**Working title: Positive feedbacks cause collapse of tree cover in a temperate forest**

Main message: Transition to non-forest state depends on positive feedbacks: loss of mature trees causes lower recruitment and tree death increases likelihood of death of nearby trees

**Working abstract**

There is increasing concern about forest dieback, especially related to transitions to non-forest states it may cause. Positive feedbacks are thought to be an important component of such transitions, but there is relatively empirical work on the topic.

Here we used a unique 50 year dataset from a forest that shows signs of transition to grassland. We used to statistical models to find correlates of tree death and recruitment. We then used these results along with information from the literature to build an individual based model to investigate the impact of positive feedbacks on forest persistence.

We found that tree death was negatively correlated with tree growth rate, distance to nearest dead tree and sand content of soils, but positively correlated with tree size. Seedling density was negatively related to canopy cover, but sapling density was higher in areas of high canopy cover. There was relatively little evidence of self-thinning in the forest suggesting that exogenous disturbances are likely be to the main cause of mortality observed. Our individual based model showed that when juvenile survival in treeless areas was reduced and mature trees were more likely to die when close to other dead trees forest structure collapsed. Otherwise forest structure remained stable.

These results show that positive feedbacks that influence both recruitment of juveniles and death of mature trees are likely to be responsible for a transition to non-forest state in our study site.To enhance forest resilience management should attempt to stop the development of such positive feedback loops, or break them where they have become established. In our study area practical measures to encourage recruitment of trees such as fencing off forest areas to reduce seedling mortality caused by browsing of ponies and deer may reduce feedbacks related to juvenile death. However, reducing the feedbacks related to mortality of larger trees will be more challenging as these may be related to interactions between drought and novel fungal pathogens.

**Figures**

Figure 1 - Relationships between Tree/canopy cover and (a) seedling density and (b) sapling density

Figure 2 - Correlates of mature beech death (a) growth rate, (b) size, (c) distance to dead tree and (d) sand content

Figure 3 - Figure showing effect of changing feedbacks on forest structure under (a) low browsing pressure, (b) medium browsing pressure and (c)  high browsing pressure

Table 1 - Summary of recruitment and mortality of juveniles for all species

Table 2 - Summary of coefficients for mortality model

**Introduction (600 words)**

1. Concern about transition to non-forest states, but little known about mechanisms that cause it (100-150 words)
2. Previous work has shown that positive feedbacks can induce regime shifts (100-150 words)
3. How feedbacks scale up from individual trees to a stand scale transition is unclear (100 -150 words)
4. We used statistical models and IBMs to show the importance of feedbacks in a forest undergoing transition (100-150 words)

**Methods (900 words)**

1. We used data from a 50 year data set collected in Denny Wood in the Southern UK (150 words)

For this study we used data collected over a 50 year period in Denny Wood, which is located in the New Forest National Park, in Southern England (Lat: 50o 51.5’ N and 1o 32.5’ W). The site is gently sloping (1-3 degrees), with clay rich brown earth soils. Woodland vegetation is dominated by old-growth beech (*Fagus sylvatica*) with frequent pedunculate oak (*Quercus* robur) and birch (*Betula pendula, B. pubescens*), and an understory primarily of holly (*Ilex aquifolium*). In open areas the ground vegetation is mostly comprised of *Agrostis*-dominated grassland or stands of bracken (*Pteridium aquilinum*). There are large populations of deer, ponies and cattle in the New Forest, resulting in high herbivore pressure. The site which we used for this study is likely to have experienced high browsing pressure since the 1960’s (Mountford & Peterken 2003). More detail on the site is given in Mountford *et al*. (1999), Mountford and Peterken (2003) and Martin et al. (2015).

1. Data were collected over two transects on tree status, size, seedling density, canopy openness and soil

Measurements were conducted in one 20 m-wide 1 km long transect, which was originally established in the 1950s. The transect was subdivided into contiguous 45 20 x 20 m (0.04 ha) subplots and surveyed in 1964, 1984, 1988, 1996 and 2014. Details of measurements are presented by Mountford *et al.* (1999) and Mountford and Peterken (2003) and 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 diameter tapes, and their status assessed as either alive or dead. Each stem >1.3m height was given a unique ID number to allow individual trees to be tracked. Stems <10 cm DBH were classified as saplings and those >10 cm DBH as mature.

In 2014 we collected data on seedling density, canopy openness, and soil characteristics. The density of tree seedlings of all species present in 10 x 10 m plots located in the centre of the 20 x 20 m plots was recorded. Canopy openness of subplots was assessed using a concave spherical densitometer in all four corners and the centre of 20 x 20 m plots, and the mean calculated for each subplot. Soil type was assessed by collecting 3 soil samples from within each 20 x 20m subplot using a 5 cm diameter soil corer. The first 20 cm of the mineral layer was retained. Soil samples were sent to the Forest Research laboratories in Surrey, UK where particle size distribution of the soil was determined by suspending 30 g of soil in water which was passed through the flow cell of a laser diffraction particle size analyser (Beckman Coulter LS13320).

1. We used statistical models to test the importance of variables for juvenile density

**Statistical analysis**

**Recruitment of juveniles**

Our assessment of tree recruitment focussed on saplings (woody stems >1.3 m height and <10 cm DBH) and seedlings. We tested for relationships seedling density and canopy openness and grazing pressure using generalised linear models. We also tested the the effect of the density and basal area of mature trees (stems >10 cm DBH) on sapling density using generalised mixed models with a poisson error structure for the three major woody species present: beech, holly and oak. These models included interactions with survey year to identify if the slope of the relationship between mature tree density and sapling density changed over time. To determine whether the widespread loss of smaller stems seen in a previous study at the site (Martin *et al.* 2015) was largely attributable to growth of individuals into other size classes or mortality we tracked the fate of each sapling recorded. As part of this we also calculated the annual mortality rate, , as defined by Sheil, Burslem & Alder (1995):

where  and  are the number of stems at the first and second surveys respectively and  is the number of years between censuses.

1. We used statistical models to test the influence of variables on mature tree mortality

**Individual tree mortality**

We assessed whether some of the mature tree mortality observed in Denny wood could be explained by the self-thinning process using a linear mixed model with subplot number as a random effect to relate stem density to basal area. A negative slope suggests a gain in BA with a loss of stem density while a positive slope suggests a gain in BA with increasing stem density.

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 1964-2014 with a mean (± SD) census interval period of 12.5 ± 6.7 years (range 4-20 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). 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. To correct for the variation in census interval we used a complementary log-log link with an offset equal to the census interval so that predictions from models were equivalent to the annual probability of mortality (Fortin *et al.* 2008). Subplot ID number was used as a random effect to account for repeated sampling of the same plots (Fortin *et al.* 2008).

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 4 groups:

* 1. tree size – DBH (cm), Basal area (m2), and tree size relative to other trees in the transect (bounded between 0 and 1)
  2. tree growth - Annual diameter growth rate (mm year-1), basal area growth rate (mm2 year-1), relative DBH growth rate (% DBH increase year-1), and relative BA growth rate (% BA increase year-1)
  3. proximity to dead trees - distance of an individual tree to a dead tree and abundance of dead trees in a 10m buffer
  4. soil type - percentage of each soil sample classified as sand

For more detail on the calculation of these variables see the supplementary materials. All model variables were standardised using the methods of Schielzeth (2010) by subtracting the mean of the variable and dividing by its standard deviation. This allows coefficients to be interpreted as effect sizes, reduces collinearity between variables and improves model convergence (Schielzeth 2010).

In step 2 we selected the best predictor for each group by choosing the univariate logistic mixed effect models which had the lowest AICc (Burnham & Anderson 2002; Chao *et al.* 2008). This step reduces intercorrelation of variables which can lead to difficulty in interpreting effects (Chao et al., 2008). In step 3 a full multivariate model was developed using these selected variables using additive terms only. In step 4 model averaging was used to produce parameter estimates for models with a ΔAICc≤7.

1. We used an individual based model to test the importance of feedbacks - ODD protocol

**Individual based model**

The model description follows the ODD protocol for describing individual based models (Grimm et al., 2006).

**Purpose**

We used the model to investigate under what conditions loss of tree cover and basal area (BA) might occur in a simplified representation of a New Forest beech woodland. The only species represented is beech, as this is the dominant species found in the area, and mortality of the species has caused the majority of BA loss from 1964-2014 (Martin et al., 2015).

**Entities, state variables and scales**

The model comprises of two types of entities: grid cells and individuals. Individuals represent beech trees. Each individual is characterised by its location, development stage (juvenile or mature), age (in years), DBH (cm), basal area (m2), mean seed dispersal distance (mean distance from the source, in number of cells), growth rate in previous year (mm year-1), local basal area and stem density of mature trees, and distance to nearest dead tree (m) . DBH of mature trees and juveniles is derived from the age of trees using an equation for beech growth defined in Holzwarth *et al.* (2013) and BA defined as . Local basal area and stem density represent the total BA and stem density within a circle with an area of 400 m2 – equivalent to the plot size used in data collection. Dispersal distance is a random number drawn from an exponential distribution with a mean of 5 m.

All grid cells in the model are considered suitable for individuals. Each grid cell is characterised by its location, whether a tree has died in that patch and the time since last tree death on that patch. When a tree dies the patch value changes from 0 to 1 and after 10 ticks if no other tree has died on this cell this value returns to 0. Each grid cell can only contain one mature individual, but may contain multiple juveniles. The model landscape consists of 100 x 100 grid cells, with each cell representing 1 m2, thus the entire area represents 1 ha. Each model time step represents one year.

**Process overview and scheduling**

Initially the distribution of individuals is determined by randomly distributing 115 mature individuals with a random age drawn from an exponential distribution with a mean of 160 years assigned to each individual. This was approximately the density and age structure of Denny Wood when last surveyed in 2014. At the same time 1000 juvenile trees are randomly distributed across the space. Then in each time step the following events are processed in the given order: increase age of individuals by one year, increase individual DBH & BA, identification of whether the time step represents a mast year, seed dispersal from mature trees > 40 years old, and death.

**Design concepts**

The total number of mature trees and basal area *emerge* from changes in the probability of mature tree mortality that occur as they age and increase in size, as well as from changes in the mortality of juvenile trees. *Interactions* between individuals are the result of density dependant mortality processes, which show size asymmetry. For juveniles this is modelled by defining a maximum number of juveniles that can coexist in the area as 1000, and a maximum number of juveniles per cell as 100. When these numbers are exceeded the smallest juveniles are killed. Similarly, for mature trees the local maximum BA was set at 75 m2 ha-1, the maximum observed for any plot during 1964-2014. When this maximum is exceeded the smallest mature tree in an area of 400m2 is killed. In addition our model tests the impact of reduced survival of juveniles in areas with few mature trees (as seen at our site) by allowing the user to switch this on and off. When turned on this causes juveniles in locations where mature tree density is <5 in the surrounding 400 m2 to have a 0.02 annual chance of survival. Additionally, our model tests what impact an increase in the probability of mature mortality as a result of being close to a dead tree would have on forest structure. This can be switched on and off. When switched on this causes the annual mortality to be increased as a function of distance to nearest cell with a dead tree. The parameter estimate for this was derived from our statistical model of mature tree mortality.

*Stochasticity* is used in the model to define whether a given time step represents a mast year. Beech trees produce large amounts of seed once every 2-3 years in the UK (Packham et al., 2012) and thus we set a probability of 0.3 of each year being a mast year.

To test the model we first initiated the model so that forest structure was similar to that seen in 1964. We then ran different scenarios with and without differential juvenile mortality and spatial mortality feedbacks and compared the change in BA and forest structure after 50 time steps to those we observed in 2014. Following this we ran the models using the same parameterisation for a further 100 years to investigate possible future changes in BA and tree cover under the different scenarios. Each model run had 100 iterations and median values were used to summarise model results.

**Results (500 words)**

1. Seedlings recruit in gaps, but saplings denser under trees
2. Large, slow growing trees, near other dead trees on sandy soil are more likely to die
3. IBM results show that forest collapses only when feedbacks are included

**Discussion (800 words)**

1. Feedbacks are important in our system, as seen in other transitions (~200 words)
2. This means that degradation of the forest could be self-perpetuating (~200 words)
3. Managers should attempt to break these feedback loops or stop them from being established (~200 words)

**Conclusion (200 words)**

1. Feedback loops can be important in causing transitions to non-forest states and need to be managed carefully (~200 words)