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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. However, understanding of the processes of 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 over 50 years along two transects in a temperate forest ecosystem, in which the canopy dominant beech (*Fagus sylvatica* L.) has demonstrated significant dieback. Our results show that basal area in the forest has declined by 33%, and juvenile tree densities have also been reduced by approximately 70%. Growing season temperatures have steadily increased and there have been a number of droughts causing climatic water deficits in recent decades, particularly in 1995. We hypothesise that these droughts may have interacted with novel pathogenic fungi to cause mortality of large trees. Curvilinear responses to BA loss were observed in tree community change, ground flora species richness, and percentage cover of grass, providing evidence of thresholds associated with stand dieback. Evidence also suggested that BA failed to recover once it declined. Critical values of basal area for a change in ground flora species richness and grass cover were around 40% decline from initial values. While these changes are dramatic, they cannot be considered a regime shift as the pressures that may have contributed to the ecosystem transition, drought, pathogenic fungi and overgrazing, are on-going. 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 and ecosystem service provision.

1. 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 (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, as a result of regional warming and water deficit (Peng et al., 2011; van Mantgem et al., 2009). Changing climatic conditions have also 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). Although invertebrate herbivores play an important role in ecosystem functioning, when these species' ranges expand beyond their native range this can result in widespread damage. 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 forest dieback is projected to occur in many regions over the 21st century, and that this is likely to pose risks for biodiversity, carbon storage and other ecosystem services (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 whether forest ecosystems can recover from disturbances. 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). Once a regime shift has occurred, because an ecological threshold has

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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 (Scheffer and Carpenter, 2003), their existence in forest ecosystems remains the subject of debate (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 – a term which is increasingly being incorporated into environmental policy – which is 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 potential consequences both for biodiversity and the associated provision of ecosystem services (Groffman et al., 2006).

Given the increasing evidence of widespread increases in tree mortality in many forest ecosystems, there is a need to understand its potential impacts (Thrush et al., 2009). In particular, there is a need for long-term field data collected in ecosystems undergoing dieback, in order to provide insights into the links between key processes, and to provide information to support both management and policy responses (Groffman et al., 2006; Thrush et al., 2009). Such data could also contribute to an understanding of the mechanisms involved in sudden transitions, which is currently lacking for ecosystems such as forests (Rietkerk et al., 2004). Very few long-term data are available for forest stands that have undergone collapse (e.g. see Goetsch et al., 2011). As a consequence, the processes by which forest dieback occurs are not well understood.

Here we use 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. Here we build on data collected from 1964 to 2001 (Mountford and Peterken, 2003; Mountford et al., 1999) 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.

2. Methods

2.1. Site history and characteristics

The site used in this study, Denny Wood, is located in the New Forest National Park in Southern England (Lat: 50°51.5′N and 1°32.5′W). It has a temperate oceanic climate. Mean annual precipitation between 1957 and 2014 ±SD at the Hurn weather monitoring station approximately 23 km from Denny Wood was 832 ± 150 mm 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*) with frequent pedunculate oak (*Quercus robur*) and occasional birch (*Betula pendula, Betula 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 has 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 (Mountford and Peterken, 2003).

2.2. 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 × 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) was 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 × 10 m plot was located in the central part of each 20 × 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, but only in 2014 for the unenclosed transect. In 2014 tree seedling abundance was also recorded for Denny Inclosure within the same 10 × 10 m plots used to assess ground flora.

2.3. Data preparation

Basal area (BA) for all tree species ⩾10 cm DBH was calculated for each subplot following Cantarello and Newton (2008). The percentage change in basal area for all species since 1964 for each subplot was calculated using the formula:

$$BA_{perc} = \frac{BA_{i,t2} - BA_{i,1964}}{BA_{i,1964}}$$

where $BA_{i,1964}$ represents the BA of a subplot i in 1964 and $BA_{i,t2}$ represents the BA of a subplot i in any of the subsequent survey years.

To examine 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. To assess changes in tree community composition since 1964 we used the Tanner Index as defined by Chai et al. (2012) which is the mean of the Sørensen similarity indices calculated using BA and stem density. This metric avoids the problems of using the quantitative Sørensen similarity Index noted by Chai et al. (2012) by accounting for both the stem density and BA of species. The quantitative