



Herbivory and seedling establishment in Pyrenean forests: Influence of micro- and meso-habitat factors on browsing pressure



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ABSTRACT

Browsing damage is among the most determinant factors that limit the establishment of tree seedlings in forests. In some areas, this process leads to massive mortalities that can reduce or even completely prevent the regeneration of some tree species. Mediterranean mountain forests have undergone during the last decades important changes in land-uses that have significantly altered the type and abundance of herbivore populations. In this study we assessed the impact of current grazing conditions in forest regeneration using a set of experimental plantations established in the Eastern Pyrenees in areas visited by domestic livestock (cattle and horses) and wild ungulates (mainly roe deer and chamois). We analyzed during 4 years the role of seedling species and size, mesohabitat (elevation and type of forest cover) and microhabitat (herbaceous cover, distance to shrub, and light availability) on the browsing-induced mortality of more than 500 seedlings of *Pinus sylvestris*, *Pinus uncinata*, *Betula pendula* and *Abies alba*, the most common tree species in the study area. Browsing-induced mortality for the three conifer species was much lower (<15%) than the one observed for *B. pendula* (>40%) and depended on both microhabitat – mainly on the distance to protective elements such as shrubs; and mesohabitat, with an interaction between the elevational belt (site) and the type of forest cover (gaps vs. understory). In the subalpine belt, browsing on *A. alba* and *P. uncinata* was higher during summer at plots located in the forest understory whereas, during winter, it was higher at plots located in gaps. The study shows that both mesohabitat and microhabitat can exert an effect on the patterns of plant damage by herbivores, providing useful information to adapt forest management in areas particularly exposed to them.

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1. Introduction

Forests regeneration is limited by several environmental constraints. Among them, browsing by large herbivores is often one of the most determinant factors, particularly in mountain areas, where tree establishment and growth are already constrained by unfavorable environmental conditions (Ameztegui and Coll, 2013). In the last decades, many European mountains have undergone major changes in the type, abundance and behavior of their main herbivore populations – including both wild and domestic animals – as a consequence of the profound socioeconomic changes that have affected these systems (Casals et al., 2009). For instance, the Pyrenees have recently changed from a transhumant system – in which sheep for wool production were favored against

cattle, and there was an extensive utilization of most available food sources – to a system in which the overall livestock pressure is notably lower, and beef cattle and breeding mares have partially substituted sheep herds (García-Ruiz and Lasanta, 1990; Lasanta, 1990). Under this new organization of the landscape, intensive grazing pressures concentrate in very limited areas (mainly sub-alpine pastures), whereas many pastures that were suitable for sheep are now unused (Balcells, 1983). The abandonment of these lands together with a reduction of logging pressure on forests have led to important forest expansion processes and to a generalized increase in canopy closure (Ameztegui et al., 2010; Poyatos et al., 2003). Wild ungulates such as roe deer (*Capreolus capreolus*) or chamois (*Rupicapra pyrenaica*) find in these dense forests a suitable habitat and have sharply increased their populations in the last decades (Apollonio et al., 2010; Putman et al., 2011).

The progressive increase in ungulate populations during the last decades has already caused some concern due to the consequences it could entail for the regeneration of European temperate forests (see, for example Motta, 1996; Putman, 1996 or Bugmann and

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Weisberg, 2003). At high stocking densities, herbivory can even completely prevent regeneration of some species and lead to a reduction of plant species diversity (Ammer, 1996; Danell, 2003; Reimoser, 1996). Changes in herbivore populations – both in livestock and wildlife – can severely affect the patterns of seedling consumption and lead to shifts in forest composition on the mid-term (Gill, 1992; Motta, 1996; Senn and Suter, 2003), and patterns of seedling predation by large herbivores can themselves be affected by other environmental factors (Weisberg and Bugmann, 2003). Available tree species, forest structure, type of habitat, period of grazing or the amount of alternative food sources, among others, affect how frequently and intensely herbivores browse young trees (Liss, 1988; Mayer, 2005a; Mayer et al., 2003; Reimoser, 1996). Yet, we are still far from a complete understanding of the combined effect that these environmental factors can exert on browsing patterns (Bergström and Edenius, 2003; Kräuchi et al., 2000).

In this study, we aim at shedding some light on the role that the complex ungulate-habitat interactions play on the dynamics of mountain forests. For this purpose, we planted seedlings of the main tree species in the Eastern Pyrenees in an area grazed both by livestock and wild ungulates, and under contrasting environmental conditions. By planting even-aged seedlings in areas with non-modified browsing conditions, we wanted to assess the effect of specific seedling selection by herbivores (Kupferschmid et al., 2014). Mortality of seedlings due to browsing, although often non-visible, can be more determinant on forest dynamics than mortality of saplings, but the later has been more studied because the damages are more evident and easier to determine (Reimoser, 2003; Senn and Suter, 2003). More specifically, the study aimed to (i) assess the impact of current grazing conditions (both of livestock and wild ungulates) in forest establishment; (ii) detect if some tree species were preferred by herbivores over others; (iii) determine how variations in meso-habitat (elevation and type of forest cover) and microhabitat (herbaceous cover, distance to shrub, light availability) may engender different patterns of plant consumption by herbivores; and (iv) discuss the potential implications of the observed patterns for forest dynamics. We expect a highly selective predation on silver fir and birch, which can prevent the diversification of pine forest described elsewhere in the absence of management (Navarro-González et al., 2013). At the meso-habitat scale, we expect livestock to cause less damage than wild ungulates at forest gaps; whereas at the micro-habitat scale, the predation rate is likely to be positively affected by herb abundance and negatively by shrubs.

2. Material and methods

2.1. Study area and species

We conducted the experiment at two sites with different elevations in the northern slopes of the Serra del Cadí, a Pyrenean mountain range in the Cadí-Moixeró Natural Park (42°17'N; 1°42'E). The Sant Romà site corresponds to a montane pine forest located at 1500 m a.s.l. (near the *Pinus sylvestris* – *Pinus uncinata* transition zone), while the Prat d'Aguiló site is a typical subalpine forest located close to the optimum elevational distribution for *P. uncinata* (around 2000 m a.s.l.; Fig. 1). The forest in Sant Romà was dominated by *P. sylvestris*, with some *P. uncinata* and *Betula pendula* individuals, and the main species in the understory were common box (*Buxus sempervirens* L.) and common juniper (*Juniperus communis* L.). Prat d'Aguiló forests were dominated by *P. uncinata* and the shrub layer was almost exclusively composed by *J. communis*.

Despite being a protected area, herds of cows and horses graze every summer in both sites (Table 1), since the authorities have

promoted animal husbandry as a major source of income for local communities. The area also hosts important populations of chamois (*R. pyrenaica*), and roe deer (*C. capreolus*), with a lower presence of wild boar (*Sus scrofa*), and red deer (*Cervus elaphus*).

We used for this study the four most common tree species in the study area: Scots pine (*P. sylvestris* L.), mountain pine (*P. uncinata* Ram. ex DC), silver fir (*Abies alba* Mill.) and silver birch (*B. pendula* Roth). These species have different ecological requirements in terms of tolerance to shade, drought and cold temperatures (see Ameztegui and Coll, 2013 for further details) but they can coexist between 1600 and 2000 m a.s.l., where they constitute the montane–subalpine ecotone.

2.2. Experimental design

A total of 1152 seedlings of the study species were planted in the early summer of 2008. Seedlings were distributed along 24 plots (12 at the montane site and 12 at the subalpine), located at less than 300 m from grasslands highly frequented by livestock (Fig. 1). At each site, half of the plots (6) were established in the forest understory and the other half (6) in naturally occurring gaps, whose size ranged between 150 and 350 m². Each plot contained 48 seedlings (12 per species) randomly distributed in a grid pattern, and seedlings were planted at least 1 m one from another to avoid above- and below-ground interaction. All the seedlings were two years old at the moment of plantation, and had been grown in a local nursery (Forestal Catalana, Pobla de Lillet, Spain) from seeds collected in neighboring forests, i.e., seed source, nursery, and plantation area were all inside the same provenance region (Alfía et al., 2005). To ensure enough seedling survival to assess the role of climate and microsite on seedling performance (see Ameztegui and Coll, 2013), half of the seedlings in each plot were protected from browsing with an individual protector (90 cm height and 33 cm of diameter) with a mesh net of 20 × 20 mm (Nortène, Lille, France). The remaining half ($n = 576$) was left unprotected and constitute the sample of this study, since they allowed us to assess for the effects of browsing by large herbivores on seedling performance.

2.3. Presence of herbivores in the study area

Both sites are highly frequented by livestock during summer, when a total of 95 cows and 60 mares – i.e. 124 adult livestock units – take advantage of the pastures located close to the experimental sites under a free-range, extensive system. During summer, the high presence of domestic cattle forces most wildlife to take refuge in the rocky areas located above the main grazing areas. On the contrary, wild ungulates are the unique large herbivores in the study area during winter, when livestock is stabled in the valley. Although there are no recent censuses of wild ungulates in the study area, the populations of roe deer, chamois, red deer and wild boar have increased in the last decades (DGMNB, 2014). The study area is located inside the Cadí National Game Reserve, created in 1966 to protect a population of 78 specimens of chamois. The last census of this species performed in 1999 revealed that the population had risen up to 2551 individuals (5.4 chamois km⁻²).

2.4. Seedling monitoring and characterization of the habitat

Individual seedling damage and mortality were monitored at the beginning and at the end of each growing season during four years since the moment of plantation. The likely cause of damage or death was recorded when apparent as whether due to (i) herbivores (browsing, trampling or other type of physical damage caused by browsers); (ii) lack of adaptation (i.e., showing

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