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Incorporating stochasticity from extreme climatic events and multi-species competition relationships into single-tree mortality models

Rubén Manso [a,c,*], François Morneau [b], François Ningre [a,c], Mathieu Fortin [c,a]

[a] INRA, UMR 1092 LERFoB, 1 Rue de l'Arboretum, 54280 Champenoux, France
[b] Office National des Forêts, Département R&D, 100 Boulevard de la Salle, 45760 Boigny sur Bionne, France
[c] AgroParisTech, UMR 1092 LERFoB, 14 Rue Girardet, 54042 Nancy, France

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ABSTRACT

Extreme climatic events, such as windstorms and drought, and competition are some of the main factors underlying tree mortality in Atlantic and Central European forest stands. However, current empirical tree mortality models are not adapted to separately consider the different causes of mortality. In addition, these approaches do not distinguish between intra- and inter-specific competition. In this study, we present a comprehensive empirical single-tree mortality model that incorporates all of the aforementioned features. On the one hand, extreme events can enter the model via fixed effects and random effects. The latter allows taking the stochasticity of the process into consideration. The distribution of these random effects can be seen as an extreme event severity distribution, which is of great interest for carrying out stochastic simulations on tree mortality. On the other hand, intra- and inter-specific competition is taken into account through linear interactions of species-specific competition indexes and species factors. In order to test this approach, we selected the beech–oak mixture in France as a case study. Beech–oak mixed forests are a common type in France which provides owners with significant economic benefits. Our findings confirm that drought and, especially, windstorm occurrence are major causes of tree mortality in these forests. The model was able to capture the stochasticity of windstorm events by means of random effects. In terms of competition, the probability of mortality in beech understories was expected to decrease in the presence of oak overstories with respect to pure beech stands. This result reveals the importance of complementarity processes in tree mortality.

1. Introduction

Tree mortality has been traditionally classified in relation to the causes that trigger the process: catastrophic mortality and background mortality. Catastrophic mortality is normally related to the occurrence of extreme events (Vanclay, 1994), while background mortality would be the result of different factors that are detrimental for tree survival and that may become more pernicious due to individual tree competition (Jutras et al., 2003).

The occurrence of extreme climatic events is a serious concern for forest managers. In the absence of wildfires, windstorms have been reported to be the most important cause of catastrophic mortality in Atlantic and Central Europe by far. According to Schelhaas et al. (2003), 18.8 million m^3 of timber were damaged in European forests per year in the second half of the 20th century. The impact of windstorms exceeds that of direct damage on growing stocks. Indeed, dead wood accumulation may favour pest outbreaks (Peñuelas et al., 2001). Carbon balance may also be affected, especially in old-growth stands (Fortin et al., 2014).

Another important extreme climatic event is drought. Drought is usually acknowledged as a tree mortality risk factor in the Mediterranean basin (Peñuelas et al., 2001). However, findings from recent studies reveal that the impact of drought in the forests of Atlantic and Central Europe is not negligible (Bréda and Badeau, 2008). In these regions, extreme drought events are expected to increase (Planton et al., 2008). This suggests that drought may become a major concern for managers in these areas in the future.

With regard to background mortality, competition reduces tree survival of individuals already at risk due to other factors.

* Corresponding author at: INRA, UMR 1092 LERFoB, 1 rue de l'Arboretum, 54280 Champenoux, France.
E-mail addresses: ruben.manso@nancy.inra.fr, rmgforestal@hotmail.com (R. Manso), francois.morneau@onf.fr (F. Morneau), ningre@nancy.inra.fr (F. Ningre), mathieu.fortin.re@gmail.com (M. Fortin).

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Increasing single-tree competition leads to lower diameter increments, which eventually may end up in vigour loss of suppressed individuals (Bigler and Bugmann, 2003). In contrast to pure stands, competition effects in mixed forests do not just depend on the hierarchical position of individuals in the stand. For example, intra-specific competition has often been reported to be more intense than inter-specific competition (Larocque et al., 2013). This phenomenon is a consequence of the more efficient use of resources in mixed stands (complementarity; Vandermeer, 1989). A common case of complementarity occurs when differences in shade tolerance among species in the mixture exists (Kelty, 2006). In such a case, small trees of shade-tolerant species can efficiently compete for light (Das et al., 2008). As a result, they can thrive in the understory of stands dominated by shade-intolerant trees better than small individuals of the dominant species. Given the extent of mixed stands in Atlantic and Central Europe and the growing interest in these forest types, the study of the effect of complex competition interactions on mortality cannot be ignored.

Current approaches for modelling tree mortality have focused either on the physical processes that govern damage (mechanistic models) or on the stand and tree factors that increase mortality risk (empirical models). A review of both model types can be found in Hanewinkel et al. (2010). Mechanistic models have proved useful to study damage by both windthrow and drought. In the case of wind-mediated damages, the mechanistic approach is obvious, given the physical resistance of trees to wind (Gardiner et al., 2008). Concerning drought, it has been hypothesized that hydraulic failure and carbon starvation determine tree mortality in the short term (see McDowell, 2011, for a review). Detailed physiological data have allowed studying these processes from a mechanistic point of view (see McDowell et al., 2013, for a multi-model case study). However, a major shortcoming of mechanistic models is that they require very precise, not always available data (e.g. wind speed, local irradiation). On the contrary, empirical models can take different sources of risk into account and are definitely more accessible to forest managers. In spite of this flexibility, empirical models have very rarely attempted to account for both extreme event-mediated mortality and background mortality.

A number of empirical models have been specifically addressed at predicting windthrow damage through data from seriously damaged forests. Factors considered are those directly affecting canopy roughness and wind firmness: tree size, anchorage type, harvesting operations, stand density, stand composition and structure (Albrecht et al., 2012; Hanewinkel et al., 2008; Nagel and Diaci, 2006) or mechanical features (Bonnesoeur et al., 2013; hybrid model). In contrast, empirical modellers have paid much less attention to drought damage. In this respect, climatic variables such as temperature and precipitation or water deficit have only recently been used to predict tree mortality (Williams et al., 2012; Yaussy et al., 2013).

A major issue in empirical approaches is that they use data from damages produced by a limited number of extreme events (Hanewinkel et al., 2008; but see Rich et al., 2007). Extrapolation of these models may therefore result in biased predictions. The alternative would be to supplement tree and stand risk factors with a quantification of the actual phenomena that give rise to tree damage – wind speed or water deficit – at stand level. However, extreme events and their local effects are highly stochastic and difficult to measure (Bréda and Badeau, 2008). For example, wind profile may dramatically change during the same windstorm due to local stand structure (Gardiner et al., 2008), while similar wind speed would blow down more trees in shallower soils (Bonnesoeur et al., 2013). With regard to drought, a short but intense event may result in damage similar to that of a longer and moderate drought event (Vidal et al., 2010).

Competition in most empirical mortality models has been included through competition indexes at the stand and tree levels (e.g. Fortin et al., 2008; Rose et al., 2006). Among them, few examples are to be found where species-specific competition indexes were used (Jutras et al., 2003; Yang and Huang, 2013). However, none of these efforts has distinguished between intra- and inter-specific competition. A precise formulation of these competition types can be found in empirical growth models, though. For example, Canham et al. (2004) managed to modulate the net effect of a neighbour individual on the growth of a given target tree through a species-dependent estimable parameter. A non-spatial, more or less modified version of this approach is due to Palahi et al. (2008). A major drawback of these approaches is that different models are actually fitted for each of the target species. Therefore, simultaneous estimation of the parameters involved in intra- and inter-specific competition is not possible.

Given this background, it seems important to develop comprehensive statistical methods to efficiently deal with the main causes of tree mortality in Atlantic and Central Europe. Potential users of these methods are forest managers. In this respect, inputs for the resulting model should be easily available from forest inventories. Therefore, our objective is to fit an accessible single-tree mortality model that considers the effect of intra- and inter-specific competition and the stochasticity linked to extreme events. The main hypothesis to be tested is that the probability of a tree dying is higher when the individual is exposed to intra-specific competition than to inter-specific competition.

In order to accomplish our objective, we chose the case study of oak (*Quercus petraea* (Matt.) Liebl.) and beech (*Fagus sylvatica* L.) mixtures in France. This forest type is common and economically important in Europe (Pretzsch et al., 2013). According to the French National Forest Inventory definition, oak–beech mixed forests amount to 740,000 ha, which represents more than 10% of French mixed forests (Morneau et al., 2008). We used these data to develop a mixed-modelling approach that permitted us to incorporate extreme events in a stochastic fashion. The model also made it possible to include multi-species competition interactions.

2. Material and methods

2.1. Data and study area

Data from the permanent-plot network maintained by the *Laboratoire d'Etude de Ressources Forêt-Bois* (LERFoB) were used in the present study. The dataset consists of a compilation of thinning experiments originally aimed at studying growth patterns in even-aged oak and beech stands across France. These trials were set up between 1883 and 1956 (Table A1). The network was designed to cover the entire oak and beech distribution in continental France (Fig. 1). Because the dataset was made up of different experiments, dbh distribution within plots ranged from unimodal to J-shaped. Similarly, both plot size and measurement intervals varied across the plots (0.2–2.0 ha and 1–24 years, respectively). For the purpose of reducing errors related to overly long, scarcely represented intervals lengths, intervals longer than 10 years were discarded from the analysis.

In brief, the data used in the present study comprises over 180,400 dbh (diameter at breast height: 1.3 m) records from some 33,100 trees in 85 plots during the period 1922–2012. Mortality events were also recorded together with dbh measurements. The dominant species was either beech or oak in most cases. However, almost half of the sampled plots presented a certain proportion of mixture between beech and oak trees. Species other than beech and oak also existed in the sample plots. The most abundant was the European hornbeam (*Carpinus betulus* L.). Besides hornbeam, up to eight other less frequent taxa were