

Limits of pine forest distribution at the treeline: herbivory matters

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Abstract Herbivores can affect future forest composition by feeding selectivity. At temperature-sensitive treelines, herbivory can exacerbate or constrain climate-driven distributional shifts in tree species. This study analyses the impact of herbivory in a Mediterranean treeline of widespread *Pinus sylvestris* and *P. nigra* pinewoods, testing whether herbivory damage reinforces or inhibits the climatic responses of these trees. We used naturally occurring sapling pairs of similar size and age of both species, thereby isolating plant characteristics from environmental effects in herbivore behaviour. Herbivory damage by ungulates proved higher than that caused by insects in saplings of both species. Low plant density and extreme abiotic conditions at the treeline could in part be responsible for the observed low incidence of insect herbivory. Ungulates preferred *P. sylvestris* over *P. nigra*, implying heavier browsing damage for a large number of *P. sylvestris* saplings, suffering reduced internode growth as a consequence. In addition, *P. sylvestris* could not compensate height-growth reductions due to browsing with higher growth rate than *P. nigra*. In fact, *P. sylvestris* showed similar or lower relative height growth with respect to *P. nigra*.

Under a scenario of increasing aridity and maintenance of ungulate populations, the upward migration of *P. sylvestris* in its southern range could be restricted by higher drought vulnerability than *P. nigra*, a situation exacerbated by ungulate herbivory. Our results indicate that ungulate herbivory reinforces climatic response of coexisting *P. sylvestris* and *P. nigra* at treeline, favouring a potential change in community dominance towards Mediterranean *P. nigra*.

Keywords Ungulate browsing · Insect herbivory · Treeline dynamics · Mediterranean mountain · *Pinus sylvestris* · *Pinus nigra*

Introduction

Herbivores can affect future forest composition by feeding selectivity and/or differential response to damage by plant species (Schowalter et al. 1986; Danell et al. 2003; Cote et al. 2004). In fact, several studies report a reduction of recruits of the more palatable or sensitive species, and/or increase of unpalatable or tolerant species (Tilghman 1989; Vasconcelos and Cherrett 1997; Ritchie et al. 1998; Kay and Bartos 2000; Rooney and Waller 2003; Potvin et al. 2003). Therefore, if herbivores exert a differential impact on dominant plant species of a forest ecosystem, they could determine vegetation dynamics (Davidson 1993), blocking forest expansion

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(Speed et al. 2010) or changing tree-species composition (Danell et al. 2003).

Herbivory and its influence in plant-community dynamics could be a noteworthy factor in ecotones and the margins of species ranges, where rapid distributional changes have been detected in recent years in response to increasing warmer conditions (Parmesan and Yohe 2003; Peñuelas and Boada 2003). Climatic conditions which limit or promote establishment of a particular tree species at the edge of its distribution could be exacerbated or inhibited by herbivory, directly influencing its performance and/or recruitment, or altering the competitive ability of a coexisting species. For example, a tree species at its southernmost distribution limit could present limited establishment due to drought impairing height growth, this in turn being exacerbated by herbivory damage diminishing photosynthetic tissue. On the other hand, another species in its uppermost distribution limit could find favourable conditions for its establishment mediated by higher rainfall, but inhibited by repeated severe browsing or defoliation. Therefore, the analysis of the impact of herbivory at the limits of species ranges could help in the assessment of range shifts under the current climatic-change scenario (Speed et al. 2010; Olofsson et al. 2009).

Treelines are temperature-sensitive ecotones between forest and alpine vegetation states (Korner and Paulsen 2004), where tree-species distributional changes have already been recorded and further are expected in response to increasing warmer conditions (Harsch et al. 2009). Studies demonstrating the effect of herbivory exacerbating or constraining such distributional changes have been conducted at high latitudes (Cairns and Moen 2004; Dalen and Hofgaard 2005; Tømmervik et al. 2009; Speed et al. 2010), but little attention has been paid to water-stressed areas such as Mediterranean ecosystems, where marked changes in plant-community composition are expected in response to drought and warming (Thuiller et al. 2005). In fact, many tree species have their southern distribution limit in the Mediterranean Basin, and thus might be more vulnerable to increasing aridity (IPCC 2007) as they are far from optimum conditions (Hampe and Petit 2005).

The objective of this study is to analyse the impact of herbivory at the Mediterranean treeline of wide-spread mixed pinewoods of *Pinus sylvestris* L. and *P. nigra* Arnold (Blanco et al. 1997; Barbéro et al. 1998),

testing whether herbivory damages reinforce or restrain the climatic response of these species. Whilst *P. sylvestris* is a boreo-alpine species reaching its southern distribution limit in the Mediterranean basin (Boratynski 1991), *P. nigra* is a Mediterranean pine species distributed mainly in southern Europe (Barbéro et al. 1998). The study focuses on saplings, as this ontogenetic state represents the near-future forest and the possibilities for forest expansion and treeline advance. First of all, we compare sapling performance between the two species to explore species responses to climatic conditions. Then, we analyse herbivory impact and the associated guild of herbivores in saplings of both species. Since the study area is at the treeline, we expect a higher impact of vertebrate herbivores on pine saplings, due to temperature limitation for insects (Bale et al. 2002), and larger body size, individual bite size and mobility of vertebrates (Danell and Bergström 2002). Regarding the species studied, previous study in the area showed *P. sylvestris* to be a more palatable species for ungulates than *P. nigra* (Baraza et al. 2009). Therefore, we predict greater damages at least for this herbivore guild in *P. sylvestris*. Within this framework, the specific objectives of this study are: (1) to test the relative impact of vertebrates and invertebrates on pine saplings; (2) to test the preference by herbivores for the two target species.

Materials and methods

Study site and sampling design

The study was conducted at Sierra de Baza Natural Park (SE Spain, 2°51'48" W, 37°22'57" N). Sierra de Baza, together with Sierra Nevada, represents the absolute southernmost distribution limit for *P. sylvestris* (Boratynski 1991). The climate is Mediterranean, characterized by cold winters and hot summers, with pronounced summer drought (June–August). Precipitation is concentrated mainly in autumn and spring. The annual and summer rainfall is 495 ± 33 and 31 ± 9 mm, respectively (mean \pm SE for 1991–2006 period; Cortijo Narváez meteorological station, 1360 m a.s.l.). The bedrock is predominantly calcareous. Both wild and domestic ungulates are present in Sierra de Baza. Amongst wild ungulates, red deer (*Cervus elaphus* L.) population reaches a density of

15.35 individuals km⁻² [Consejería de medioambiente (CMA) 2008], whereas Spanish ibex (*Capra pyrenaica* Schinz) maintain only a small population of 0.39 individuals km⁻² (CMA 2009). On the other hand, from May to December, herds of domestic goat (*Capra hircus* L.) and sheep (*Ovis aries* L.) notably intensify the grazing pressure with a density of 40 individuals km⁻² (CMA 2008).

The study was performed in three different sites of approximately 1 ha, at least 900 m apart from each other in three different valleys. All three sites are situated at ca. 2000 m of elevation with a south-west orientation. These sites are forest ecotone areas, close to mixed forests of both species, representing the treeline for both *P. sylvestris* and *P. nigra* in the Mediterranean mountain. Therefore, selected sites represent areas for potential forest expansion towards higher altitudes. The woody vegetation of the study sites is formed mainly by saplings (defined as non-reproductive individuals) of *P. sylvestris* and *P. nigra* of different ages and sizes, with some scattered individuals of *Juniperus communis* L., *J. sabina* Sibth & Sm and *Erinacea anthyllis* Link (see Table 1 for further details about sites). In October 2008, we choose 30 pairs of both species at each site (a total of 180 pines). Each pair of saplings contained one individual from each species of similar age and size, being the closest sapling in the surrounding area (see Table 1 for further details about selected pairs). Therefore, each pair represents a set of one individual of each species growing under similar conditions, to test herbivore preference for *P. sylvestris* and *P. nigra*.

Plant performance

Height and axis internode growth of the last 11 years (2008–1998) were measured in each selected pair of saplings. Both species showed one flush per year in the study area, so we were able to estimate height corresponding to 11 years earlier based on measurements of annual internode growth. Annual internode growth (or trunk elongation) is easily identifiable by yearly whorls and bud scars. Relative height growth (RHG) for 2008–1998 series was calculated for each sapling using the following formula (Leopold and Kriedemann 1975) as a measure of long-term sapling performance:

$$\text{RHG} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where W_2 and W_1 are sapling heights at times 2 and 1, respectively. Age was estimated counting the number of annual bud scars or whorls (Edenius et al. 1995; Zamora et al. 2001; Debain et al. 2007). The estimated age ranged from 14 to 31 years and height from 0.27 to 4.05 m. The estimated age and height of saplings of each pair is very similar (see Table 1 for mean differences in age and height for each site). Age and height differences between individuals of each pair were evenly distributed amongst the three sites.

Ungulate herbivory

Browsing damage was recorded for the selected paired saplings in October 2008, after summer, the main browsing period in the study area (Zamora et al. 2001). The intensity of ungulate herbivory was quantified using the following estimates: (1) risk of herbivory, (2) damage intensity, and (3) leader browsing. Risk of herbivory was estimated as the percentage of herbivorized plants in 2008 (annual) and in the last 3–4 years (accumulated) for the total of sampled individuals. Damage intensity was estimated as the proportion of apical shoots consumed by ungulates. This was quantified by counting the number of apical shoots as well as the number of apical shoots herbivorized by ungulates (shoots browsed in 2008 for annual damage intensity, and shoots browsed in the last 3–4 years for accumulated damage intensity). Leader browsing was estimated as the percentage of terminal leader shoots lost to herbivory. This type of herbivory caused a loss in the apical dominance of the pine sapling. We estimated the leader browsing of the last 11 years (1998–2008 series). Old losses of apical dominance were detected by clear bifurcation or strong changes of direction in the main stem (therefore a conservative measurement).

Insect herbivory

All selected paired saplings were checked for current insect damage. For damages caused by *Retinia resiniella* L. (*Lepidoptera: Tortricidae*) the number of galls were counted per sapling. We considered galls formed in 2008 and 2007 due to their two-year generation

Table 1 Location and characteristics of the selected sites and pairs of saplings

Variable	Site		
	1	2	3
Geographical position	2°51'42.841" W 37°22'23.16" N	2°50'33.874" W 37°22'27.091" N	2°50'48.359" W 37°21'59.927" N
Sapling density (ind ha ⁻¹) ^a	318 ± 61.3	174 ± 47.9	250 ± 42
Relative proportion (<i>P. sylvestris</i> / <i>P. nigra</i> ; %) ^a	72.3 ± 0.8/27.7 ± 0.8	62.4 ± 2.1/37.6 ± 2.1	54.2 ± 10.3/45.8 ± 10.3
Distance (m) ^b	1.19 ± 0.18	2.05 ± 0.29	1.26 ± 0.24
Age difference (years) ^c	1.7 ± 0.18	1.7 ± 0.26	1.83 ± 0.25
Height difference (cm) ^c	43.23 ± 7.21	60.37 ± 8.99	43.23 ± 6.13

Geographical position, sapling density, and relative proportion of *P. sylvestris* and *P. nigra* are related to whole sites. Longitudinal distance and height and age differences between saplings of selected pairs are related to pairs of saplings of each site. Values are shown as mean ± standard error

^a Sapling density and relative proportion of *P. sylvestris* and *P. nigra* were measured with 10 transects of 50 m length and 10 m wide

^b Longitudinal distance between saplings of selected pairs

^c Height and age differences between saplings of selected pairs. Those values are calculated using absolute values, as differences were not always in the same direction

cycle (Kletecka 1992). In the case of *Rhyacionia duplana* Den. et Schiff. (*Lepidoptera: Tortricidae*), we counted the number of shoots affected by the feeding of the caterpillar in each sapling. Affected shoots were hook shaped from severe deformation (Dajoz 2001). For *Thaumetopoea pityocampa* Den. et Schiff. (*Lepidoptera: Notodontidae*), we counted the number of silk nests, which contain the larvae aggregations (Dajoz 2001). Finally, we measured the damage caused by leaf feeders belonging to *Acantholida* (*Hymenoptera: Pamphiliidae*) and *Diprion* (*Hymenoptera: Diprionidae*), estimating the percentage of needles affected of the total for the entire individual.

Data analysis

Differences in herbivory risk were analysed using a generalized linear model (GLM) with a Poisson probability distribution and logarithmic link function. RHG, damage intensity and leader browsing were analysed with generalized linear mixed models (GLMM), with species and site as fixed factors and pair as a random factor. For the RHG, we pooled browsed and unbrowsed saplings, as no differences between them were recorded. Whilst log-transformed RHG was analysed with a Gaussian probability distribution and identity function, damage intensity and leader browsing were analysed with a binomial probability distribution and a logit link function. The significance of individual fixed effects was determined

by sequentially removing fixed effects from the model and comparing AIC values. In addition, the likelihood ratio test (analysis of deviance) was applied to test models against one another in ascending order of complexity. Finally, annual internode growth of the last 4 years (2005–2008), standardized by internode age, was compared for browsed and unbrowsed saplings of each species using a MANOVA, with the dependent variable as a repeated measure. Year was the repeated factor, and category (browsed/unbrowsed) and category interaction with year sources of variation. Saplings of the three sites were pooled for this analysis. Internode growth was transformed using the natural logarithm (ln) to improve homogeneity of variances. All the analyses except GLMM were performed using JMP 7.0 (SAS Institute Inc.). GLMM were performed with R software (R Development Core Team 2010, version 2.11.1), using lme4 package (Pinheiro and Bates 2000). All results throughout this article are given as mean ± standard error.

Results

Plant performance

Significant differences in RHG for 2008–1998 series were found between the different sites (Table 2; $t = -2.95$ and $t = -3.25$, $P < 0.05$). In addition, the differences between species varied with the site

considered as shown by the significant site \times species interaction (Table 2; $t = -3.26$ and $t = -4.41$, $P < 0.05$). *P. nigra* showed higher values than *P. sylvestris* in site 2 and especially in site 1, whilst similar values were detected in site 3 (Fig. 1). No differences between browsed and unbrowsed saplings (pooled for this analysis) were found, perhaps because we measured damage intensity only for the last 3–4 years whilst the calculated RHG encompassed the last 11 years.

Ungulate herbivory

P. sylvestris presented a significantly higher risk of herbivory than *P. nigra* (Fig. 2), for both accumulated ($\chi^2 = 18.66$, $P < 0.0001$) and annual herbivory

($\chi^2 = 32.58$, $P < 0.0001$). In addition, significant differences were recorded between the sites for accumulated ($\chi^2 = 9.47$, $P = 0.0088$) and annual herbivory ($\chi^2 = 7.11$, $P = 0.0286$; Fig. 2).

Accumulated and annual damage intensity was higher for *P. sylvestris* than for *P. nigra* in all the cases, as was leader browsing (Tables 2, 3; Fig. 2). There were differences amongst sites, as reported by the significant site factor and site \times species interaction. Nevertheless, in all the cases the differences amongst two pines were clear, with *P. sylvestris* showing consistently higher and often much higher damage than *P. nigra* (Tables 2, 3; Fig. 2).

Internode growth of the last 4 years standardized by internode age differed between browsed and unbrowsed saplings, pooling individuals of the three sites

Table 2 Model selection for accumulated and annual damage intensity (% browsed buds), leader browsing (% apical losses) and RHG (year⁻¹)

Model	Random effect	Fixed effects	<i>K</i>	AIC	Δ AIC
<i>Accumulated damage intensity</i>					
ACDI1	Pair	Species \times Site	6	402.3	0.0
ACDI2	Pair	Species + Site	4	409.8	7.5
ACDI3	Pair	Species	2	410.4	8.1
ACDI4	Pair	Site	3	847.7	445.4
ACDI5	Pair	None	1	848	445.7
<i>Annual damage intensity</i>					
ANDI1	Pair	Species \times Site	6	296.6	0.0
ANDI2	Pair	Species + Site	4	322.4	25.8
ANDI3	Pair	Species	2	319.2	22.6
ANDI4	Pair	Site	3	516.6	220
ANDI5	Pair	None	1	513.3	216.7
<i>Leader browsing</i>					
LB1	Pair	Species \times Site	6	268.5	0.0
LB2	Pair	Species + Site	4	272.1	3.6
LB3	Pair	Species	2	278.2	9.7
LB4	Pair	Site	3	304.9	36.4
LB5	Pair	None	1	304.9	36.4
<i>Relative height growth</i>					
RHG1	Pair	Species \times Site	6	-102.4	0.0
RHG2	Pair	Species + Site	4	-95.94	6.46
RHG3	Pair	Species	2	-67.15	35.25
RHG4	Pair	Site	3	-87.44	14.96
RHG5	Pair	None	1	-58.65	43.75

RHG data were log-transformed to fit a Gaussian distribution. The number of estimated parameters (*K*), AIC value and the difference between AIC value of a model and that of the most parsimonious (Δ AIC) are shown for each model. Likelihood ratio test support the results presented here

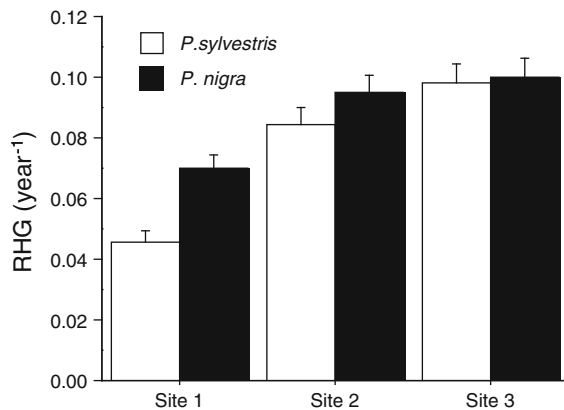


Fig. 1 RHG (year⁻¹) for 1998–2008 series for *P. sylvestris* and *P. nigra* saplings. Untransformed data are shown to allow easy interpretation. Bars indicate the standard errors of calculated means ($n = 30$)

($F = 12.98$, $P = 0.0005$ and $F = 35.31$, $P < 0.001$ for *P. sylvestris* and *P. nigra* saplings, respectively; Fig. 3). In addition, significant differences were found between different years ($F = 2.72$, $P = 0.0494$ and $F = 4.39$, $P = 0.0064$, respectively).

Insect herbivory

The percentage of saplings affected by *Rhyacionia duplana* and *T. pityocampa* was very low for both species (Table 4). Although the incidence of herbivory by *Retinia resiniella* (only for *P. sylvestris*) and leaf feeders was considerable, both the number of galls and the percentage of damaged needles per sapling were rather low (Table 4).

Discussion

This study analyses the influence of herbivory in two coexisting pine species at the treeline. According to our first hypothesis, the impact of ungulates on pine saplings was higher than the impact of insect herbivores, which caused minor damage. As predicted by our second hypothesis, ungulates inflicted heavier damage in *P. sylvestris* than in *P. nigra*. Lower internode growth for browsed saplings reflects the retarded height growth that can result from ungulate browsing. Thus, ungulate herbivory appears to be the most harmful type during pre-reproductive years in the pine species studied. Although *R. resiniella* presented

a high incidence in *P. sylvestris* saplings, the number of galls per saplings was low, and a gall did not always imply the breakage of the shoot or bud, which would translate as a loss of biomass. Leaf-feeder damage was recorded for a considerable number of saplings for both species, but the percentage of needles affected was very low, and normally only some portions of the needles were damaged (authors' personal observation). By contrast, ungulate herbivory affected a higher number of saplings, inflicting considerable damage in browsed saplings, as indicated by the reduction in internode growth.

Three different factors can explain the low incidence of insect herbivores found in this study: first, pine density was low at the treeline, which can hamper the movements of insects between trees (Dalin et al. 2009); second, abiotic conditions at the treeline are extreme, and, despite the trend of climatic change, temperature is still the prime factor influencing the physiology of insect pests (e.g. Bale et al. 2002); and third, for the case of *T. pityocampa*, our sampling coincided with a lower phase of incidence of this plague in S Spain (e.g. Hódar and Zamora 2009). In contrast, most of these factors do not affect ungulates. They are quite generalist, have a higher movement capacity, and select food in a hierarchical fashion: plant communities at the landscape scale, feeding stations at the plant-community, and individual plants or plant parts at the bite scale (Senft et al. 1987; Provenza et al. 2002). Thus, ungulates foraging at the treeline find a landscape composed of stunted scrubs, most of them spiny and/or unpalatable, and scattered young pines attracting attention from this background, which concentrates all the attacks of the ungulates even taking into account the relatively low palatability of pines (Gómez et al. 2001). Taken all together, the result is a much higher herbivory intensity by ungulates than by insects.

It is clear from our results that ungulates preferred *P. sylvestris* over *P. nigra*, in agreement to previous studies in the area (Baraza et al. 2009). This preference involves higher browsing damage for large number of *P. sylvestris* saplings, which consequently suffered a reduction in height growth, and therefore an increase in pine saplings risk of herbivore damage. In Mediterranean areas, *P. sylvestris* saplings presented low growth rates in comparison with northern latitudes (Danell et al. 1991; Väisänen et al. 1992; Edenius et al. 1995), thus aggravating the effects of herbivory.

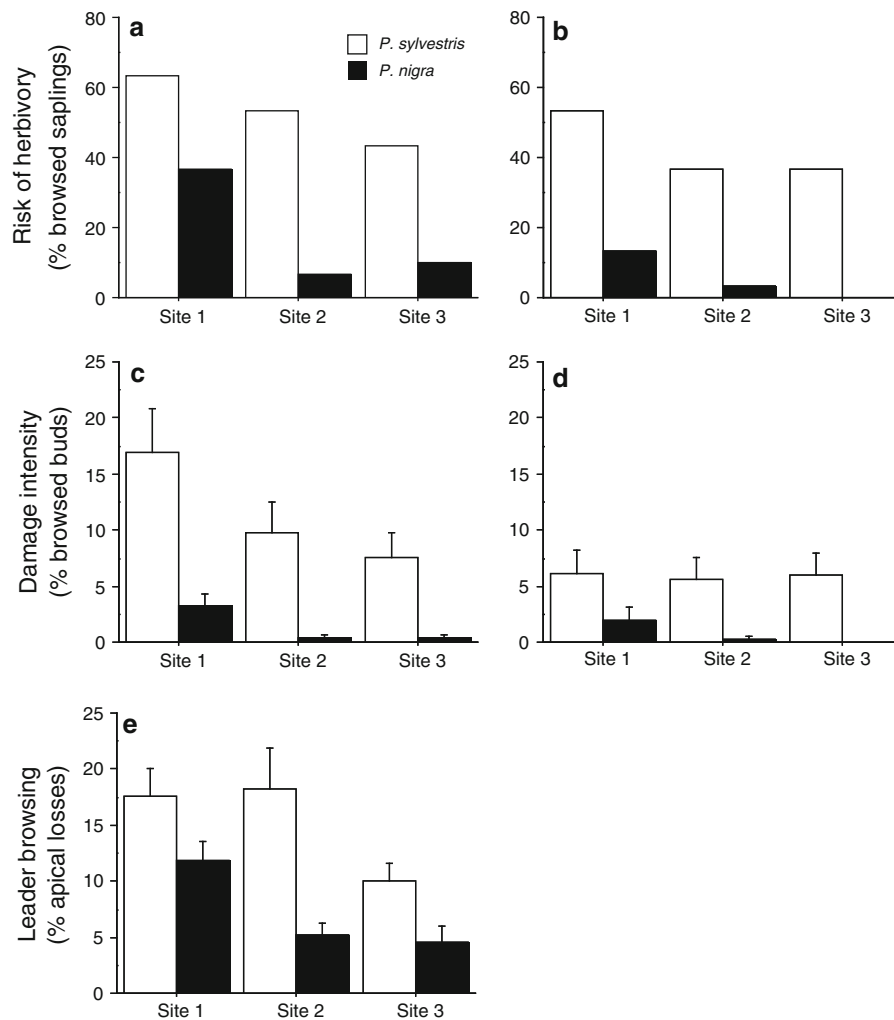


Fig. 2 Accumulated (a) and annual (b) risk of herbivory represents the percentage of browsed saplings for *P. sylvestris* and *P. nigra* in the study sites taking in account browsing of the last 3–4 years and browsing of 2008, respectively. Accumulated

(c) and annual (d) damage intensity show the percentage of browsed buds, and leader browsing (e) the percentage of apical losses since 1998. Bars indicate the standard errors of calculated means ($n = 30$)

Furthermore, browsing in Mediterranean areas is more severe in summer when other food resources for ungulates are less abundant, leaving less time to recover from damages (Hester et al. 2004). All these factors exacerbate browsing damage, which reduces height growth, thereby increasing the time needed for saplings to achieve maturity (Zamora et al. 2001). *P. nigra* becomes sexually fertile later than *P. sylvestris*, but once mature, *P. nigra* effective fecundity is greater than that of *P. sylvestris* (Debain et al. 2005, 2007; Boulant et al. 2008). Therefore, the delay in reaching reproductive age for *P. sylvestris* due to ungulate

browsing diminishes its competitiveness with respect to *P. nigra*. Finally, *P. nigra* showed higher or similar RHG than *P. sylvestris* at the treeline. Thus, at sites where *P. sylvestris* presented lower growth rates than *P. nigra*, higher browsing damages for *P. sylvestris* will accentuate the differences in performance and time of maturity between the two species.

Furthermore, several studies showed worse response to drought for *P. sylvestris* than for *P. nigra* both at the seedling and sapling stage (Castro et al. 2002, 2004), and at the adult stage (Martínez-Vilalta and Piñol 2002) in seasonal dry Mediterranean

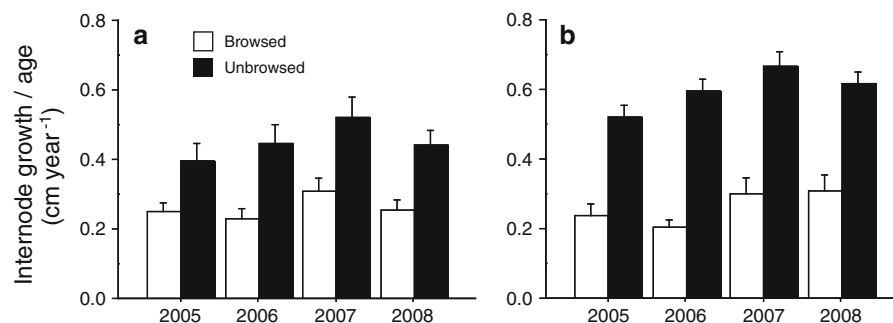
Table 3 Fixed-effects estimates for each parameter included in the most parsimonious models of annual and accumulated damage intensity (% browsed buds) and leader browsing (% apical losses)

Parameter	Estimate	SE	z-value	P
Accumulated damage intensity (ACDI1)				
Intercept	-5.1982	0.5282	-9.841	<2e-16***
<i>P. sylvestris</i>	2.2087	0.1901	11.621	<2e-16***
Site 2	-2.5023	0.8825	-2.835	0.00458**
Site 3	-2.3876	0.8902	-2.682	0.00732**
<i>P. sylvestris</i> : Site 2	1.3560	0.5084	2.667	0.00765**
<i>P. sylvestris</i> : Site 3	0.9623	0.5136	1.874	0.06100
Annual damage intensity (ANDI1)				
Intercept	-6.0617	0.5838	-10.382	<2e-16***
<i>P. sylvestris</i>	1.4446	0.2667	5.416	6.1e-08***
Site 2	-2.1536	0.9759	-2.207	0.02733*
Site 3	-16.5191	715.5196	-0.023	0.98158
<i>P. sylvestris</i> : Site 2	1.6893	0.5982	2.824	0.00474**
<i>P. sylvestris</i> : Site 3	16.2249	715.5192	0.023	0.98191
Leader browsing (LB1)				
Intercept	-2.1489	0.2127	-10.102	< 2e-16***
<i>P. sylvestris</i>	0.4847	0.2286	2.120	0.03396*
Site 2	-1.0001	0.3581	-2.793	0.00522**
Site 3	-1.0630	0.3680	-2.888	0.00387**
<i>P. sylvestris</i> : Site 2	1.0021	0.3759	2.666	0.00768**
<i>P. sylvestris</i> : Site 3	0.3818	0.4040	0.945	0.34463

* P < 0.05

** P < 0.01

*** P < 0.001

**Fig. 3** Differences between unbrowsed and browsed saplings for internode growth standardized by internode age (cm year^{-1}) for *P. sylvestris* (a) and *P. nigra* (b). Untransformed data are shown to allow easy interpretation. Bars indicate the standarderrors of calculated means. *P. sylvestris*: unbrowsed, $n = 44$; browsed, $n = 46$. *P. nigra*: unbrowsed, $n = 74$; browsed, $n = 16$

mountains. This vulnerability to drought is of special relevance under the prediction of increased frequency and severity of droughts in the Mediterranean Basin

[Moreno 2005; Fundación para la Investigación del Clima (FIC) 2006; IPCC 2007]. In fact, drought-induced mortality and decline symptoms have been

Table 4 Summary for insect herbivory incidence (percentage of affected saplings) and damage intensity for *P. sylvestris* and *P. nigra* saplings pooling the three sites ($n = 90$)

Organism	Incidence (%)	Damage intensity (Mean)	SE	Range
<i>Retinia resiniella</i>				
<i>P. sylvestris</i>	61.11	2.01	0.29	16
<i>P. nigra</i>	1.11	0.05	–	–
Leaf feeders (<i>Achantolida</i> / <i>Diprion</i>)				
<i>P. sylvestris</i>	24.44	1.72	0.38	20
<i>P. nigra</i>	40	3.39	0.63	30
<i>Rhyacionia duplana</i>				
<i>P. sylvestris</i>	2.22	0.02	0.01	1
<i>P. nigra</i>	15.56	0.31	0.09	6
<i>T. pityocampa</i>				
<i>P. sylvestris</i>	2.22	0.02	0.01	1
<i>P. nigra</i>	8.89	0.11	0.04	3

In the case of *Retinia resiniella* the damage intensity was measured as number of galls per sapling, for leaf feeders as percentage of damaged needles, for *Rhyacionia duplana* as number of affected shoots, and for *T. pityocampa* as number of silk nests

observed in several *P. sylvestris* Mediterranean populations in recent years (Martínez-Vilalta and Piñol 2002; Thabeet et al. 2009; Galiano et al. 2010). Thus, *P. sylvestris* is the species most prone to suffer both drought- and ungulate-induced damages. This reinforcement of climatic responses by ungulate browsing can have major consequences for the dynamics of treelines in widespread *P. sylvestris*–*P. nigra* mixed forests. Under the scenario of increasing aridity and maintenance or increase of ungulate populations (due to the lack of predators and difficulties to perform adequate management; Cote et al. 2004), *P. sylvestris* upslope movements could be impeded. By contrast, the less herbivorized, more drought-tolerant *P. nigra* may have an opportunity for altitudinal expansion to other areas currently dominated by *P. sylvestris* (see Debain et al. 2005, 2007; Boulant et al. 2008).

In conclusion, our field sampling design enabled us to disentangle the effects of invertebrate and vertebrate herbivory in Mediterranean pine treelines formed by *P. sylvestris* and *P. nigra*. This study demonstrates that saplings of both species at Mediterranean treelines suffer a weak invertebrate herbivore pressure, but a high, species-specific ungulate damage, concentrated on *P. sylvestris*. Thus, ungulate herbivory reinforce climatic response of coexisting *P. sylvestris* and *P. nigra*, and could favour a change in community dominance towards Mediterranean *P. nigra* at the upper altitudinal margin.

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