**Mortality and recruitment in a woodland undergoing collapse**

**Introduction**

* Mortality and recruitment are vital for understanding forest dynamics and recent studies have suggested alteration of both

Understanding tree mortality and recruitment is fundamental to an understanding of forest dynamics. As a result of changes in fire regimes, increases in water deficit and nodel pests and pathogens numerous recent studies have shown increases in tree mortality and reductions in recruitment (van Mantgem *et al.* 2009; Peng *et al.* 2011; Mcintyre *et al.* 2014). In forests where individual species recruitment has not kept pace with mortality, such as in the Western USA, this can lead to alteration of forest composition (Mcintyre *et al.* 2014). Where mortality is particularly high, as seen in Eastern Amazonian forests where repeated fires have taken place, this can result in shifts to relatively treeless states (Barlow & Peres 2008; Brando *et al.* 2014). Any such transitions from forest to a non-forest ecosystem would inevitably result in large emissions of carbon as well as potentially negative impacts on other ecosystem services and conservation priorities.

* Identification of what drives tree recruitment and mortality could aid production of indicators of resilience

While numerous studies give details of increases in mortality over recent decades relatively few identify what factors determine the likelihood of tree death when a transition is occurring. Coomes *et al.* (2003) suggest that in the event of disturbance larger trees are likely to be more prone to death than small or intermediate trees and this appears to be true in many cases where transitions to non-forest states are occurring (Barlow *et al.* 2002; Mcintyre *et al.* 2014). Given that large trees produce large amounts of seeds (Greene & Johnson 1994) and play a vital role in maintaining the microclimatic conditions of forests by limiting the light reaching the forest floor their loss may have important consequences for recruitment. In addition to tree size it has been widely seen that slow growing trees tend to have increased risk of mortality. This observation may be particularly useful in the context of forests at risk of transitions to non-forest states since it may serve as an early warning indicator of low resilience (Camarero *et al.* 2015).

* In addition there is a potential in systems that positive feedbacks can drive system transitions

Positive feedbacks are important for maintaining ecosystems in their state. For example in forests the presence of a canopy maintains relatively moist, dark conditions on the forest floor which results in relatively low ground flora biomass. However, when ecosystems transition from one state to another this can be the result of unfavourable positive feedbacks. These feedbacks can occur at multiple scales and can thus be difficult to identify.

* Though there are numerous studies on forests in a state of transition to relatively treeless states few investigate the processes that affect individual trees to cause such changes.

Ultimately shifts in the species composition of an ecosystem require that individual species recruitment does not keep pace with loss as a result of mortality. In the context of forest dieback this has been the case in the Western USA where increases increased mortality of large pine trees, apparently as a result of water deficits, has led to increased abundance of oak species. Indeed evidence suggests that large trees are particularly likely to be killed by droughts, which given their importance for biodiversity and carbon storage is a major concern. Though there is evidence of increased tree mortality from drought in all forested continents few studies have examined what influences tree mortality and recruitment in these studies.

Understanding tree mortality and recruitment is fundamental to an understanding of forest dynamics. While numerous studies have characterised

* There are many different mechanisms that have the potential to influence tree mortality. It has been widely seen that mortality is high amongst small trees as a result of asymmetric competition, relatively low in trees of intermediate size and higher for large trees as a result of senescence. Recent work has also shown that trees that show reduced growth may be more likely to die, with reduced growth rate indicative of low tree vigour.
* In addition to individual tree characteristics the characteristics of the ecosystem and its disturbance regime can have profound effects on tree mortality. For example mortality of large trees in fragmented landscapes is elevated by increased wind throw and higher physiological stress (e.g. lower moisture availability, higher evapotranspiration etc).
* However, relatively few studies that have investigated shifts in forest systems have been able examine mortality since they are largely space-for-time studies.

**Statement of aims**

* To test the influence of tree size, growth rate, competition and proximity to dead trees on determining tree mortality.
* To test the factors what influenced seedling and sapling density to enable an understanding of recruitment
* Test the influence of tree size and competition on growth rate
* Use parameter estimates from these models along with estimates from the literature to produce an individual based model to look at the potential for regime shift in the system, in particular:
  + Hysteresis – does the system recover along the same trajectory it declined over

**Hypotheses**

* Recruitment did not keep pace with mortality for any species during any of the survey periods
* Mortality likelihood is u-shaped in relation to tree size
* Slow growing trees are more likely to die
* Proximity to trees that have died is more likely to result in tree death
* Under current conditions the woodland will show increased loss of tree cover. In situations where recruitment is maximized dramatic losses will be averted.

**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). Detailed site descriptions are provided by 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 old-growth beech (*Fagus sylvatica*)withfrequent pedunculate oak (*Quercus* robur) and birch (*Betula pendula, B. pubescens*), and an understorey primarily of holly (*Ilex aquifolium*). Other tree species present at lower frequencies include apple (*Malus sylvestris*), ash (*Fraxinus excelsior*), blackthorn (*Prunus spinosa*), alder buckthorn (*Frangula alnus*), hawthorn (*Crataegus monogyna*), sycamore (*Acer pseudoplatanus*), rowan (*Sorbus aucuparia*), willow (*Salix caprea, S. cinerea*)and yew (*Taxus baccata*). 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), owing to its history as a Royal Forest and the long-term maintenance of a traditional commoning system (Newton 2011, Newton et al. 2013). Although the site surveyed here has largely been untouched by silvicultural treatment, since 1870 it has been divided into two portions, one of which was enclosed by fencing (Denny Inclosure) to exclude livestock, but not deer. Although browsing pressure is likely to have been higher in the unenclosed part of the site during the early 20th century, since the 1960s browsing pressure has been high in both parts, though with different main herbivores (ponies in the unenclosed part; deer in the enclosed) (Mountford and Peterken 2003).

* Data were collected from 1964-2014 with each tree marked and given an ID number and at each time period DBH and status were assessed.

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 51 subplots and the shorter transect 20. 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) and those for 2014 in Martin et al. (2015). In each survey, the location and species name of all woody stems >1.3 m in height were recorded, their diameter at breast height measured using measuring tapes, and their status assessed as either alive or dead. Each stem >1.3m height was given a unique ID number to allow changes in individual trees to be tracked.

* Binomial mixed effects models were used to assess factors influencing likelihood of tree death using workflow similar to Chao et al in which alternative variables (e.g. DBH, BA etc) were tested against each other and then included in the model

Statistical models of individual tree mortality were developed using logistic mixed effects models, which describe the probability that a tree dies in a given period of time.

For this model we tested only individual-level predictors of mortality. Models were developed in a four-step process similar to the workflow of Chao et al. (2008). In step 1 we prepared predictors classified into 3 groups: (i) tree size, (ii) tree growth, (iii) proximity to dead trees. Tree size represented diameter based measurement prior to death, specifically diameter at breast height, basal area and relative size. Tree growth was based on measurements of diameter at two separate time periods prior to death and represented both relative and absolute growth rates. Proximity to dead trees related to the prior to death distance of an individual tree to a dead tree or the abundance of dead trees in a 10m buffer. In step 2 we selected the best predictor for each group using univariate logistic mixed effects models using AICc values (Burnham & Anderson 2002). In step 3 a full multivariate model was developed using these selected variables. In step 4 model averaging was used to produce parameter estimates using the most parsimonious models. Each of these steps is described in more detail below.

During data processing tree status (alive or dead) was coded at census time . Only trees with diameter measurements at both and prior to time were included in analyses. Censuses on the transect were undertaken 5 times from 1964-2015 with a mean (± SD) census interval period of 12.5 ± 6.7 years. Since trees used in mortality models required censuses at both and prior to time we selected three non-overlapping census periods: 1984-1988, 1988-1996 and 1996-2014 (mean census period 10 ± 5.9 years). To correct for the variation in census interval a random effect was included in models to identify census period.

Tree size metrics used were (i) DBH (cm): diameter at height of 1.3m of tree at time ; (ii) BA (m2): basal area of tree at time ; (iii) DBH (cm) and DBH2 (m2) – used to indicate possible u-shaped mortality curve (Holzwarth *et al.* 2013) and; (iv) The relative size of tree at time given with the equation:

For the biggest tree in the transect is close to 1 for the smallest it is close to 0 (Monserud & Sterba 1999).

Tree growth rate metrics used were: (i) Annual diameter growth rate (mm year-1) calculated as:

where and are the *DBH* values for a tree at time and respectively; (ii) Basal area growth rate (cm2 year-1) calculated as:

where and are the *DBH* values for a tree at time and respectively; (iii) relative DBH growth rate (% DBH increase year-1) calculated as:

and; (iv) relative BA growth rate (% BA increase year-1) calculated as:

Metrics of proximity to dead trees were: (i) *deadSD*=stem density of dead trees at time within 10 metres of the target tree; (ii) *deadSD45*=stem density of dead trees ≥45cm DBH at time of death at time within 10 metres of the target tree; (iii) *deadDist*=distance to nearest dead tree (m) at time ; (iv) *deadDist45*=distance to nearest dead tree ≥45cm DBH at time of death (m) at time . Our rationale for focussing on dead trees ≥45cm DBH was that this represents the upper quartile of tree diameters in the woodland and we hypothesised that the death of larger trees plays a stronger role in altering local microclimate conditions.

* Poisson mixed models were used to assess how density of saplings and seedlings changed over time and with density of mature trees

**Individual based models of recruitment and mortality**

* An individual based model built in netlogo was parameterised using values from these analyses to investigate the potential changes in the woodland

**Results**

**Discussion**

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