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Spatial variation in tree demography associated to domestic herbivores and topography: Insights from a seeding and planting experiment

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ABSTRACT

Tropical and subtropical high mountains forests are mainly situated within ravines. Two alternative and often confronted explanations have been proposed for this pattern: that abiotic environmental conditions are favourable for tree establishment only within ravines, or that ravines are less affected by grazing and fires which negatively affect establishment in other sites. Here we propose a mixed explanation and hypothesize that abiotic environmental conditions associated to spatial variation are important during early seedling establishment and that grazing is the main determinant during later stages through its negative effect on survival and growth of larger saplings. We sowed 302,400 seeds and planted 360 saplings of the dominant tree species from the upper Córdoba Mountain range (Central Argentina) with and without grazing in three contrasting sites: a ravine, a valley and a ridge. We monitored seeding plots 5 years until the seedlings reached the height of the planted saplings and we monitored the planted saplings for 12 years. We integrated life stages using matrix multiplications, which resulted in data simulating 17 years of the trees' early development. Our results showed that seedling establishment was lower in the ravine and ridge sites and higher in the valley site with negative differences due to grazing only in the valley. Planted sapling survival increased but growth decreased from ravine to valley and ridge sites in the absence of large herbivores, while both survival and growth were substantially lower in the presence of large herbivores. Matrix multiplications indicated that differences between sites were 5.0 times more important than grazing when integrating up to year 5, but grazing by large herbivores was 5.4 times more important than differences between sites when assessed across the whole 17 year period. We conclude that there could be a strong influence of grazing in restricting high montane forests to sites like ravines where large herbivores are less frequent and show how the relative importance of site characteristics and grazing changes as a result of the length and the differing life stages which are monitored.

1. Introduction

Subtropical and tropical mountains forests situated above the continuous timberline are often found in ravines, with little or no tree cover in open sites such as valley floors, gentle slopes, ridges and convex summits (Körner, 2012). In South America much debate exists on the causes of this prevalence of forests to ravines and the issue has been termed "the *Polylepis* problem" (Kessler, 2002) because in this continent it is mainly species of the genus *Polylepis* which dominate the canopy of the high mountain forests above the timberline in a 5400 km forest belt which ranges from Venezuela to Central Argentina.

Proponents of the natural distribution explanation suggest that *Polylepis* forests are mainly situated within ravines due to a combination of more favourable micro climate conditions including protection from freezing, wind and radiation, and due to deeper soils with better moisture conditions (review in Kessler, 2002). Studies supporting this view have been performed in absence of grazing and fires. For example, better microclimatic growing conditions were determined within forest as compared to forest gaps and surrounding paramo vegetation for *Polylepis sericea* in Venezuela (Rada et al., 2009). Also, better soil nutrient and water conditions are reported within ravine woodlands as compared to shrublands

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situated in higher topographies for *Polylepis australis* in Argentina (Enrico et al., 2004).

Proponents of the anthropogenic explanations note that in most tropical and subtropical mountains herbivory is largely exerted by free roaming domestic livestock (Messerli and Ives, 1997) and that it is well established that in alpine environments browsing by herbivores affects woodland regeneration by retarding or even hampering juvenile growth (Cairns and Moen, 2004; Speed et al., 2011). Forest restriction to ravines could be explained at least in part because here trees may find protection from browsing because at these sites domestic herbivores are more exposed and vulnerable to predation than in open sites (i.e. for wild herbivores; Ripple and Beschta, 2003). Also, in ravines fire incidence is reduced due to higher moisture content and the tendency of fire to spread uphill, and hence in ravines we find fewer domestic herbivores which are attracted to post-fire plant re-growth (Renison et al., 2006; Coblentz and Keating, 2008). Studies performed in sites with differing herbivore densities show mixed support for the anthropogenic explanation. In Ecuador more *Polylepis incana* seedlings are found in sites with higher livestock impact (Cierjacks et al., 2007). In central Argentina more *P. australis* seedlings are found at intermediate livestock densities than without livestock or at high livestock densities (Torres et al., 2008; Zimmermann et al., 2009), but juvenile growth is severally hampered by livestock (Giorgis et al., 2010). Thus, seedling studies do not seem to support the anthropogenic explanation and juvenile studies support it.

Population filters due to microclimate, soil conditions and browsing may exert their effects at different plant life stages. Small seedlings may be more vulnerable to stressing microclimatic conditions such as wind, strong radiation and lack of moisture, which could easily desiccate a seedling in its early stages. When seedlings grow larger (i.e. >3 cm) they become accessible to large herbivores and thus became vulnerable to browsing (Fenner and Thompson, 2005). Fires may affect all life stages in complex patterns where some life stage may be more affected than others. The use of fire to sustain grazing areas and improve forage quality is certainly very relevant to understand the spatial pattern of *Polylepis* forests (i.e. Renison et al., 2002; Cierjacks et al., 2008; Coblentz and Keating, 2008). The forest belt occupied by small *Polylepis* forest patches and isolated trees found above the continuous timberline in subtropical and tropical mountains forms part of what has been termed the "ecosystem uncertain" climate envelope where vegetation types dominated by grasses and by different types of woody vegetation coexist (Whittaker, 1975). Under these climatic conditions the balance between vegetation types may be driven to a certain extent by large herbivores but also by fires which can be thought of as a non-selective consumer (Bond, 2005).

Here, we experimentally manipulate livestock presence and control for seed and plant density at different sites. We report elsewhere the important influences of fire (Alinari et al., in press). Our objective is to gain insight into demographic filters that show the relative importance of site characteristics as compared to grazing, and discuss its implications in the debate over the causes of the restriction of *Polylepis* forests to ravines. We hypothesised that differences between sites would be the main driver during early establishment, when seedlings are most vulnerable to harsh micro climatic and abiotic conditions prevalent out of ravines (Enrico et al., 2004). We additionally hypothesized that grazing would be the main driver of survival and growth after the seedling stage, as grazers are known to eat parts of tree saplings when accessible (Giorgis et al., 2010; Marcora et al., 2013). We therefore predict a greater influence of contrasting site characteristics at the early life stages with an increasing influence of livestock at the later stages.

Polylepis forests contain an important richness of endemic species which in many cases is endangered, forest extension and density has been reduced in many regions and soil loss has been prominent in extended areas within the *Polylepis* forest belt (Jameson and Ramsay, 2007; Gareca et al., 2010; Robledo and Renison, 2010; Renison et al., 2013). Obtaining insights into the drivers of high altitude *Polylepis* forest distribution is important to provide information to assist the many ongoing *Polylepis* forests restoration projects by pointing at the spatial variation in tree demography associated to domestic herbivores and topography.

2. Materials and methods

2.1. Study area and species

The Córdoba mountains in Central Argentina (31°34′ S; 64°50′ W; 500–2800 m) have a mean temperature of 5.0 and 11.4 °C at 2100 m for the coldest and warmest months, respectively, with occurrence of below zero temperatures all year round. Mean annual precipitation from 1992 to 2010 averaged 900 mm. The long, dry and cold season lasts from May to September and 83% of the rainfall is concentrated in the warmer months between October and April (Colladon et al., 2010). Soils are mainly derived from weathering of the granite substrate and fine-textured Aeolian deposits (Cabido et al., 1987). The main economic activity is livestock rearing (cattle, sheep, horses and goats), which began in the 17th century, and all large native herbivores went extinct by the 1920s. At present, local livestock densities range from 0.1 to 4.8 cattle equivalents/ha (von Müller et al., 2012). The main livestock predator in the area is the puma (*Puma concolor*) which is still fairly abundant in the higher mountains (Pia et al., 2013) and according to local ranchers is often found within forested ravines (personal communications).

The vegetation belts in the study area have been traditionally described as a lower seasonally dry forest dominated by trees such as *Lithraea molleoides* and *Celtis ehrenbergiana* with a timberline at around 1300 m asl (Luti et al., 1979). The areas above the timberline, up to the highest altitudes of 2884 m asl, consist of a mosaic of tussock grasslands, short grazed grasslands, exposed granite surfaces and rock outcrops. In addition, around 12% of the area comprises scattered forest stands and shrublands largely restricted to ravines and gorges (locally called "quebradas"), but also found in rock outcrops and in the slopes of open valleys in areas with less human disturbance (Cingolani et al., 2008). The canopy of the forest patches above the continuous timberline is dominated by *P. australis*, which at lower altitudes mixes with other tree species, mainly *Maytenus boaria* (Renison et al., 2011).

P. australis is endemic to the mountains of Central and North-Western Argentina (Renison et al., 2013) and is strongly consumed by livestock which on average browses from 85% of the accessible shoots when at moderate stocking rates and 98% of the accessible shoots under the heavy grazing pressures typical of the area (Giorgis et al., 2010). *P. australis* can reach up to 14 m in height, the fruits are single seeded nutlets (hereafter referred to as seeds) that ripen and fall from the trees between January and April; they usually germinate immediately after dispersal at the end of the wet season in March and April. Seed viability is variable, ranging from 0% to 60% with an average viability of around 20% (Renison et al., 2004).

2.2. Seeding and planting experiments

We performed two seeding and one planting experiments in the northern part of the higher Córdoba Mountain range (Los Gigantes, 31°25′ S; 64°48′ W; 2270 m asl) in three sites of contrasting topography: the bottom of a ravine, the lower slopes of an open valley, and a flat ridge site (hereafter ravine, valley and ridge, respectively). We selected these particular sites because they were