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

Authors: Philip Martin1, Adrian C. Newton1, Elena Cantarello1, Paul Evans1, Edward Mountford2.

Journal: Journal of Applied Ecology

1Centre for Conservation Ecology and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole, BH12 5BB, UK.

2Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough, PE1 1JY, UK.

Keywords: forest dieback; regime shift; forest collapse; ecosystem resilience;

Corresponding author email: martinp@bournemouth.ac.uk

**Introduction**

In recent decades tree mortality has increased in many parts of the world. In forests in the western USA mortality rates have more than doubled over the past 30 years (van Mantgem *et al.* 2009) and have approximately tripled in boreal Canada since the 1960’s (Peng *et al.* 2011). Drought-induced tree mortality linked to recent climate change has now been seen on all wooded continents and is thought to be increasing in prevalence (Allen *et al.* 2010; Steinkamp & Hickler 2015). At the same time intensity and regularity disturbances has also been increasing. Large wildfires have quadrupled in frequency in the Western USA in the past 30 years (Westerling *et al.* 2006) and bark beetle damage in the same region has reached unprecedented levels (Meddens, Hicke & Ferguson 2012). Similarly in Europe the negative effects of wildfire, windthrow, and pathogen and pest species have all increased over the last two decades (Seidl *et al.* 2014). The intensity of disturbances and the severity of climate change are both predicted to increase over the coming decades resulting in further increases in tree mortality.

In forests where recruitment has not kept pace with increased mortality, such as in the Western USA, this has led to changes in the dominant tree species (Mcintyre *et al.* 2014). When tree mortality is particularly high or recruitment low this can result in shifts to relatively treeless savannah or grassland states (Barlow & Peres 2008; Brando *et al.* 2014). There are widespread concerns that such ‘regime shifts’ in forests may be more likely to occur as a result of interactions between changes in disturbances, land-use and climate (Staver, Archibald & Levin 2011; Scheffer *et al.* 2012). Though the consequences of transitions to non-forest states are severe, relatively little is known about the mechanisms underlying such shifts (Reyer *et al.* 2015). Improving this understanding would aid our ability to predict when transitions may occur and how to stop them before they occur.

The occurrence of a regime shift is determined by the balance between recruitment and mortality for each species in a community. As such, it is important to understand what determines these vital rates. In forests undergoing disturbance larger trees are likely to be prone to an increased probability of death (Coomes *et al.* 2003). Following the mortality of large trees gaps in the canopy tend to stimulate recruitment of seedlings. However, in systems undergoing a transition there must be some recruitment limitation of the previously dominant species. This has been seen in forests when disturbances are large, leading to unfavourable microclimatic conditions for seedling growth and in some cases a lack of propagules for dispersal limited species (Coates 2002; Acácio *et al.* 2007). Seedling recruitment may also be limited by grazing of domesticated animals, which in some cases can be so severe that it leads to a transition from woodland to grassland that resembles a regime shift (Fischer *et al.* 2009).

* The impact of climate on tree mortality and recruitment

Changes in temperature and water supply can alter the growth of trees. Slow growing trees tend to have increased risk of mortality, since this measure provides a proxy of tree vigour. Previous studies have suggested that widespread slow growth of trees may be an early-warning signal of tipping points in response to climatic change (Camarero *et al.* 2015).

* Potential for feedback between disturbances and climate

When regime shifts occur there is evidence that that mortality and recruitment are governed in part by feedback loops. 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, some positive feedbacks can cause transition from one ecosystem state to another such as when forest canopies are subject to large disturbances leading to reduced seedling recruitment and invasion by grasses and shrubs in Mediterranean climates (Acácio *et al.* 2007). Positive feedbacks can also occur between different drivers such as when degradation and fragmentation increase fire risk in forests (Benchimol & Peres 2015). However, feedbacks such as these can occur at multiple different scales and thus are difficult to identify (Reyer *et al.* 2015).

* Brief description of study site

**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 that 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 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 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*); *Rubus fruticosus* agg., *Juncus effusus* and *Molinia caerulea* are also locally abundant. There are large populations of deer, ponies and cattle in the New Forest, resulting in high herbivore pressure. The portion of the site which we used for this study is likely to have experienced high browsing pressure since the 1960s (Mountford & Peterken 2003).

**Data collection**

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 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 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 a number of variables that were not recorded in previous surveys were collected: seedling density, canopy openness, soil characteristics, and herbivore pressure. 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. In addition the canopy openness of plots was assessed using a concave spherical densitometer in all four corners and the centre of 20 x 20 m plots. The mean of these measurements for each subplot was subsequently calculated for use analyses. The soil type in each subplot 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). To estimate herbivore abundance a manual dung count was carried out in each sub-plot following the commonly used faecal standing crop method (Marques *et al.* 2001; Campbell, Swanson & Sales 2004). Following Jenkins & Manly (2008), the individual pellets/bolus and their condition were recorded. The faecal matter of different animal species was recorded separately. The condition of each dung patch was classified as one of 4 groups:

1. surface smooth and shiny, interior firm;
2. dung surface pitted, interior friable (easily crumbled), < 10% of pellets/ bolus partially decomposed;
3. dung surface cracked, 10–50% of pellets/ bolus partially or completely decomposed;
4. > 50% of pellets/ bolus partially or completely decomposed.

**Statistical analysis**

**Individual tree mortality**

To determine whether some of the mortality observed in Denny wood could be explained by the self-thinning process we produced a statistical model of the relationship between log subplot stem density and log subplot basal area. To do this we used 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. 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.

**Recruitment**

To assess recruitment of trees we focussed on saplings (woody stems >1.3 m height and <10 cm DBH) and seedlings. To test the effect of the density of mature trees (stems >10 cm DBH) on that of saplings we produced generalised mixed models with a poisson error structure for the three major woody species present in Denny, beech, holly and oak. These models also included interactions with survey year to identify if the slope of the relationship between mature tree density and sapling density changed over time. To investigate the impact of canopy openings and grazing pressure on recruitment we produced generalised linear models of seedling density using dung count and canopy cover as explanatory variables.

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.

**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.

**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 (seedling, sapling, mature), age (in years), DBH (cm), basal area (m2)and, mean seed dispersal distance (mean distance from the source, in number of cells). DBH of mature trees and saplings is derived from the age of trees using an equation for beech growth defined in Holzwarth *et al.* (2013) and BA defined as . All grid cells in the model are considered suitable for individuals. Dispersal distance is a random number drawn from an exponential distribution with a mean of 5. Each grid cell can only contain one mature individual, but may contain multiple seedlings and saplings. 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 400 mature individuals with a random age drawn from an exponential distribution with a mean of 160 years assigned to each individual. At the same time 10,000 seedlings 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, seed dispersal from mature trees > 20 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 both seedlings and saplings. *Interactions* between individuals are the result of density dependant mortality processes, which show size asymmetry. This is modelled by defining a maximum number of saplings that can coexist within the area as 274, following Putman et al’s (1989) estimation of sapling density in ungrazed plots in the New Forest.

**Results**

**Tree mortality**

The slope of the relationship between log subplot stem density and log subplot basal area was positive (slope=0.41 ± 0.05, marginal R2=0.24, Figure 1). However, in general subplots lost both stem density and basal area between 1964 and 2014 (Figure 1). Given that self-thinning processes tend to be strongest when plots are increasing in biomass and losing stem density at the same time (Coomes & Allen 2007) such processes are unlikely to be responsible for the majority of tree death seen in Denny wood from 1964-2014.

When predicting the mortality of individual beech trees growth rate was considered the most important predictor, as it was included in all models with a ΔAICc≤7. Trees that grew slowly or shrunk were more likely to die than those that grew relatively quickly (slope=-0.59 ± 0.06, P value <0.001, Figure 2a). Next most important was tree DBH with an importance value of 0.8, and models suggested that tree size was positively correlated with probability of mortality (slope=0.21 ± 0.05, P value<0.001, Figure 2b). Distance to nearest dead tree and soil type were of similar importance with importance values of 0.52 and 0.45 respectively, with models indicating that trees closer to dead trees were more likely to subsequently die (slope=-0.24 ± 0.06, P value<0.001, Figure 2c) and trees located in areas of the forest where soils had higher sand content were less likely to die (slope=-0.27 ± 0.01, P value<0.001, Figure 2d).

**Tree recruitment**

There was a positive relationship between mature beech density and sapling density (slope= 1.27 ± 0.14, P value<0.0001), and sapling density tended to be reduced over time (slope= -0.69 ± 0.10, P value<0.0001). The relationship between mature beech density and sapling density grew more positive over time (interaction term=0.38 ± 0.09, P value<0.001), though since the density of mature trees was also reduced over this time period this effect was relatively unimportant in determining sapling densities. As the number of beech saplings declined during the years 1964-2014, so did the mortality rates of these saplings (Table 2). Conversely the proportion of saplings that became mature trees (>10 cm DBH) showed an increase over this time period.

Mean beech seedling density (± SE) in 2014 was 115.22 ± 32.14 seedlings ha-1. Canopy openness was positively related to beech seedling density (slope=0.56 ± 0.09, P value <0.001), but no other variables were included in models which had ΔAICc≤7 and thus were considered to have poor support. No metrics of deer or pony density were related to seedling density in any way.

* Plots of the relationship between Beech sapling density and Beech mature tree density
* Table showing the fate of sapling for each species
* Plots of the relationship between canopy openness and seedling density

**Discussion**

**References**

Acácio, V., Holmgren, M., Jansen, P.A. & Schrotter, O. (2007) Multiple Recruitment Limitation Causes Arrested Succession in Mediterranean Cork Oak Systems. *Ecosystems*, **10**, 1220–1230.

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. *Forest Ecology and Management*, **259**, 660–684.

Barlow, J. & Peres, C. a. (2008) Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 1787–94.

Benchimol, M. & Peres, C.A. (2015) Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation.

Brando, P.M., Balch, J.K., Nepstad, D.C., Morton, D.C., Putz, F.E., Coe, M.T., Silvério, D., Macedo, M.N., Davidson, E.A., Nóbrega, C.C., Alencar, A. & Soares-Filho, B.S. (2014) Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 6347–52.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*.

Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Oliva, J. & Vicente-Serrano, S.M. (2015) To die or not to die: early warnings of tree dieback in response to a severe drought (ed D Gibson). *Journal of Ecology*, **103**, 44–57.

Campbell, D., Swanson, G.M. & Sales, J. (2004) Methodological insights: Comparing the precision and cost-effectiveness of faecal pellet group count methods. *Journal of Applied Ecology*, **41**, 1185–1196.

Chao, K.J., Phillips, O.L., Gloor, E., Monteagudo, A., Torres-Lezama, A. & Martínez, R.V. (2008) Growth and wood density predict tree mortality in Amazon forests. *Journal of Ecology*, **96**, 281–292.

Coates, K.D. (2002) Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. *Forest Ecology and Management*, **155**, 387–398.

Coomes, D. a. & Allen, R.B. (2007) Mortality and tree-size distributions in natural mixed-age forests. *Journal of Ecology*, **95**, 27–40.

Coomes, D. a., Duncan, R.P., Allen, R.B. & Truscott, J. (2003) Disturbances prevent stem size-density distributions in natural forests from following scaling relationships. *Ecology Letters*, **6**, 980–989.

Fischer, J., Stott, J., Zerger, A., Warren, G., Sherren, K. & Forrester, R.I. (2009) Reversing a tree regeneration crisis in an endangered ecoregion. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 10386–91.

Fortin, M., Bedard, S., DeBlois, J. & Meunier, S. (2008) Predicting individual tree mortality in northern hardwood stands under uneven-aged management in southern Québec , Canada. *Annals of Forest Science*, **65**, 205.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe’er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U. & DeAngelis, D.L. (2006) A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, **198**, 115–126.

Holzwarth, F., Kahl, A., Bauhus, J. & Wirth, C. (2013) Many ways to die - partitioning tree mortality dynamics in a near-natural mixed deciduous forest (ed P Zuidema). *Journal of Ecology*, **101**, 220–230.

Jenkins, K.J. & Manly, B.F.J. (2008) A double-observer method for reducing bias in faecal pellet surveys of forest ungulates. *Journal of Applied Ecology*, **45**, 1339–1348.

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 (New York, N.Y.)*, **323**, 521–524.

Marques, F.F.C., Buckland, S.T., Goffin, D., Dixon, C.E., Borchers, D.L., Mayle, B.A. & Peace, A.J. (2001) Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. *Journal of Applied Ecology*, **38**, 349–363.

Martin, P.A., Newton, A.C., Cantarello, E. & Evans, P. (2015) Stand dieback and collapse in a temperate forest and its impact on forest structure and biodiversity. *Forest Ecology and Management*.

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.

Meddens, A.J.H., Hicke, J.A. & Ferguson, C.A. (2012) Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications*, **22**, 1876–1891.

Monserud, R. a. & Sterba, H. (1999) Modeling individual tree mortality for Austrian forest species. *Forest Ecology and Management*, **113**, 109–123.

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.

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). *Perspectives in Plant Ecology, Evolution and Systematics*, **2**, 223–272.

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. *Nature Climate Change*, **1**, 467–471.

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 (ed D Coomes). *Journal of Ecology*, **103**, 5–15.

Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E.H. & Chapin, F.S. (2012) Thresholds for boreal biome transitions. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 21384–9.

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, **1**, 103–113.

Seidl, R., Schelhaas, M., Rammer, W. & Verkerk, P.J. (2014) Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, 1–6.

Sheil, D., Burslem, D.F.R.P. & Alder, D. (1995) The Interpretation and misinterpretation of mortality rate measures. *Journal of Ecology*, **83**, 331–333.

Staver, a C., Archibald, S. & Levin, S. a. (2011) The global extent and determinants of savanna and forest as alternative biome states. *Science (New York, N.Y.)*, **334**, 230–2.

Steinkamp, J. & Hickler, T. (2015) Is drought-induced forest dieback globally increasing? (ed D Gibson). *Journal of Ecology*, **103**, 31–43.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. (2006) Warming and earlier spring increase western U.S. forest wildfire activity. *Science*, **313**, 940–3.

Figures



Figure 1 – Relationship between subplot stem density and total subplot basal area. Points represent individual plots in 1964 (red circles), 1996 (green triangles) and 2014 (blue squares). The solid line represents the prediction from a mixed model of this relationship with the grey band representing the coefficient confidence intervals. Note that that both x and y axes are log transformed.

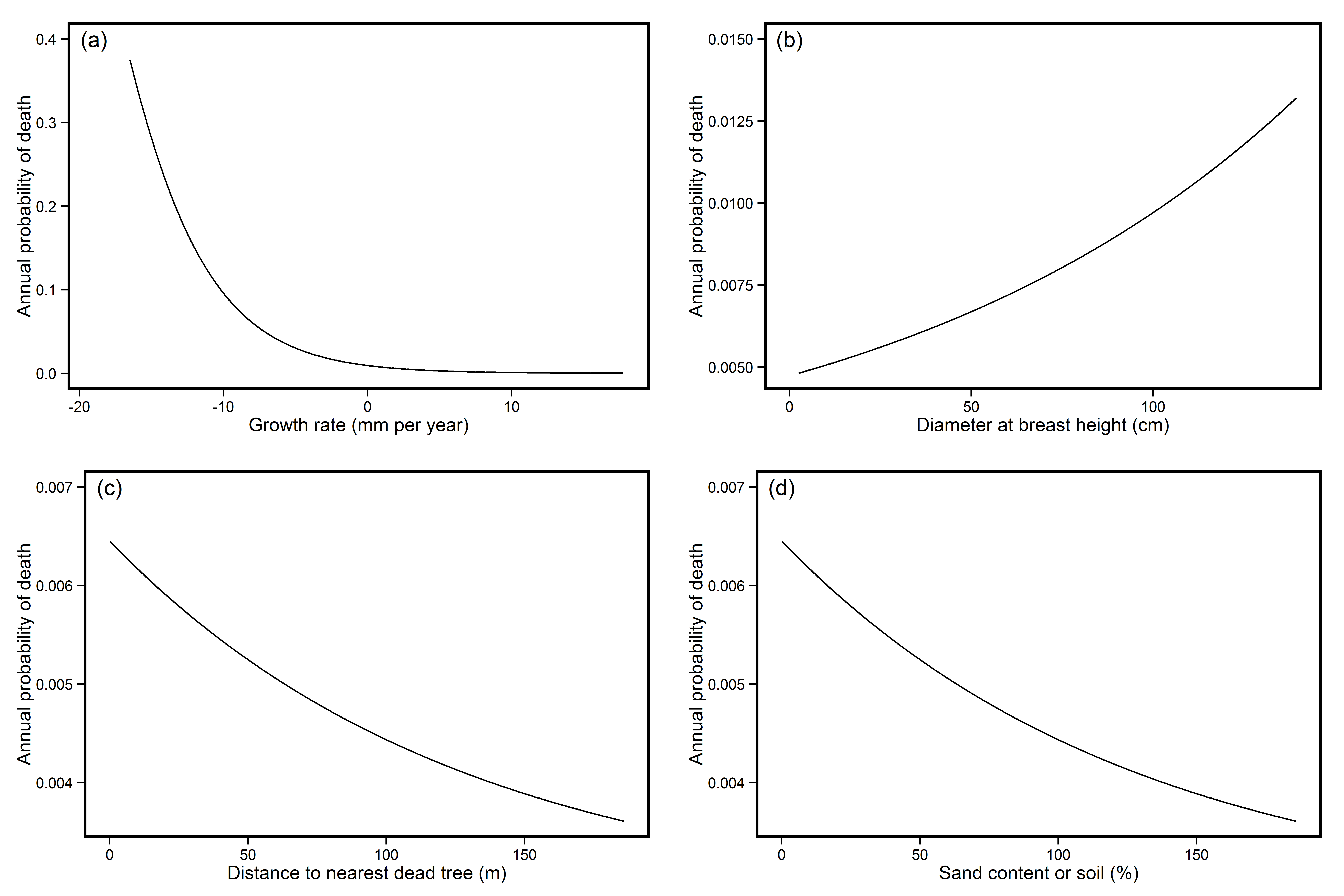


Figure 2 – Relationship between annual probability of beech tree death (a) growth rate per year, (b) diameter at breast height, (c) distance to nearest dead tree and (d) sand content of soil. Lines represent predictions generated from model-averaged parameter estimates.

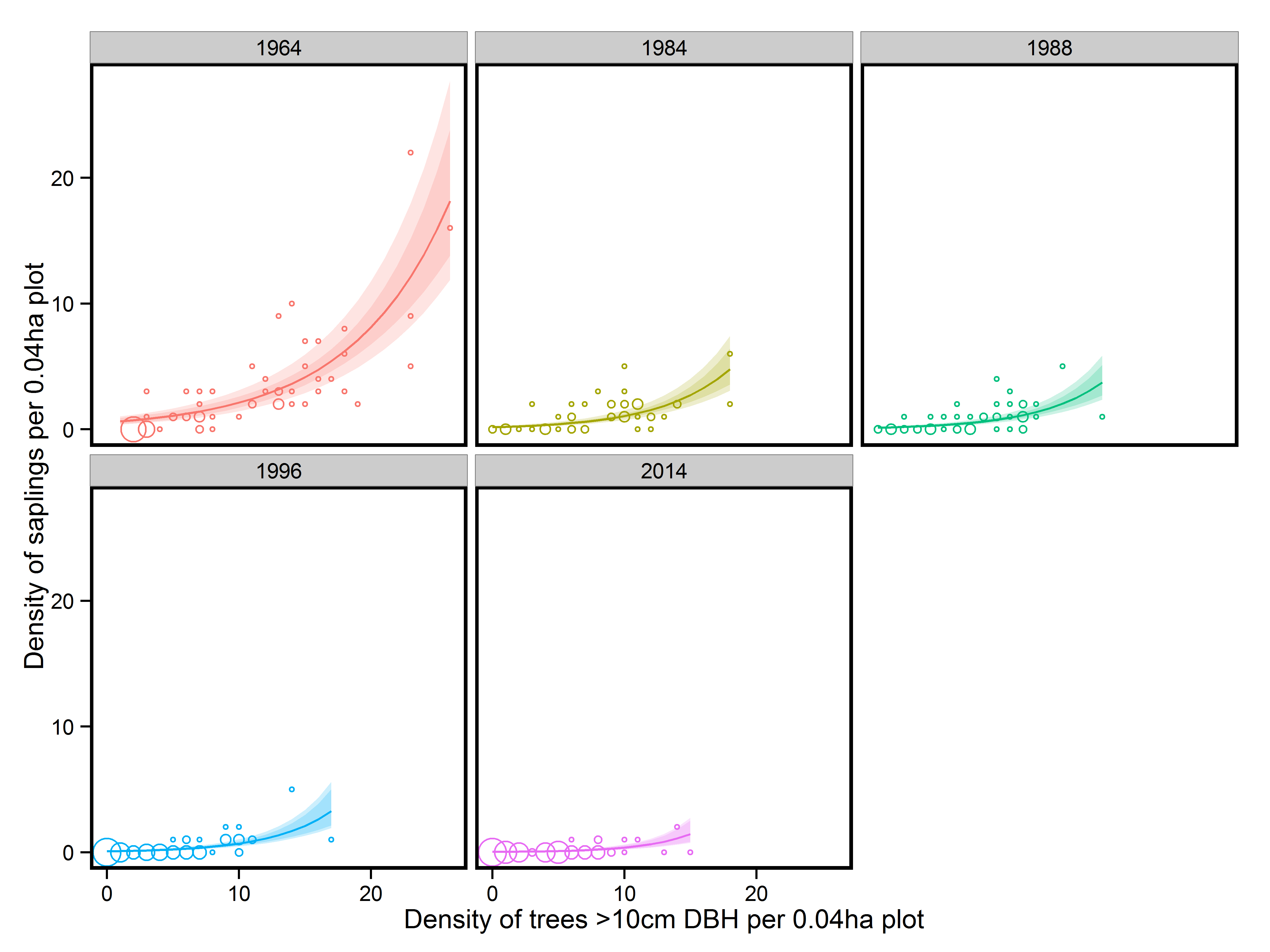


Figure 3 – The change in the relationship between the density of beech trees >10 cm DBH and the density of beech saplings. While the relationship between the two is clear in 1964 by 2014 this relationship has disappeared. Solid lines represent predictions from a mixed model containing an interaction between year and density of trees >10 cm. Coloured bands represent confidence intervals of the coefficients. Points represent plots, with the size of the point indicating the number of plots with the same density values in order to ease interpretation.

Tables

Table 1

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Variable** | **Estimate** | **Std. Error** | **Lower CI** | **Upper CI** | **p value** | **Importance value** |
| Intercept | -5.12 | 0.16 | -5.43 | -4.82 | <0.0001 | 1 |
| DBH | 0.21 | 0.05 | 0.11 | 0.31 | <0.0001 | 0.8 |
| Distance to dead tree | -0.24 | 0.06 | -0.36 | -0.12 | <0.0001 | 0.53 |
| Growth rate | -0.59 | 0.06 | -0.70 | -0.47 | <0.0001 | 1 |
| Sand content | -0.27 | 0.01 | -0.29 | -0.26 | <0.0001 | 0.45 |

Table 2

|  |  |  |  |
| --- | --- | --- | --- |
| Census period | Proportion died | Proportion increased to >10 cm DBH | Annual mortality rate |
| 1964-1984 | 0.56 | 0.14 | 4.07% |
| 1984-1988 | 0.11 | 0.2 | 2.79% |
| 1988-1996 | 0.15 | 0.32 | 2.01% |
| 1996-2014 | 0.09 | 0.61 | 0.50% |

**Supplementary materials**

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.

As well as individual based variables that may affect tree mortality we assessed the importance of soil properties as well, given that finer soils may be prone to water logging in the winter, which impedes root growth and consequently reduces the ability of trees to take advantage of water deeper in the soil in dry summers. To do this we used data on the proportion of each soil sample that was classified as sand during laboratory analyses.