers. 2013, 1–15. doi:10.1155/2013/273948

Pautasso, M., Aas, G., Queloz, V., Holdenrieder, O., 2013. European ash (Fraxinus excelsior) dieback – A conservation biology challenge. Biol. Conserv. 158, 37–49. doi:10.1016/j.biocon.2012.08.026

Pedersen, B.S., 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. Ecology 79, 79–93. doi:10.1890/0012-9658(1998)079[0079:TROSIT]2.0.CO;2

Pedersen, B.S., 1999. The mortality of midwestern overstory oaks as a bioindicator of environmental stress. Ecol. Appl. 9, 1017–1027. doi:10.1890/1051-0761(1999)009[1017:TMOMOO]2.0.CO;2

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. Nat. Clim. Chang. 1, 467–471. doi:10.1038/nclimate1293

Peterken, G., Mountford, E.P., 1996. Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. Forestry 69, 125–136. doi:10.1093/forestry/69.2.125

Petraitis, P., 2013. Multiple Stable States in Natural Ecosystems. Oxford University Press.

Power, S.A., Ashmore, M.R., Ling, K.A., 1995. Recent trends in beech tree health in southern Britain and the influence of soil type. Water, Air, Soil Pollut. 85, 1293–1298. doi:10.1007/BF00477160

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J. a., Turner, M.G., Romme, W.H., 2008. Cross-scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. Bioscience 58, 501. doi:10.1641/B580607

Reyer, C.P.O., Brouwers, N., Rammig, A., Brook, B.W., Epila, J., Grant, R.F., Holmgren, M., Langerwisch, F., Leuzinger, S., Lucht, W., Medlyn, B., Pfeifer, M., Steinkamp, J., Vanderwel, M.C., Verbeeck, H., Villela, D.M., 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. J. Ecol. 103, 5–15. doi:10.1111/1365-2745.12337

Rietkerk, M., Dekker, S.C., de Ruiter, P.C., van de Koppel, J., 2004. Self-organized patchiness and catastrophic shifts in ecosystems. Science 305, 1926–1929. doi:10.1126/science.1101867

Sala, A., Piper, F., Hoch, G., 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. New Phytol. 186, 274–281. doi:10.1111/j.1469-8137.2009.03167.x

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–6. doi:10.1038/35098000

Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol. Evol. 18, 648–656. doi:http://dx.doi.org/10.1016/j.tree.2003.09.002

Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., van de Koppel, J., van de Leemput, I. a., Levin, S. a., van Nes, E.H., Pascual, M., Vandermeer, J., 2012. Anticipating Critical Transitions. Science (80-. ). 338, 344–348. doi:10.1126/science.1225244

Schimming, C.-G., Augustin, S., Karez, R., 2010. The Scientific Potential of Environmental Monitoring, in: Müller, F., Baessler, C., Schubert, H., Klotz, S. (Eds.), Long-Term Ecological Research SE  - 4. Springer Netherlands, pp. 39–55. doi:10.1007/978-90-481-8782-9\_4

Scholes, R., Settele, J., Betts, R., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J., Taboada, M.G., 2014. Terrestrial and inland water systems, in: Field, C., Barros, V., Mach, K., Mastrandrea, M. (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Cambridge University Press, Cambridge, pp. 271–360.

Staver, a C., Archibald, S., Levin, S. a, 2011. The global extent and determinants of savanna and forest as alternative biome states. Science 334, 230–2. doi:10.1126/science.1210465

Thrush, S.F., Hewitt, J.E., Dayton, P.K., Coco, G., Lohrer, A.M., Norkko, A., Norkko, J., Chiantore, M., 2009. Forecasting the limits of resilience: integrating empirical research with theory. Proc. Biol. Sci. 276, 3209–3217. doi:10.1098/rspb.2009.0661

Toms, J.D., Lesperance, M.L., 2003. Piecewise regression: a tool for identifying ecological thresholds. Ecology 84, 2034–2041. doi:10.1890/02-0472

Tubbs, C.R., 2001. The New Forest: history, ecology and conservation. New Forest Ninth Centenary Trust.

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 of tree mortality rates in the western United States. Science 323, 521–524. doi:10.1126/science.1165000

Walker, B., Holling, C.S., Carpenter, S.R., Kinzig, A., 2004. Resilience, adaptability and transformability in social--ecological systems. Ecol. Soc. 9, 5.

Warton, D.I., Hui, F.K.C., 2011. The arcsine is asinine: The analysis of proportions in ecology. Ecology 92, 3–10. doi:10.1890/10-0340.1

Wickham, H., 2009. ggplot2: elegant graphics for data analysis. Springer, New York.

Zimmermann, J., Hauck, M., Dulamsuren, C., Leuschner, C., 2015. Climate Warming-Related Growth Decline Affects Fagus sylvatica, But Not Other Broad-Leaved Tree Species in Central European Mixed Forests. Ecosystems 1, 560–572. doi:10.1007/s10021-015-9849-x

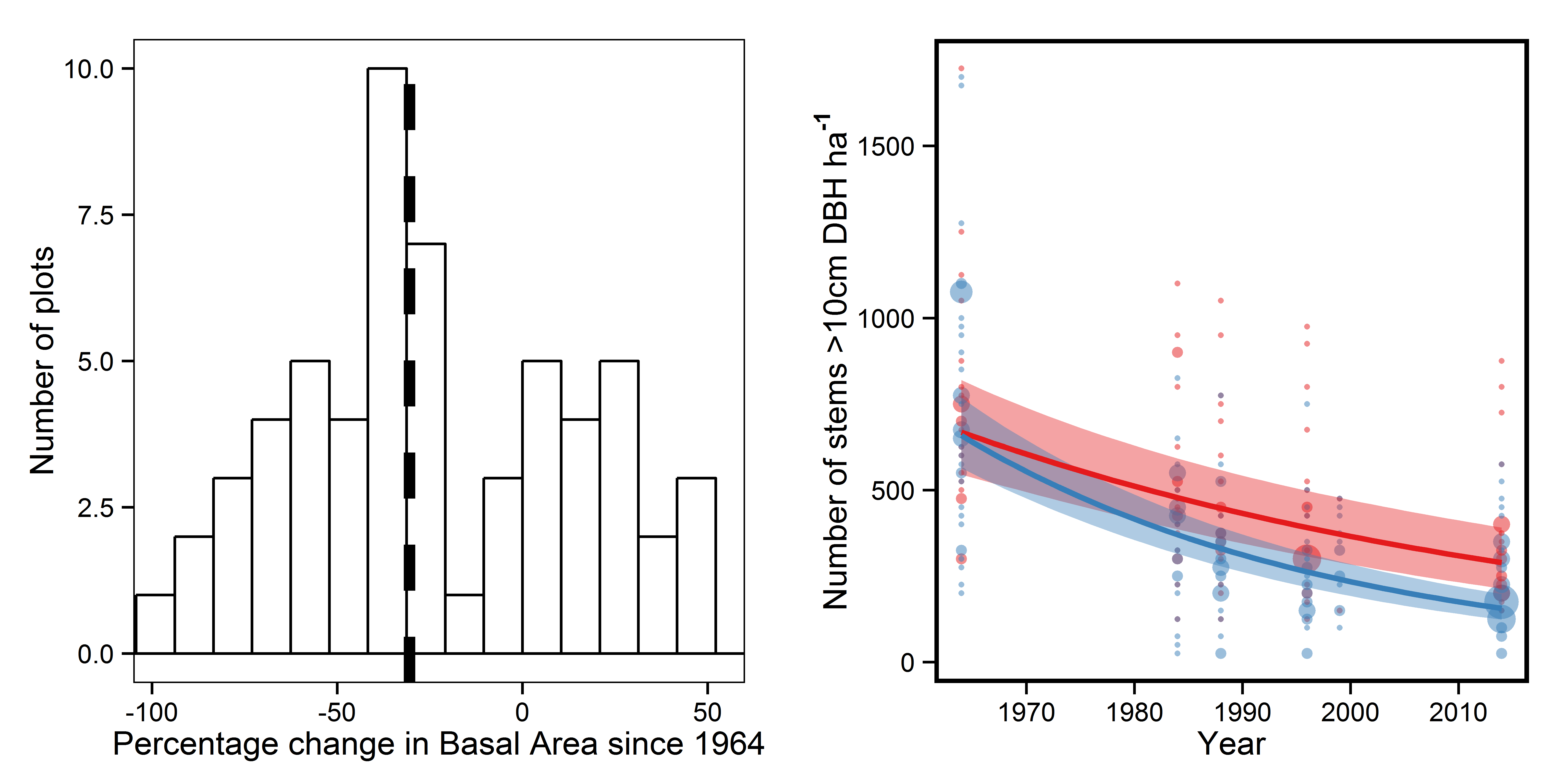


Figure 1 – Changes in (a) basal area and (b) stem density for subplots over the period 1964-2014. In (a) the dashed line represents the median change in basal area. In (b) points represent individual subplots, with collapsed subplots coloured red and stable subplots blue, lines represent predictions from the most parsimonious model and bands the 95% confidence intervals of these predictions (marginal R2=0.37).

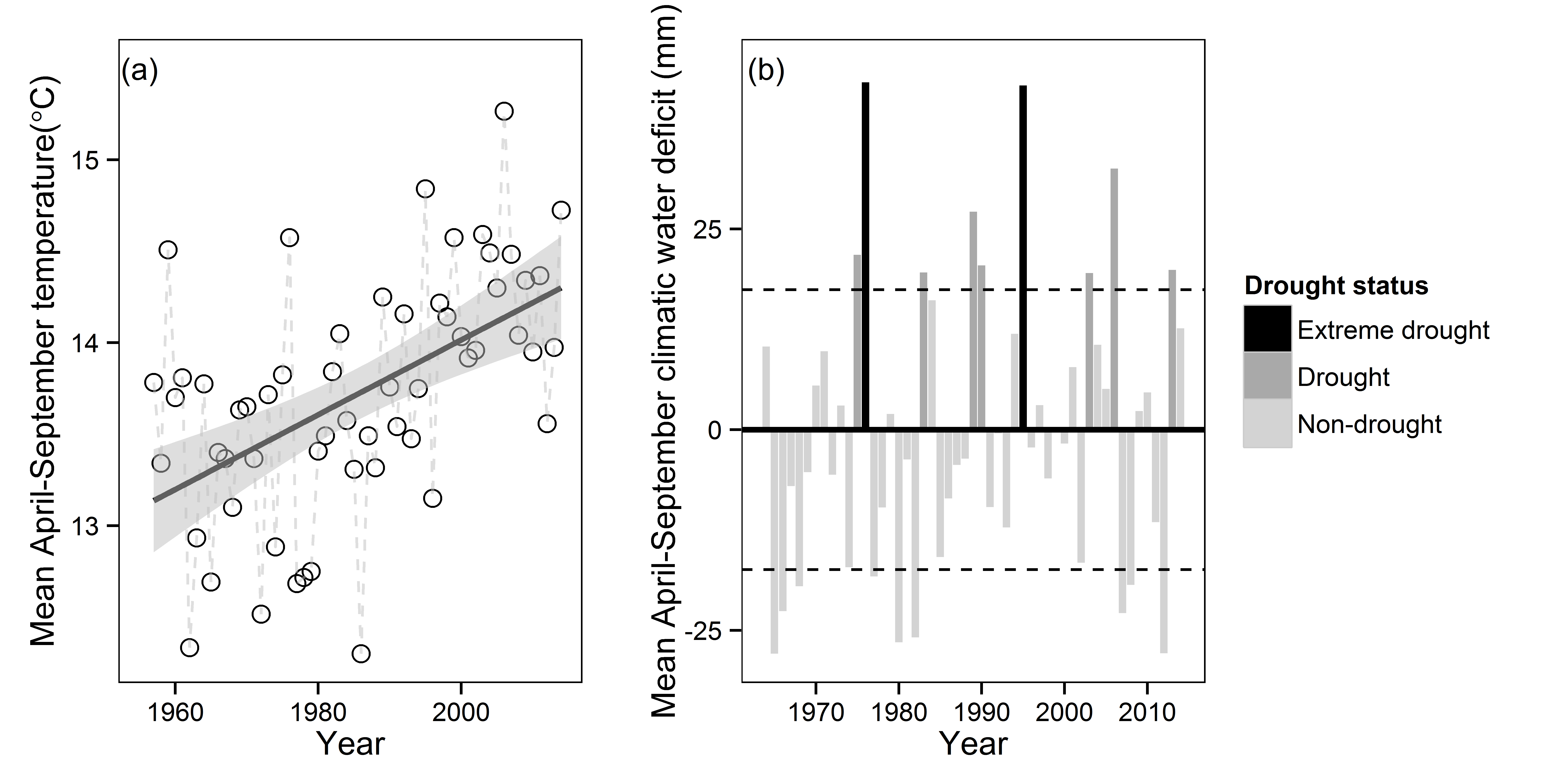


Figure 2 – Climate records from 1964-2014 showed that (a) mean temperature during April-September increased from 1960’s to present day at a rate of 0.02 ± 0.004°C year-1 (model R2=0.28); and (b) there were numerous drought years (water deficit > 1 SD from mean deficit) post 1976. In (a) points represent means of each year, with the solid line representing predictions from a regression; the band around this represents the 95% confidence intervals of the prediction. In (b) dotted lines represent the mean April-September water deficit ± 1SD. Refer to methods section for definitions of drought status. Data taken from the Hurn weather station, 24km from the study site (data available from www.metoffice.gov.uk/public/weather/climate-historic/ - accessed 16/04/2015).



Figure 3 – Relationship between percentage loss in plot basal area and species composition changes as measured using the Tanner Index (n=210). Where Tanner Index values are closer to 1 species composition is more similar to the same plot in 1964. Points represent individual plots surveyed in 1984 (red), 1988 (blue), 1996/9 (green), or 2014 (purple). Circles represent plots on the enclosed transect and triangles circles those on the unenclosed transect. The line represents the most parsimonious model fit (R2=0.47), with dashed lines representing the 95% confidence intervals around the coefficient. For more details of model see Tables S13 and S14.



Figure 4 – Changes in mean subplot percentage grass cover for the enclosed area of Denny wood, for subplots that collapsed at some point from 1964-2014 (red bars) and those that were stable during this period (blue bars). Error bars represent 95% confidence intervals of the most parsimonious model explaining changes in grass cover (marginal R2=0.44). There was no difference amongst subplot grass cover in 1964 but by 1996 collapsed subplots had significantly greater grass cover than stable subplots (P=0.009) and this difference increased by 2014 (P<0.001). Only subplots from the enclosed transect are included in this figure as data on ground cover was missing for the unenclosed transect for 1964.



Figure 5 – Relationship between percentage loss in subplot basal area and (a) percentage grass cover and (b) ground flora species richness. Circles represent individual subplots on the enclosed transect surveyed in 1996 (red) or 2014 (blue). The line represents prediction using model averaged coefficients and grey shading the 95% confidence intervals of the coefficients (marginal R2=0.39 and 0.15 for grass cover and ground flora richness respectively). Only data from enclosed transect subplots are included in this figure.