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Disentangling drivers of tree population size distributions

Duane A. Peltzer [a,*], Robert B. Allen [a], Peter J. Bellingham [a], Sarah J. Richardson [a], Elaine F. Wright [b], Phil I. Knightbridge [c,1], Norman W.H. Mason [d]

[a] *Landcare Research, P.O. Box 69040, Lincoln 7640, New Zealand*
[b] *Department of Conservation, P.O. Box 13049, Christchurch 8141, New Zealand*
[c] *Department of Conservation, Private Bag 701, Hokitika 7842, New Zealand*
[d] *Landcare Research, Private Bag 3127, Hamilton 3240, New Zealand*

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ABSTRACT

There are pressing needs to evaluate and manage the effects of biological invaders in forest ecosystems in the face of long-term changes and anthropogenic influences on these systems. Hence, disentangling the effects of different drivers is critical for understanding the relative importance of biological invaders on shaping future forest structure and composition, and how management of these invaders changes forest ecosystem functioning. We evaluated the effects of major drivers of changes in tree population structure in New Zealand forests using a national grid of permanent vegetation plots and long-term (>15 year) ungulate exclosures. The long-term effects of disturbance and other drivers leave imprints in tree population dynamics and size class structure. For example, the effects of natural disturbance are expected to have different effects from those of browsing or folivorous animals. We quantified variation in tree size class distributions for common tree species, and plant functional groups defined by mammal diet selection, in 986 permanent forest plots and in 88 paired ungulate exclosure and control plots. Our analyses revealed that: (i) strong changes in size class distributions have occurred in recent decades, (ii) tree species selected or preferred by invasive ungulates (primarily red deer) demonstrate particularly strong shifts, (iii) inclusion of climate or soil variables into statistical models of exclosure effects on size class distributions were overwhelmed by temporal changes and effects of forest stand successional stage. These findings demonstrate that the effects of invasive herbivores can be distinguishable from other drivers such as disturbance or successional stage, and suggests that these changes will ultimately be manifested in altered forest community composition and ecosystem processes.

1. Introduction

Forests are increasingly managed for multiple goals including biodiversity and carbon sequestration in the face of global change (e.g., Houghton, 2005; Schumacher and Bugmann, 2006; Lindenmayer et al., 2006; Hyvönen et al., 2007; Pichancourt et al., 2014). These goals depend on community and ecosystem processes that are controlled by tree populations, and are thus driven by both short- and long-term biotic and abiotic processes. Changes in tree populations are difficult to quantify directly because there are often different controls or filters on recruitment, growth and mortality of individuals (Clark, 1990; Silvertown et al., 1993; Coomes and Allen, 2007; Kuijper et al., 2010). Despite this, there is an increasing desire to manage and monitor tree populations for purposes such as the maintenance of forest ecosystem processes or to determine the long-term effects of management activities (e.g., Kurz et al., 2008; Luyssaert et al., 2008; Peltzer et al., 2010). For example, the effects of disturbance, animal hyperabundance and biological invasions alter forest species composition and successional processes (Waller and Alverson, 1997; Augustine and McNaughton, 1998; Côté et al., 2004; Kuijper et al., 2010; Martin et al., 2010; Nuttle et al., 2014). An unresolved issue is how to quantify and monitor the imprint of these drivers on longer-term tree population processes, and ultimately to forest species composition and ecosystem processes. An important family of indicators to accomplish this is to predict and quantify drivers of variation in tree size class distributions (Condit et al., 1998; Souza, 2007; Bin et al., 2012; Helm and Witkowski, 2012).

Species and functional group size class structures can be used to assess drivers of population change in tree species (e.g., Knox et al., 1989; Condit et al., 1998; Niklas et al., 2003; Helm and Witkowski, 2012; Cousins et al., 2014). Changes in the size class distributions

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[*] Corresponding author. Tel.: +64 3 321 9773; fax: +64 3 321 9998.
E-mail address: peltzerd@landcareresearch.co.nz (D.A. Peltzer).
[1] Deceased.

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of plant populations have been widely applied in ecology and evolutionary biology to quantify the effects of self-thinning, allometric scaling of resources, and abiotic influences on population demographic processes (e.g., Hara, 1984, 1988; Lomnicki, 1988; Cyr et al., 1997; Menning et al., 2007; Muller-Landau et al., 2006; Coomes et al., 2012). For example, the "inverse J-shaped" size class distribution reflects the relatively high abundance of juveniles relative to adults, and can indicate healthy, growing populations whereas other distributions may not (Condit et al., 1998; Beschta, 2005; Feeley et al., 2007; but see Venter and Witkowski, 2010). Here, we use this approach to evaluate the effects of invasive herbivores and several putative major drivers of changes in tree population structure throughout New Zealand forests using a national grid of permanent vegetation plots and long-term ungulate exclosures (Coomes et al., 2002; Allen et al., 2003; Mason et al., 2010). More specifically, we determine whether the impacts of mammalian herbivores can be distinguished from other drivers such as tree species, physical disturbance, environmental and community compositional effects (Pickett and White, 1985; Allen et al., 2002; Lewis et al., 2004; Way and Oren, 2010; Malizia et al., 2013). For example, increasing elevation and latitude both structure forest composition and size-class distributions through environmental effects whereby trees at higher latitudes or elevation are longer-lived and skew size class distributions towards increasing dominance by larger trees (e.g., Bellingham et al., 1999; Coomes and Allen, 2007; see also Fig. 1). Although there are multiple potential drivers of variation in size class distributions that influence tree populations through alteration of population vital rates (i.e., recruitment, growth or mortality of individual tree stems), a major focus of management and monitoring internationally is to determine the effects of herbivores on forest properties and processes (Weisberg and Bugmann, 2003; Danell et al., 2006; Beschta and Ripple, 2009; Condit et al., 2014; Nuttle et al., 2014).

Understanding the consequences of increasing abundance of mammalian herbivores and their effects in forest ecosystems is a widespread phenomenon: recent examples include the hyperabundance of white-tailed deer in eastern North America (Côté et al., 2004; White, 2012) and elk in Yellowstone (Beschta, 2005; Beschta and Ripple, 2009), restoration of large mammals to savanna systems in southern Africa (Loarie et al., 2009), multiple ungulate species in the Białowieża Primeval Forest (Poland) (Jedrzejewska et al., 1994; Kowalczyk et al., 2011), overabundance of Sika deer in Japan (Takatsuki, 2009), and the well-documented invasion by non-native ungulates and brushtailed possums in New Zealand's indigenous forests (Holloway, 1950; Mark and Bayliss, 1975; Nugent et al., 2001; Allen and Lee, 2006). One challenge is that the 'palatability' of species is context-dependent, i.e. can vary with environment, neighbouring species composition, apparency, or abundance of competing herbivore species, making it somewhat difficult to compare results among different studies at relatively small spatial scales (Bee et al., 2007; Parkes and Forsyth, 2008; Wright et al., 2012; Castagneyrol et al., 2013). However, changes in size class distributions of plant taxa or functional groups should be predictable from the long-term influence of different herbivores. For example, ungulates should reduce the number of small stems for susceptible (i.e. palatable) species, which then results in lower recruitment of stems into larger size classes (Fig. 2). Furthermore, the rate of these changes will depend on features of the plant taxa (i.e. population vital rate, speed of transition from seed to sapling to mature stem, frequency of successful reproduction) and on animal density, functional response, and efficacy (Crawley, 1983; Danell et al., 2006; Bee et al., 2007; Martin et al., 2010; Tanentzap et al., 2012; Holland et al., 2013). Here, we do not determine these demographic parameters for individual species or populations, but rather, use size class distribution as a well-documented method for understanding changes in forest ecosystems (Condit et al., 1998; Hutchings, 1997; Coomes et al., 2012).

We determined which major drivers operate at a national scale using long-term and large-scale datasets from New Zealand forests. More specifically, we test the influence of common invasive herbivores and other major drivers on the size class distributions of trees through consideration of effects of: (1) species, (2) physical disturbance and successional stage, (3) herbivory by ungulate browsers and an invasive mammalian folivore, (4) reproductive failure or decoupling, (5) environmental effects climate soil fertility, and (6) compositional influences including compensatory growth, sampling bias (all of which are detailed further in Table 1). We do not develop a detailed rationale for inclusion of these drivers because their effects on tree population demography and size class distributions have been previously synthesized (e.g., Coomes et al., 2012; Malizia et al., 2013). The primary motivation for this paper is to determine whether the effects of invasive herbivores can be distinguished from other processes or drivers affecting tree size class distributions.

Fig. 1. Representative photograph illustrating how multiple drivers operate to control tree demographic processes and size class distributions (summarized in Table 1). The view is looking west near the Main Divide of the Southern Alps, New Zealand. Debris from the nearby "fallen mountain" disturbed the forest vegetation in the foreground. An obvious elevational treeline is also seen; less evident are the influences of invasive herbivores (e.g., red deer) are also having in these forests. A national network of forest vegetation plots and long-term exclosures was used to determine the effects of these various drivers on tree size class distributions.

2. Methods

2.1. Data for New Zealand forests

Indigenous forests cover approximately 6.4 million ha or 23% of the land surface area of New Zealand (Wardle et al., 1983). These forests are dominated by one or more species of southern beech (Nothofagaceae), broadleaved tree species such as *Beilschmiedia tawa*, *Griselinia littoralis*, *Melicytus ramiflorus*, *Weinmannia racemosa*, *Metrosideros umbellata* and *Metrosideros robusta*, and admixtures with conifer species (mostly Podocarpaceae, also some Cupressaceae and Araucariaceae; plant names follow the Allan Herbarium 2002–2014). Comprehensive descriptions of New Zealand's forests are given in Wardle et al. (1983), Wardle (1984, 2002), and Wiser et al. (2001). These forests were sampled using permanent plots (20 m × 20 m) located on a systematic 8-km grid across the area mapped as indigenous forest. The sampling approach is described in Coomes et al. (2002) and Allen et al. (2003); see also Payton et al. (2004), Hurst and Allen (2007). These