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Impact of introduced herbivores on understory vegetation along a regional moisture gradient in Patagonian beech forests

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ABSTRACT

Introduced ungulates can alter understory structure and composition posing a serious threat to forest biodiversity. Yet how large-herbivore impacts in forested regions vary along major environmental gradients remains little explored. If ungulate effects shift with habitat conditions, then management could be tailored to protect most vulnerable forests. We tested the hypothesis that the extent of livestock impact on understory vegetation increases with habitat moisture across *Nothofagus dombeyi* forests in Nahuel Huapi National Park, NW Patagonia, Argentina. Understory composition and species diversity were compared for paired sites ($N = 5$), which were historically used by cattle or remained free of livestock for more than 50 yr, and were located along a regional precipitation gradient (1500–2800 mm/yr). Long-term cattle presence reduced the cover of sub-canopy trees, shrubs and bamboo by 57–83%, and increased the relative cover of ground-layer herbs, regardless of habitat moisture. Livestock effects on species composition increased towards the wettest forests, which contained more species exclusive to either browsed or unbrowsed sites. Livestock presence increased species richness (α diversity) and within-site heterogeneity (β diversity) in some locations, but mostly reduced species evenness (30%) throughout the moisture gradient. Species turnover at the gradient scale was lower across browsed sites than for livestock-free sites. Our results indicate that the historical presence of domestic cattle induced region-wide changes in understory communities, highlighting the vulnerable nature of the local flora to ungulate disturbance. The greater impact of livestock browsing on the species composition of wetter forests was consistent with the role of plant growth–defence trade-offs along resource gradients. We suggest that the erosion of understory vegetation attributed to domestic herbivores in Patagonian beech forests can be mitigated by adjusting current animal stocks, while moister forests should be given the highest conservation priority.

1. Introduction

The ecological impacts of exotic herbivores are a major conservation concern in forests worldwide. The introduction of ungulate herbivores may drastically alter understory structure and composition, affecting biodiversity from local to regional scales (Vázquez, 2002; Spear and Chown, 2009; Martin et al., 2010; Nuttle et al., 2011; Hegland et al., 2013), with consequences on multiple ecosystem functions (Pastor and Cohen, 1997; Wardle and Bardgett, 2004). Large herbivores interact with environmental conditions in creating the spatial patterning of vegetation observed at various scales (Senft et al., 1987; Adler et al., 2001; Frank, 2006). Yet, how grazing/browsing impacts in forest communities vary across relevant ecological gradients remains little explored (Randall and Walters, 2011). If ungulate effects depend on environmental context as determined by habitat moisture or productivity, then management options could be tailored to prevent biodiversity loss from the most vulnerable forest sites.

Herbivore effects are expected to change with environmental conditions according to dominant plant species' traits and susceptibility to herbivory (Coley et al., 1985; Pastor and Cohen, 1997; Díaz et al., 2006). Several models predict an increase in the magnitude of grazing effects on plant composition along productivity or moisture gradients (Milchunas et al., 1988; Leibold et al., 1997; Chase et al., 2000). Weaker effects in less productive or drier systems may be explained by dominant species having traits that provide tolerance to low resource supply as well as resistance to

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herbivory (Coley et al., 1985). Conversely, herbivore-driven compositional changes in productive or moister habitats would reflect the prevalence of plant traits for aboveground competition, which render dominant species more susceptible to herbivory (Milchunas et al., 1988; Díaz et al., 2006). Thus, a dominance shift towards well-defended, less palatable species may be apparent under intense herbivory in productive sites (Leibold et al., 1997; Olff and Ritchie, 1998). In addition, ungulate herbivory may either increase or decrease plant diversity, depending on the balance between local colonization and extinction processes, and herbivore selectivity for competitive dominant *vs.* subordinate species (Milchunas et al., 1988; Olff and Ritchie, 1998). Herbivore effects on species richness and evenness are predicted to shift from negative to positive with increasing habitat productivity (Proulx and Mazumder, 1998; Hillebrand et al., 2007).

While hypotheses for context-dependent herbivore effects have gained support in grass-dominated systems (e.g. Milchunas and Lauenroth, 1993; Anderson et al., 2007; Lezama et al., 2014), they have barely been tested in forested landscapes (Randall and Walters, 2011). Studies in temperate and boreal forests often focus on ungulate density as a major driver of understory community structure (Wardle and Bardgett, 2004; Royo et al., 2010; Didion et al., 2011; Wright et al., 2012; Hegland et al., 2013). Few have addressed the interactive effects of herbivory and environmental gradients in shaping regional patterns of understory composition and diversity (Randall and Walters, 2011; Suzuki et al., 2013). In aspen forests of Michigan (USA), deer herbivory decreased forb biomass and plant richness mostly in high-productivity sites, but increased fern and sedge biomass in low-productivity ones (Randall and Walters, 2011). In contrast, in warm-temperate forests of Japan, deer herbivory was the main determinant of ground-layer species composition, irrespective of canopy openness and habitat moisture (Suzuki et al., 2013). In the latter study, plant richness peaked at intermediate herbivore densities (Suzuki et al., 2013), whereas in cool-temperate forests of Patagonia, the effect of exotic ungulates on species richness may vary with canopy cover (Vázquez, 2002). These examples suggest that general patterns for herbivore impacts in forested systems may be more elusive than expected from current grazing models.

Mechanisms affecting herbivore effects along productivity or moisture gradients in forest ecosystems may differ from those reported in grasslands due to differing dominant plant life forms. In grassland communities, large herbivores often suppress dominant grasses, making resources available to less competitive species (Milchunas and Lauenroth, 1993; Olff and Ritchie, 1998). In contrast, in closed-canopy forests, ungulates consume subordinate understory species (shrubs, trees) and ground-layer herbs, while canopy trees remain largely inaccessible. Further, understory species are generally constrained by their tolerance to shading (Grime, 2001; Coomes et al., 2009), and may be ill-equipped to regrowth after browsing, although they may still possess effective structural defenses (Bryant et al., 1983; Hanley et al., 2007). Browsing could thus exert similar impacts in forest communities along broad habitat gradients (Suzuki et al., 2013), unless higher light availability in less productive or drier sites favors fast-growing species with greater susceptibility to herbivory (Coley et al., 1985; Coomes et al., 2009). Ungulate browsers may also release low-growing herbs from shrub (Hegland et al., 2013) or bamboo competition (Darabant et al., 2007), and this indirect effect could be stronger in wetter forests with greater light limitation (Vázquez, 2002; Randall and Walters, 2011). At the regional scale, whether ungulate herbivores exacerbate or reduce vegetation patchiness will depend on the interplay between animal densities, the steepness of underlying environmental gradients, and the size and composition of plant species pools (Adler et al., 2001; Frank, 2006; Suzuki et al., 2013).

By changing the structure and composition of understory communities, large ungulates may also alter the amount and diversity of litter material transferred to the forest floor (Pastor and Cohen, 1997; Wardle and Bardgett, 2004). Herbivore-induced shifts in leaf-litter biomass and composition may affect belowground communities and ecosystem attributes such as soil carbon and nutrient cycling (Tanentzap and Coomes, 2011; Lessard et al., 2012; Hatton et al., 2014). Although interactions between above- and belowground processes have attracted much recent attention (Wardle and Bardgett, 2004), there is still little evidence to ascertain whether ungulate impacts at the level of the forest litter layer vary predictably along environmental gradients (Persson et al., 2005).

In this study, we examine the long-term impact of introduced livestock on understory vegetation of southern beech *Nothofagus* forests distributed along a region-wide moisture gradient in northern Patagonia, Argentina. Exotic ungulates were introduced into the study region during the late 1800s, and have been found to alter the structure and composition of understory communities (Veblen et al., 1989, 1992; Vázquez, 2002; Raffaele et al., 2007, 2011; Relva et al., 2008, 2010). Yet, previous studies inferred ungulate impacts from browsing metrics and short-term exclosures in single habitats, and were thus limited by the lack of historical reference sites in various environmental contexts (cf. Veblen et al., 1992). Here we examine the hypothesis that the impact of domestic herbivores on understory communities increases with habitat moisture. *Nothofagus dombeyi* stands that were either historically (>50 years) used by or remained free of livestock were compared along a 1300 mm/yr precipitation gradient. It was assumed that this moisture gradient encompassed a range of ecological conditions and species composition that were relevant for vegetation responses to livestock disturbance (Veblen et al., 1992; Speziale et al., 2010). We expected differences in vegetation attributes between (paired) browsed and unbrowsed sites to increase from drier to wetter forests, while differences across forest habitats would be mostly apparent for livestock-free sites. Specifically, we examined livestock impacts on (a) cover of plant functional types, (b) overall species composition, (c) species richness and evenness, (d) spatial species turnover within and among sites, and (e) ground litter composition and diversity.

2. Materials and methods

2.1. Study area

The study was conducted in Nahuel Huapi National Park, which is located on the eastern foothills of the Andes (40°15′–41°30′S) in north-western Patagonia, Argentina (Veblen et al., 1992). The landscape topography was carved by Quaternary glaciations, including the last glacial retreat some 14–12 K yr BP. Soils are poorly developed Andisols derived from volcanic ash layers. The climate is cool temperate, with average temperatures around 8.3 °C. Mean annual precipitation decreases markedly from west to east, ranging from ~3500 mm/yr near the Andean divide to ~800 mm/yr at the woodland–steppe ecotone, some 60 km eastward (Barros et al., 1983; Jobbágy et al., 1995; Veblen et al., 1996). Most precipitation falls during autumn and winter (April–September), being usually sparse from October through March. Study sites were spread over a 1500–2800 mm precipitation gradient, and were representative of mid-elevation (800–900 m), broadleaved evergreen forests dominated by *N. dombeyi* (Table 1). This species forms monotypic, 20–30 m height stands; the conifer *Austrocedrus chilensis* occurs as subordinate canopy tree, increasing towards drier sites. Moister forests near the Andean divide are enriched with elements from the Valdivian rainforests of Chile, including *Maytenus magellanica*, *Drimys winteri*, and *Weinmannia trichosperma* (Veblen et al., 1996;