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Cattle affect early post-fire regeneration in a *Nothofagus dombeyi–Austrocedrus chilensis* mixed forest in northern Patagonia, Argentina

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ABSTRACT

In forest ecosystems where infrequent, severe fires have been an important process in shaping ecosystem structure, understanding the effects of introduced livestock on post-fire recovery of the vegetation is essential for effective forest resource management and preservation. In Nahuel Huapi National Park in northwestern Patagonia, we studied the effects of livestock on the post-fire recovery of a *Nothofagus dombeyi–Austrocedrus chilensis* forest that was burned in 1999. We experimentally excluded cattle by fencing plots and compared the vegetation characteristics of fenced and unfenced control plots over a 5-year period. Although cattle did not significantly reduce total plant cover or total species richness, they did reduce maximum heights of woody species including the dominant tree species. *Chusquea culeou*, a tall understory bamboo, can impede establishment and height growth of the dominant tree species. Although *C. culeou* accounts for the largest percentage of cattle diet, its mean cover and mean maximum height were not strongly affected by cattle. The reduction in the height growth of seedlings of *N. dombeyi* and *Austrocedrus* in the unfenced areas implies that presence of cattle in the recently burned areas may contribute to a post-fire transition from tall forest to bamboo-dominated shrubland that is already widespread in this landscape. Thus, these results provide support for the fencing of recently burned *Nothofagus* and *Austrocedrus* forests in the national parks for periods long enough to allow the dominant tree species to grow to heights at which they are no longer severely inhibited by cattle browsing.

1. Introduction

A major challenge in community ecology is improved understanding of species interactions in the context of fluctuating environmental conditions created by large, severe disturbances (Agrawal et al., 2007). In many ecosystems infrequent, broad-scale natural disturbances are important in driving ecological processes and patterns that persist for decades or centuries (Attiwill, 1994; Perera and Buse, 2004). It is widely recognized that in many temperate forests, severe fires occurring at intervals of many decades or centuries are key natural disturbances that trigger massive tree establishment and allow the development of long-lasting ecological structure. However, in widespread areas of temperate forests in the southern Andes of Argentina and Chile, the introduced large herbivores (livestock and deer) have potentially altered the

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early phases of plant community responses to wildfire in forested habitats (Ramirez et al., 1981; Veblen et al., 1989; Raffaele and Veblen, 2001). Although infrequent, severe fires may be an inherent process consistent with preservation of many native forest ecosystems, the effects of introduced animals on post-fire recovery patterns are often uncertain. Thus, where land management goals include preservation or restoration of native forest structures and processes, knowledge of how introduced animals may alter community response to infrequent, severe fires is critical.

In most terrestrial habitats worldwide, fire and large herbivores are major influences on the composition and structure of vegetation through their roles as consumers of plant material. Fire as an abiotic consumer and herbivores (e.g. large mammals) as biotic consumers may create negative feedbacks between these two disturbance types and/or may result in synergistic and more extreme influences on vegetation composition and structure (Bond, 2005). However, the nature of the interactions between these disturbance types and their consequences for plant community composition and structure are highly context specific (Bond, 2005; Agrawal et al., 2007).

In northwestern Patagonia (Argentina), two of the most important disturbances are fire (Kitzberger and Veblen, 1999; Veblen et al., 2003; Alauzis et al., 2004) and herbivory by large introduced mammals, such as livestock and red deer (Martín et al., 1985; Veblen et al., 1989, 1992a,b; De Pietri, 1995; Relva and Veblen, 1998, 2001; Vázquez, 2002). Fire, both natural and human-set, historically has played a major role in creating landscape patterns in northwestern Patagonia along the gradient from dry steppe to wet Andean rain forests (Veblen et al., 2003). The relative importance of fires set by Native Americans prior to European settlement in the late 19th century versus fires ignited by lightning, as well as the effects of fire exclusion during the 20th century, is highly variable according to ecosystem type and location along the gradient from steppe to Andean rainforests (Kitzberger et al., 1997; Veblen et al., 1999, 2003; Kitzberger and Veblen, 2003). The focus of the current study is on the *Nothofagus dombeyi–Austrocedrus chilensis* mixed forest type which occupies an intermediate position along the precipitation gradient from xeric Patagonian plains to the wet Andean cordillera. Most stands of *N. dombeyi–A. chilensis* originated after widespread fires during the 19th and early 20th centuries ignited either by humans or lightning and associated with exceptional drought (Kitzberger and Veblen, 2003; Veblen et al., 2003). However, following establishment of infrastructure for suppressing fires in the 1940s, the extent of burning in this forest type has been relatively small compared to the extent over the previous 150 years (Veblen et al., 2003).

Overlapping with the reduction of fire occurrence in these forests in the second half of the 20th century has been a major change in the use of the *N. dombeyi–A. chilensis* forest type by large mammalian herbivores. Native large mammals in this region include the guanaco (*Lama guanicoe*) and the huemul deer (*Hippocamelus bisulcus*) both of which are believed to have preferred open habitats of the steppe or the alpine timberline (Povilitis, 1978; Caviares and Fajardo, 2005) over dense forests of *N. dombeyi* and *Austrocedrus*. Among native ungulates, the miniature pudu deer (*Pudu pudu*) occurred in dense forests; however, it is not believed to have been abundant and probably did not have a major influence on forest structure (Vázquez, 2002). Thus, the introduction of cattle and several species of Eurasian deer (*Cervus elaphus*, *Dama dama* and *Axis axis*) and their abundance in dense forests, at least locally, is a major departure from the conditions under which the *N. dombeyi* and *A. chilensis*-dominated forests originated. Cattle were present in the steppe of northwestern Patagonia as early as the late 18th century, but were not abundant in forested areas until the phase of intensive European settlement and forest burning of the late 19th and early 20th century (Veblen and Lorenz, 1988). Eurasian deer were introduced as early as 1917 to create a game resource and by the 1940s they were abundant in some areas (Daciuk, 1978; Ramilo, 1985). A survey of the large area of Nahuel Huapi National Park (706,000 ha approximately) in northwestern Patagonia estimated that about 56% of the park's terrestrial surface is affected by cattle to some degree (Lauría Sorge and Romero, 1999). Studies conducted mostly during the 1980s and early 1990s have shown that cattle and cervids have greatly affected the vegetation of the northern Patagonia landscape, including *Nothofagus* and *Austrocedrus* forests (Martín et al., 1985; Veblen et al., 1989, 1992b; Relva and Veblen, 1998). This research has shown that heavy cattle pressure may locally impede or dwarf the regeneration of some arboreal species, shift dominance toward spiny shrubs, favor the abundance of introduced plants, and under some circumstances may shift community structure from tall forests to shrublands (Veblen et al., 1992b, 2003; Relva and Veblen, 1998; Kitzberger et al., 2005). Most studies have examined deer and livestock impacts on mature plant communities with relatively few studies focusing on the earliest and probably most critical stages of vegetation recovery following fire (but see Raffaele and Veblen, 2001).

The widespread occurrence of fires during the extreme drought of the late 1990s in forests in northwestern Patagonia (Administración de Parques Nacionales, 1999) provided a rare opportunity to examine the effects of introduced animals on patterns of early post-fire regeneration in the *N. dombeyi–A. chilensis* forest type. Our research presents the first experimental results on livestock browsing on early post-fire recovery in this forest type in northwestern Patagonia. Over a 5-year period, we studied the effects of cattle on post-fire vegetation by monitoring exclosures and control plots in a *N. dombeyi* and *Austrocedrus* mixed forest, situated in Nahuel Huapi National Park. The objective of this study is to determine how introduced cattle affect, directly and indirectly, the processes of early post-fire regeneration in a *N. dombeyi–Austrocedrus* mixed forest. Because both dominant tree species are obligate seeders that lack the ability to resprout vegetatively (Kitzberger and Veblen, 1999; Veblen et al., 2003), the post-fire recovery of this forest type may be particularly vulnerable to the effects of introduced cattle.

2. Methods

2.1. Study area

The study was conducted in a *N. dombeyi–A. chilensis* forest, located on the eastern side of Lago Espejo, in Nahuel Huapi