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Determinants of tree mortality in mixed old-growth *Nothofagus* forest

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ABSTRACT

Rates and spatial patterns of tree mortality were examined using long-term data from old-growth, mixed-species forests of the Maruia Valley, South Island, New Zealand. The aim of the study was to investigate patterns of tree mortality in two common, co-occurring species, *Nothofagus fusca* (Hook. f.) Oerst. and *Nothofagus menziesii* (Hook. f.) Oerst. The dynamics of three old-growth stands were followed over a 23-year period, using plots sized 0.8–1.0 ha. In total the fates of 1138 individual *N. fusca* and 1611 *N. menziesii* were recorded, which had annual mortality rates of 0.016 and 0.0089 per year, respectively. Differing spatial and size-related patterns of mortality were found between species. For both species, individual-based logistic models showed that slower growing trees were more likely to die than faster growing trees. *N. fusca* trees growing in previously disturbed stands were also more likely to die than those in undisturbed stands. Spatial point process analysis showed that dead *N. fusca* trees were spatially aggregated, and were segregated from living trees, a pattern that was consistent across both small and large trees. Dead *N. menziesii* were spatially aggregated, but were not segregated from living trees. Aggregated mortality of *N. fusca* trees should favor regeneration of this light-demanding species in large canopy gaps, perpetuating its aggregated distribution, whereas the lower mortality of shade-tolerant *N. menziesii* allows this species to persist. Our results demonstrate that performance differences in coexisting tree species can be manifested spatially. Between species, different mortality patterns may have implications for sustainable forest management.

1. Introduction

Demographic patterns and processes drive much of the spatial and temporal variation observed in forests. Tree deaths, for example, create canopy gaps and microhabitats for tree recruitment that leave legacies in forest composition and structure (Runkle, 1985; White and Pickett, 1985; Veblen, 1992). In mixed-species forest, different responses between species to such events will ultimately determine the course of stand dynamics. At juvenile life stages (e.g., seedlings, saplings and small trees) for example, interspecific trade-offs in demographic performance (i.e., growth and mortality) are well documented and occur across forest microhabitat and light gradients (Pacala et al., 1994; Lin et al., 2002). Juveniles of shade-tolerant species often have low mortality under low light conditions but only moderate growth responses to canopy openings, whereas juveniles of shade-intolerant species often have high mortality under low light but exhibit strong growth responses to canopy openings (Kobe et al., 1995; Kobe and Coates, 1997; Kneeshaw et al., 2006). These interspecific differences in juvenile demographic performance represent an important axis of niche differentiation (e.g., 'the regeneration niche'; Grubb, 1977), which influences the dynamics of mixed-species forests and may promote species' coexistence (Pacala et al., 1996). However, demographic rates also vary intraspecifically, especially, for example, with ontogeny (Boyden et al., 2009). As a consequence, performance differences among species are possible at many life stages. There remains a need to examine performance across a range of tree life-stages to comprehensively explain coexistence (Veblen, 1986; Abe et al., 1998; Lusk and Smith, 1998; Nakashizuka, 2001; Condit et al., 2006).

The mortality probability of an individual tree is commonly examined as a function of readily measured variables such as tree size, recent growth and the spatial pattern of trees or competitive neighborhood (Yao et al., 2001; Bigler and Bugmann, 2003; Wunder et al., 2008). More specifically, the importance of density-dependent mortality is often explored by studying changes in the spatial patterning of trees within a stand through time, or amongst stands of different ages (e.g., Gray and He, 2009); or by incorporating variables that describe the competitive neighborhood into models of individual tree mortality (e.g., Monserud,

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1976; Yao et al., 2001). Density dependent competition can often be inferred when the spatial pattern of surviving trees becomes more regular through time (Duncan, 1991; He and Duncan, 2000). For small trees it may be generally the case that competitive interactions drive such patterns of mortality; however, for relatively large trees it is usually difficult to determine a single direct cause of tree mortality (Franklin et al., 1987). Size-asymmetric competition for light is likely to be a relatively unimportant cause of mortality of established large canopy trees (Coomes et al., 2003), particularly in old-growth forest, where mortality results from a wide range of biotic and abiotic factors including pathogen or insect attack, mechanical failure and disturbance (Franklin et al., 2002; Busing, 2005). Furthermore, mortality in old-growth forests often operates contagiously, as evidenced by the progressive expansion of canopy gaps (Runkle, 1985, 1998). Spatial patterns of tree mortality, and interactions with previous canopy disturbances, could also be expected to vary interspecifically, for example, due to pathogen host-specificity and differing susceptibility of species to wind-throw (Canham et al., 2001; Worrall et al., 2005). Because spatial patterning of mortality events in turn influences microhabitats and light availability, and so has ongoing consequences for forest dynamics, spatial patterns of mortality must be considered in combination with tree size and competition, when examining species-specific patterns.

This study examines tree mortality for two southern beech species, *Nothofagus menziesii* (Hook. f.) Oerst. and *Nothofagus fusca* (Hook. f.) Oerst., which co-dominate extensive old-growth mixed-species forests in New Zealand. These are two of the most abundant tree species in New Zealand's remaining indigenous forest (Wardle, 1984; Ogden et al., 1996; Wiser et al., 2011) and such mixed-*Nothofagus* forest comprises >80% of privately owned indigenous forests managed for timber production (Ministry of Agriculture and Forestry, 2009). There is ongoing debate about the extent to which mortality of New Zealand *Nothofagus* spp. can be predicted, or pre-empted, in managed forests (Mason, 2000), as well as what impact silvicultural harvest will have on remaining canopy trees (Wiser et al., 2005). Large-scale forest dieback events in *Nothofagus* have been documented (Hosking and Kershaw, 1985; Jane and Green, 1986; Ogden et al., 1996), but mortality rates of *N. fusca* and *N. menziesii* trees have seldom been quantified in the forests where they co-occur. Previous demographic research in mixed-*Nothofagus* forests has focused largely on regeneration patterns and tree growth (e.g., Runkle et al., 1995, 1997; Stewart et al., 1991). Because *N. fusca* is considered relatively shade intolerant, and *N. menziesii* relatively shade tolerant, these species are considered to occupy different regeneration niches (Holloway, 1954; Wardle, 1984; Stewart and Rose, 1990; Ogden et al., 1996; Wiser et al., 2007), although both *N. fusca* and *N. menziesii* require canopy gaps to attain the canopy (Stewart and Rose, 1990; Stewart et al., 1991; Runkle et al., 1995, 1997).

Using data collected over 23 years from tagged *N. menziesii* and *N. fusca* trees on permanently marked plots (Stewart, 1992), we examine how mortality varied between the two species and with tree size. Because asymmetric competition for light is likely to be an important cause of mortality in small trees, a reasonable expectation is that the mortality of small trees will be highest in areas of intense neighborhood competition; we expect that this will be particularly apparent for shade-intolerant *N. fusca,* in contrast to shade-tolerant *N. menziesii* (Hypothesis 1). Mortality of large individuals is likely to be driven by disturbance rather than competition for light (Franklin et al., 1987; Coomes et al., 2003). If previous disturbance increases subsequent mortality risk then trees growing in disturbed stands will likely have much higher mortality than average (Hypothesis 2), and where disturbance kills multiple trees large dead trees are likely to be spatially aggregated, and segregated from living trees (Hypothesis 3). Finally, native *Platypus* spp. (Platypodidae) beetles attack *Nothofagus* individuals and provide a vector for infection by pathogenic *Sporothrix* fungi, which in turn infect the inner sapwood of trees and lead to their death or stem rot (McCracken et al., 1994). In forests managed for timber, it has been suggested that new *Platypus* infections of living trees usually occur within 5 m of a previous host tree, large trees are more frequently infected than small trees, and *N. fusca* is more frequently attacked than *N. menziesii* (Litchwark, 1978; McCracken et al., 1994; Wiser et al., 2005). However, little is known about the spatial dynamics of *Platypus* infection in unmanaged forests (McCracken et al., 1994). Based on the dynamics of managed forests, we hypothesize that tree mortality resulting from *Platypus* attack will be spatially clustered, especially for *N. fusca* (Hypothesis 4).

2. Materials and methods

2.1. Species, study area and data collection

The study was conducted in low elevation old-growth mixed *Nothofagus* forest in the Maruia Valley, South Island, New Zealand (42°13′S, 172°16′E). The study sites (Pell Stream, Rough Creek, Station Creek) were located on relatively flat and fertile alluvial terraces and were dominated, across all tree size classes, by *N. fusca* and *N. menziesii*. *N. fusca,* considered less shade-tolerant than *N. menziesii,* grows larger (e.g., the largest trees recorded are >200 cm diameter (*D*), 35 m tall vs. 150 cm diameter, 25 m tall for *N. menziesii)* but is thought to have a shorter maximum longevity (Wardle, 1984). The maximum tree diameter in the present study was 230 cm for *N. fusca* and 80 cm for *N. menziesii,* and size-class structures for both were similar to those reported for a nationally representative sample of mixed *Nothofagus* forest (Wiser et al. 2011).

Elevation across the three study sites ranges from 450 to 600 m a.s.l. Mean annual precipitation at nearby Springs Junction (425 m elevation, approximately equidistant to the three study plots) is 2280 mm, with >130 mm recorded every month (National Institute of Water and Atmospheric Research, unpublished data). Mean annual temperature is 9.8 °C, with a monthly minimum of 3.8 °C (July) and monthly maximum of 15.2 °C (January). Valley-floor soils developed on Pleistocene glacial outwash deposits contain granite, greywacke and schist (Bowen, 1964). These soils are acidic (mineral soil pH 4.0) with relatively high levels of available P.

At each of the three sites a permanent plot was established in 1986, each plot being 0.8–1.0 ha in size (100 × 80 m, 150 × 60 m and 100 × 100 m). Plots were subdivided into contiguous subplots of 5 × 5 m, within which all trees ($D \geqslant 5$ cm) were uniquely tagged, identified and measured. On the Station Creek plot, tree locations were mapped, recording *x* and *y* coordinates (to within 0.5 m) within each 5 × 5 m subplot during plot establishment in 1986, whereas at Pell Stream and Rough Creek trees were mapped in 2009–2010, taking care to locate and map dead trees wherever possible. Across these two plots a small number ($n = 72$) of dead trees, typically with $D < 10$ cm, were not re-located, and for analyses were assigned a location at the middle of the 5 × 5 m subplot where they were originally recorded. In 2001 and 2009 the diameter of each tagged tree was remeasured, and recruitment of new individuals ($D \geqslant 5$ cm) determined. In 2001 and 2009 the new recruits were tagged, measured and their location recorded.

Mortality censuses recorded the fate of each tagged individual during the austral summers of 1987–1998, 2001 and 2009. During each mortality census, stem and crown debris for trees that had died since the preceding census were examined and the incidence of *Platypus* infection recorded. *Platypus* infection was evidenced by the presence of 'frass' and small borer holes (e.g., 1–2 mm in