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Research Article

Selectivity and context dependence of Corsican red deer browsing in a Mediterranean coppice system

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Abstract

To manage potentially contrasting objectives such as ungulate conservation, habitat conservation, and forest harvesting, information about browsing patterns on vegetative regeneration of woody plants is needed. Here, we study browsing patterns of Corsican red deer on vegetative regeneration of coppices in a Mediterranean Holm oak forest. Within the forest management plan, the proportion of browsed shoots per plant was yearly monitored. Regression models were applied to estimate browsing probability of plants (BrY) and of shoots (Br), and evaluate factors though to affect red deer feeding behaviour, such as plant identity (Sp), plant height (H), years from coppicing (YfC), density of palatable (Dp) and unpalatable plants (Du), and presence of wild boars (WB). Browsing rates were unrelated to relative abundance of species (RA), and strongly affected by Sp , suggesting high feeding selectivity of Corsican red deer. High browsing rates were observed on *Quercus ilex* ($RA=0.26$; $BrY=0.81$, $Br=0.41$), and *Phillyrea latifolia* ($RA=0.07$; $BrY=0.89$, $Br=0.63$). Early successional shrubs such as *Arbutus unedo* ($RA=0.39$; $BrY=0.04$, $Br=0.01$), *Erica arborea* ($RA=0.14$; $BrY=0.06$, $Br=0.01$), *Cistus monspeliensis* ($RA=0.08$; $BrY=0.05$, $Br=0.01$), and *Cistus salvifolius* ($RA=0.05$; $BrY=0.10$, $Br=0.04$), were very seldom browsed. Browsing probability of palatable species decreased with YfC and H , and was affected by Dp and Du . WB did not seem to affect browsing probability. The effect of plant density on browsing was explained in terms of relative palatability and associational resistance, which need to be considered in forest management plans of mixed forests under browsing pressure. To improve the biological understanding underlying forest management decisions, we recommend managers monitoring browsing impact on woody plants through space and time within plans of sustainable harvesting.

Introduction

Traditional forest management in the Mediterranean basin is highly reliant on coppicing, a silvicultural practice that depends on vegetative regeneration of woody plants (Scarascia-Mugnozza et al., 2000; Sjölund and Jump, 2013). In fact, dominant evergreen trees and shrubs of the Mediterranean basin generally resprout vigorously after severe disturbances (Pausas et al., 2008). However, vegetative regeneration of coppices can be negatively affected by widespread and increasing populations of ungulate browsers (Apollonio et al., 2010). As ungulate populations tend to aggregate in coppice areas (Kuijper et al., 2009; Cutini et al., 2011) in search of preferred plants (Augustine and McNaughton, 1998; Bee et al., 2009; Martínez, 2009; Perea et al., 2014), coppice forest dynamics are likely to be affected by herbivore selectivity. Given that the main regeneration mechanisms in coppice forest management systems is vegetative (Sjölund and Jump, 2013), selective browsing on coppices could affect tree growth and forest regeneration and composition in the long term (Cutini et al., 2011; Chianucci et al., 2015). Indeed, selective browsing could negatively affect palatable woody species, providing competitive advantage to less preferred species belonging to early successional stages of vegetation (Augustine and McNaughton, 1998; Bruno et al., 2003). Such process could result in forest ecosystem homogenization, as shown in Spanish Mediterranean shrubland with high density of red deer (Perea et al., 2014). Given its economic and ecological importance, understanding patterns of ungulate browsing on woody plant species is a traditional and open issue in forest management (Bengtsson et al., 2000).

Browsing patterns are strongly dependent on feeding behavior and selectivity of browsers (Barbosa et al., 2009) as well as on species-specific resistance mechanisms of plants (Massei et al., 2000; Focardi and Tinelli, 2005). Depending on their feeding requirements and available resources (Bugalho and Milne, 2003; Storms et al., 2008), browsers make foraging decisions (Bee et al., 2009). Within this behavioral process, the likelihood of plant detection by browsers can decrease (associational resistance, AR) or increase (associational susceptibility, AS) with plant community composition and relative palatability of plants (Barbosa et al., 2009; Bee et al., 2009; Herfindal et al., 2015). Indeed, AR can be explained in terms of "repellent plant hypothesis" and "attractant-decoy hypothesis", where browsers can respectively avoid low quality patches of vegetation, or be attracted by more palatable neighbors (see Bee et al., 2009 for a nice study on red deer). Somewhat differently, AS can arise when browsers are attracted within a patch to more palatable focal plants (Barbosa et al., 2009), i.e. the spatial scale of the investigation and the selected focal plant matter. In fact, AR patterns are affected by spatial scale: moose browsing on pines has been found to be affected by abundance and/or quality of browse at multiple spatial scales (Herfindal et al., 2015). Regarding red deer (*Cervus elaphus*), it has been shown that browsing probability can be strongly affected by plant identity (species) and overall patch quality (Bee et al., 2009), supporting a "plant repellent" scenario (see also Perea et al., 2014 for selectivity patterns). The object of this investigation, the Corsican red deer (*Cervus elaphus corsicanus*), is also known to show feeding selectivity among species of the Mediterranean Holm oak (*Quercus ilex*) woodland (Beccu, 1989; Maillard, 1994; Lovari et al., 2007). Therefore, we hypothesize that red deer browsing on vegetative regeneration of coppiced plants should vary in space and time

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with the environmental context where the process develops (Barbosa et al., 2009; Bee et al., 2009; Owen-Smith, 2014), i.e. depending on plant- and patch- level features.

In general, despite the economic importance of coppice forest management (Sjölund and Jump, 2013) and red deer conservation or enhancement (Lovari et al., 2007; Perea et al., 2014), little is known about the spatial and temporal variation of red deer browsing on vegetative regeneration of coppiced Mediterranean trees and shrubs. To manage potentially contrasting objectives such as wood production and nature conservation, it is important to learn more about the interaction between red deer browsing and vegetative regeneration of coppiced plants. From a manager perspective, relevant knowledge about system functioning could arise from adaptive management (Nichols and Williams, 2006; Lindenmayer et al., 2008), with a targeted monitoring plan of coppiced stands. Within this management perspective, we attempt to understand here patterns of Corsican red deer browsing on vegetative regeneration of coppiced plants of the Mediterranean Holm oak woodland. Similarly to the mainland red deer (Apollonio et al., 2010), the Corsican subspecies was overexploited and heavily fragmented up to the 70s, which resulted in strict protection measures and subsequent population recovery with increasing impact on vegetation (Lovari et al., 2007; Mandas et al., 2008; Puddu et al., 2009, 2012).

The investigation was carried in a Site of Community Interest (SCI) of the European Natura 2000 network, where both the conservation of the Holm oak habitat and the Corsican red deer are main objectives (Council Directive 92/43/EEC, Annex I and II). To consider the social and economic dimensions of the sustainable development of this SCI (Keulartz, 2009), a forest management plan based on coppice with standards was implemented. Given previous data on similar ecosystems showing tolerance to browsing (Focardi and Tinelli, 2005; Lovari et al., 2007), the strong interest in red deer conservation, and the importance of maintaining ecological processes (Owen-Smith, 2014) that historically shaped the landscape (Blondel and Aronson, 1999), stands were not fenced to protect vegetative regeneration of plants. However, the authorizing body prescribed to monitor eventual damages due to overbrowsing: browsing pressure on the vegetative regeneration of coppiced plants was thus monitored with rapid visual inspections (Cutini et al., 2011).

Using the data gathered within this monitoring program, and considering the biological scenario hypothesized above, we investigate whether browsing probability on woody plants vary as follows:

- a) Browsing probability differs among plant species. The Corsican red deer, as well as the European red deer (Bee et al., 2009; Perea et al., 2014), shows feeding selectivity and browse differentially on plant species (Beccu, 1989; Maillard, 1994; Lovari et al., 2007).
- b) Browsing probability is affected by the density of palatable and unpalatable plants. Feeding behaviour of the Sardinian red deer could be affected by the identity and density of the neighbour plants. Patches with high density of unpalatable plants could be avoided (Bee et al., 2009), reducing browsing probability. Patches with high density of palatable plants may attract browsers, and affect browsing probability in complex ways (Herfindal et al., 2015): higher density of palatable plants may reduce browsing probability if browsers are saturated (abundant resources), or may increase browsing probability if most preferred plants are more likely to be detected (Barbosa et al., 2009).
- c) Browsing probability decreases with plant height. Plant size affects quantity and position of new shoots, and thus browsing probability (Chianucci et al., 2015). One year after coppicing plant height is very close to ground level. Red deer browsing will be easy as the area is open and shoots are well reachable by animals. With plant growth, more shoots will be available at heights that are progressively more difficult to reach by browsers.
- d) Browsing probability decreases with time from coppicing. As time could affect browsing probability with additional resistance mechanisms (Massei et al., 2000; Focardi and Tinelli, 2005), we will attempt to evaluate also a general reduction of browsing rates with time (years from coppicing).

- e) Browsing increases with increasing rooting activity of wild boars. Wild boars are widespread ungulate in Mediterranean forests and may interact with red deer by feeding on acorns and reducing the grass layers with rooting (Latham, 1999). They could reduce food resources available for red deer (Bugalho and Milne, 2003; Lovari et al., 2007; Storms et al., 2008), increasing the need for browsing.

Materials and methods

Habitat and species

Coppiced stands were located in the public forest of Marganai (Sardinia, Italy), within the SCI “Monte Linas–Marganai”, ITB041111. The forest is managed by the regional government agency Forestas. During 2011, over a total area of 542 ha, the agency started a forest management plan based on coppice with standards, with 27 year rotation length.

During the first part of the plan, three stands were coppiced (A: 2010/11; B: 2011/12; C: 2012/13). Total stand area was 8, 15, and 19 ha for A (Google Earth, centre coordinates: 32S 465154.00 m E, 4362285.00 m N), B (465247.00 m E, 4361995.00 m N), and C (465138.00 m E, 4361208.00 m), respectively.

The area is characterized by the Habitat 9340 “*Quercus ilex* and *Quercus rotundifolia* forests” (Council Directive 92/43/EEC, Annex I), with holm oaks (*Quercus ilex*) associated with shrubs such as the strawberry tree (*Arbutus unedo*), the tree heath (*Erica arborea*), and the green olive tree (*Phillyrea latifolia*). These woody species are coppiced along with Holm oaks for firewood production, and to facilitate operations. After coppicing, all species of woody plants mentioned above soon recover with root suckers. Forest opening also results in the germination of the seed bank of rockroses, *Cistus monspeliensis* and *Cistus salvifolius*.

The Corsican red deer is a subspecies endemic to Sardinia and Corsica, strictly protected under Appendix II of the Bern Convention and Annexes II and IV of the Council Directive 92/43/EEC. The species recently re-colonised the coppiced area with individuals coming from the two adjacent populations (Puddu et al., 2009). Among other large herbivores that can be found in Sardinia, sheep, goat, domestic cattle, and fallow deer (*Dama dama*) are absent, the mouflon (*Ovis gmelini musimon*) is rare (it has been occasionally recorded in the area by forest workers, and 1 faecal pellet group was observed in 2015 in a coppiced stand), whereas the wild boar (*Sus scrofa meridionalis*) is widespread. Estimates of Corsican red deer densities based on faecal pellet counts performed in the area ranged from 0.67 animals/km² before coppicing (2010) up to 1.82 (2011), 6.44 (2012), 5.04 (2013), and 4.31 (2014) after coppicing, which can be considered low densities for Mediterranean ecosystems (Lovari et al., 2007).

Browsing rates

Mandatory monitoring was performed with limited resources devoted to research activities (Cagnacci et al., 2013). Following previous studies that showed the reliability of rapid assessments based on categories of browsing pressure on single plants (Espelta et al., 2006; Cutini et al., 2011), we opted for a simple and cost effective method, as below.

Browsing rates were visually estimated as the proportion of shoots browsed per plant. A careful observation of all suckers belonging to the stool was simultaneously performed by two well trained observers. At the end of the observation, a consensus about the proportion of browsed shoots observed in the plant was reached between the two observers, and directly recorded as proportion (value ranging from 0.0, 0.1, . . . , 1). All observations were done by the same observers (A. Murgia and P. Casula). Therefore, observer-specific bias, which is reduced by the combination of two independent observations, should remain constant.

At the beginning of spring (March/April) 2013, 2014, 2015 and 2016 respectively 3 (Stand A) + 6 (Stand B), 3 (Stand A) + 4 (Stand B) + 4 (Stand C), 3 (Stand A) + 4 (Stand B) + 4 (Stand C), and 4 (Stand B) + 4 (Stand C) linear transects (25 m length and 2 m width) were randomly selected within the coppiced stands. Due to a delay in planning, monitoring started in 2013, 2 years after coppicing the first stand (A).

Stand A was also not sampled during 2016 (5th year after coppicing, which was not of interest). Stand edges and uncut areas within stands were avoided. The proportion of browsed shoots per plant was visually estimated on all coppiced plants and shrub seeders (*Cistus* spp.) found within transects. All plants that had whole or a part of their crown projection inside transects were considered. Transects were randomly selected each year, and were not repeated during subsequent years. Browsing rates were thus measured once each year after coppicing, before the main growing season of woody plants (May-June), and they can be interpreted as the cumulative browsing on plants over the year.

Variables affecting browsing rates

Plant height after coppicing (H) was measured as the maximum vertical height of plant suckers growing up from the coppice (ground level), or the highest branch of shrub seeders (*Cistus* spp.). Time was measured as the number of years from coppicing ($YfC=1, 2, 3, 4$). The density of unpalatable woody plants (Du) was measured as the total number of *Arbutus unedo*, *Erica arborea* and *Cistus* spp. individuals found within transects. As we will show in the results, these species were very seldom browsed, and their density is taken as a measure of patch resistance to red deer browsing, according to a plant repellence hypothesis (Bee et al., 2009). The density of woody palatable plants was also considered (Dp), as the presence of more abundant resources could enhance the permanence of red deer within the patch (attractant) or reduce the browsing pressure on single plants due to saturation of browsers. Dp was measured as the total number of *Quercus ilex* and *Phyllirea latifolia* individuals found within transects. Disturbance levels from wild boars were estimated as percent ground cover with rooting signs observed within the transect (WB), which can be used as proxy for wild boar densities (Amori et al., 2015; Casula et al., 2016).

Among the factors possibly affecting browsing rates, the random effects of stand (A, B, and C), year of sampling (2013, 2014, 2015, and 2016), and transect was also considered.

Statistical analysis

The proportion of browsed plants can be used to estimate browsing probability of plants (Frid and Turkington, 2001; Herfindal et al., 2015), whereas the proportion of browsed shoots per plant can be used to estimate browsing probability of shoots belonging to a given plant. Browsing probability of plants was estimated using logistic regression (Neter et al., 1996; Frid and Turkington, 2001; Bee et al., 2009; Herfindal et al., 2015), whereas browsing probability of shoots, considering that available observations lay within a open unit interval (0–1), was analysed using beta regression (Cribari-Neto and Zeileis, 2009). Possible effects of stand, year and transect were also considered in both type of regressions within a generalized linear mixed model framework (Bolker et al., 2009).

We used the software R 3.2.4 (R Core Team, 2013) packages `lme4` (Bates et al., 2015) to analyse browsing rates on plants (binomial), and `betareg` (Cribari-Neto and Zeileis, 2009) to analyse the proportion of browsed shoots per plant. `Betareg` assumes a beta distribution to model continuous response variables with values in the open unit interval (0–1) (Grün et al., 2004). Giving the software constraint of $0 < y < 1$ (i.e. $y=0$ and $y=1$ cannot be analysed), data were modified as follows, $Br = (y(n-1) + 0.5)/n$, as suggested by (Cribari-Neto and Zeileis, 2009), where Br is the corrected proportion of browsed shoots per plant and y is the real observation (see Supplemental S1).

To assess difference in browsing probability among plant species, both the proportion of browsed plants (BrY) and the proportion of browsed shoots per plant (Br) were analysed. A null model specifying that browsing probability of plants does not vary among plant species ($BrY \sim 1$; one intercept for all species), was compared with a model specifying that browsing probability of plants varies among plant species ($BrY \sim Sp$; one intercept for each species). The proportion of browsed shoots (Br) was similarly analysed: a null model specifying that browsing probability of shoots does not vary among plant species ($Br \sim 1$), was compared with a model specifying that browsing prob-

ability of shoots varies among plant species ($Br \sim Sp$). Proportion of browsed shoots were analysed with both the R packages `lme4` on logit transformed data (`lme4` does not allow to analyse proportions in continuous form, $0 < y < 1$), and `betareg`, which was used to analyse untransformed proportions. All models assumed stand, year, and transect random effects, and were compared by means of likelihood ratio test and small sample correction of the Akaike Information Criterion, AICc (Burnham and Anderson, 2002). Subsequently, Tukey contrasts between estimated species-specific intercepts were performed using the R package `multcomp` (Hothorn et al., 2008). See Supplemental S2 for additional details and R scripts necessary to repeat the analysis.

Effect of variables potentially affecting browsing rates was analysed using the proportion of browsed shoots, focussing on species that were significantly browsed. The analysis was performed separately on each browsed species, using beta regression (Cribari-Neto and Zeileis, 2009). To assess problems of collinearity among predictor variables we rested on: a) a priori selection of few biologically meaningful variables; b) confronting support and consistence of parameter estimates across univariate and multivariate regressions; c) checking correlation coefficients between covariates (Mac Nally, 2000; Burnham and Anderson, 2002; Dormann et al., 2013). Therefore, browsing patterns were analysed with both univariate and multivariate regression. All regression models assumed stand, year, and transect random effects.

Models specifying univariate beta regressions, $Br \sim Covariate$ (Du or H or YfC or WB or Dp), were compared with a null model specifying no effect of the covariates of interest, $Br \sim 1$ (one intercept, which corresponds to the average value of browsing probability of shoots). Comparison was performed by means of AICc values and likelihood ratio test (see Supplemental S3 for R scripts).

The general multiple regression model assumed that browsing probability of shoots was simultaneously affected by all covariates of interest. We thus hypothesized that plant and context specific features, such as plant identity (Sp), plant height (H), time from coppicing (YfC), wild boar density (WB), density of palatable (Dp), and unpalatable plants (Du), determine the observed browsing rates on plants: $Br \sim 1 + Du + H + YfC + WB + Dp$.

Starting from the general model above, regression variables were selected by means of backward model selection (Mac Nally, 2000; Burnham and Anderson, 2002; Hobbs and Hilborn, 2006). The general model was confronted with simplified models (-1 covariate at a time) by mean of AICc. Variables were eliminated if model simplification resulted in consistent improvement of AICc. When $\Delta AICc$ between the general and the simplified model was smaller than 2, a likelihood ratio test was used to select the most appropriated (see Supplemental S4 and Supplemental S5). The best multiple regression model retained only covariates that were supported by the backward model selection. Parameter estimates were obtained for each model run, and with model averaging, which addresses model uncertainty by using model weights to average parameter estimates across models (Burnham and Anderson, 2002; Hobbs and Hilborn, 2006).

Results

Observed browsing rates

Data about browsing on vegetative regeneration of 1101 coppiced plants (*Arbutus unedo*=Au, n=502; *Quercus ilex*=Qi, n=327; *Erica arborea*=Ea, n=177; *Phillyrea latifolia*=Pl, n=95) and 178 shrub seeders (*Cistus monspeliensis*=Cm, n=109; *Cistus salvifolius*=Cs, n=69) were recorded (see Supplemental S1). Table 1 shows relative abundance, proportions of browsed plants (BrY), and proportions of browsed shoots (Br) per species. Coppices of Holm oaks (Qi: $BrY=81\%$, $Br=41\%$) and of the Green olive tree (Pl: $BrY=89\%$, $Br=63\%$) were very often browsed by red deer. Strawberry trees (Au: $BrY=4\%$, $Br<1\%$), tree heaths (Ea: $BrY=6\%$, $Br=1\%$), and rockroses ($BrY=5\%$, $Br=1\%$ for Cm and $BrY=10\%$, $Br=4\%$ for Cs) were rarely browsed. Noteworthy, the most abundant species, the strawberry tree, is the most rarely browsed, while the relatively rare green olive tree is the most often browsed. Additionally, at stand level the proportion of browsed plants of each species is not related to relative abundance (Spearman

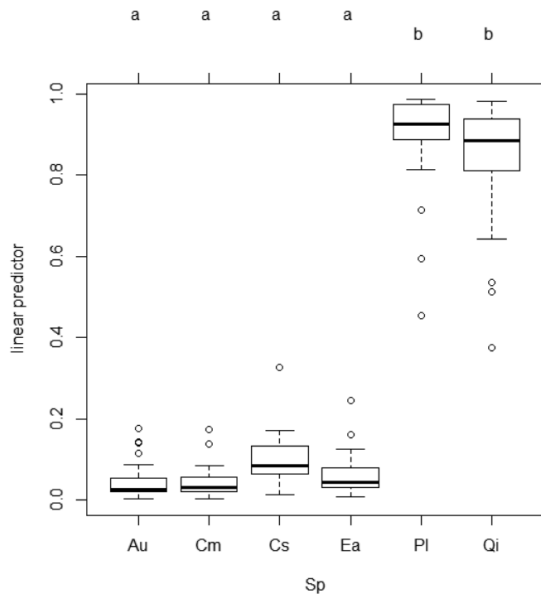


Figure 1 – Box plot with results of Tukey contrasts among species-specific browsing probabilities of plants estimated with model $BrY \sim Sp$ (“plot a cld object” function of R package multcomp; linear predictor = BrY). Browsing probability of plants differs between unpalatable (a) and palatable species (b). Plant species: *Arbutus unedo* (Au), *Cistus monspeliensis* (Cm), *Cistus salvifolius* (Cs), *Erica arborea* (Ea), *Phyllirea latifolia* (PI), *Quercus ilex* (Qi).

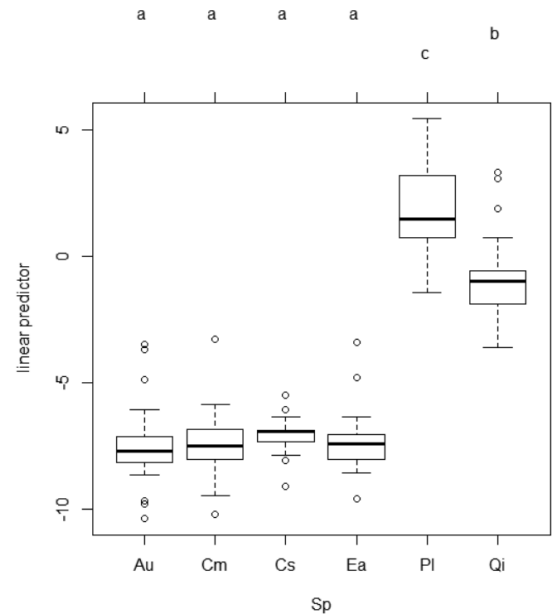


Figure 2 – Box plot with results of Tukey contrasts among species-specific browsing probabilities of shoots estimated with model $Br \sim Sp$ (“plot a cld object” function of R package multcomp; linear predictor = logit transformed Br). Browsing probabilities of shoots of palatable species differ with unpalatable species (a) and between each other (b and c). Species: *Arbutus unedo* (Au), *Cistus monspeliensis* (Cm), *Cistus salvifolius* (Cs), *Erica arborea* (Ea), *Phyllirea latifolia* (PI), *Quercus ilex* (Qi).

correlation=0.057, n=18), confirming selectivity of red deer. Browser selectivity should result in different browsing probability among plant species, as analysed below.

Browsing probability differs among plant species

The model specifying that browsing probability of plants does not differ among species ($BrY \sim 1$; AICc=1490.278) has no support if compared with the model specifying that browsing probability of plants differ among plant species ($BrY \sim Sp$; AICc=686.607). Likelihood ratio test shows that the two models are significantly different ($p=0.000$). Figure 1 shows box plot with results of Tukey contrasts among species-specific browsing probabilities of plants estimated with model $BrY \sim Sp$. Browsing probability of PI and Qi (b) significantly differs from those of Au, Cm, Cs, and Ea (a), with p values <0.001 in all contrasts between the two groups (see Supplement S2). The figure shows that there are two highly preferred species (PI and Qi), and a group of species that are rarely selected.

Similarly, the model specifying that browsing probability of shoots does not differ among species ($Br \sim 1$; AICc=7258.85) has no support if compared with the model specifying that browsing probability of shoots differ among plant species ($Br \sim Sp$; AICc=6012.281). Likelihood ratio test shows that the two models are significantly different ($p=0.000$). Figure 2 shows box plot with results of Tukey contrasts among species-specific browsing probabilities of shoots estimated with model $Br \sim Sp$ ($1m \times 4$ with logit transformed data). Browsing probability

of PI (c) and Qi (b) significantly differs between each other, and from those of Au, Cm, Cs, and Ea (a), with $p < 0.001$ in all contrasts between the two groups, and between the two palatable species. Identical results are obtained if Tukey contrasts are performed on browsing probability of shoots estimated with `betareg` on untransformed data (Supplemental S2). Likely, the more detailed information about browsing probability contained in the proportion of browsed shoots per plant confirms that there are fundamentally two groups of plants that drastically differ in palatability (hereafter we will refer to them as “palatable” and “unpalatable”), and shows that the two significantly browsed plants, Qi and PI, are browsed differentially. Below, variables affecting browsing probability will be studied separately on the two species.

Variables affecting browsing probability

Univariate regressions

Figure 3 shows how plant height increases with time, depending on species. Four years after coppicing Au, Ea and Qi median heights exceed 1.5 meters. Despite considerable browsing, Qi coppices reach in four years heights that cannot be easily browsed by red deer. On the opposite, suckers of PI, the most heavily browsed plant, remain well below one meter, at heights that can be easily browsed by the Corsican red deer.

Univariate regressions performed on the proportion of browsed shoots of each palatable species (Qi, n=327; PI, n=95) show that browsing probability: a) decreases with plant height, H (PI:

Table 1 – Relative abundance and proportion of browsed plants ($n_{Sp(Br)}/n_{Sp(tot)}$) per stand (A, B, C), and species. Plants are ranked in order of relative abundance. $Br_{(Mean)}$ refers to the average proportion of browsed shoot per species ($\Sigma Br/n_{Sp(tot)}$). ABC refers to data merged over stands.

Plant species	Relative abundance				Proportion of browsed plants (BrY)				$n_{Sp(Br)}$	$n_{Sp(tot)}$	$Br_{(Mean)} \pm SD$
	A	B	C	ABC	A	B	C	ABC			
<i>Arbutus unedo</i>	0.36	0.42	0.38	0.39	0.02	0.05	0.05	0.04	22	502	0.007 ± 0.036
<i>Quercus ilex</i>	0.33	0.24	0.22	0.26	0.62	0.88	0.93	0.81	265	327	0.410 ± 0.333
<i>Erica arborea</i>	0.10	0.13	0.18	0.14	0.19	0.04	0.03	0.06	11	177	0.013 ± 0.060
<i>Cistus monspeliensis</i>	0.13	0.08	0.06	0.08	0.05	0.07	0.00	0.05	5	109	0.014 ± 0.077
<i>Phillyrea latifolia</i>	0.03	0.11	0.06	0.07	0.60	0.93	0.93	0.89	85	95	0.628 ± 0.371
<i>Cistus salvifolius</i>	0.04	0.03	0.09	0.05	0.00	0.41	0.00	0.10	7	69	0.045 ± 0.160
$n_{(Stand)}$	318	541	420							1279	

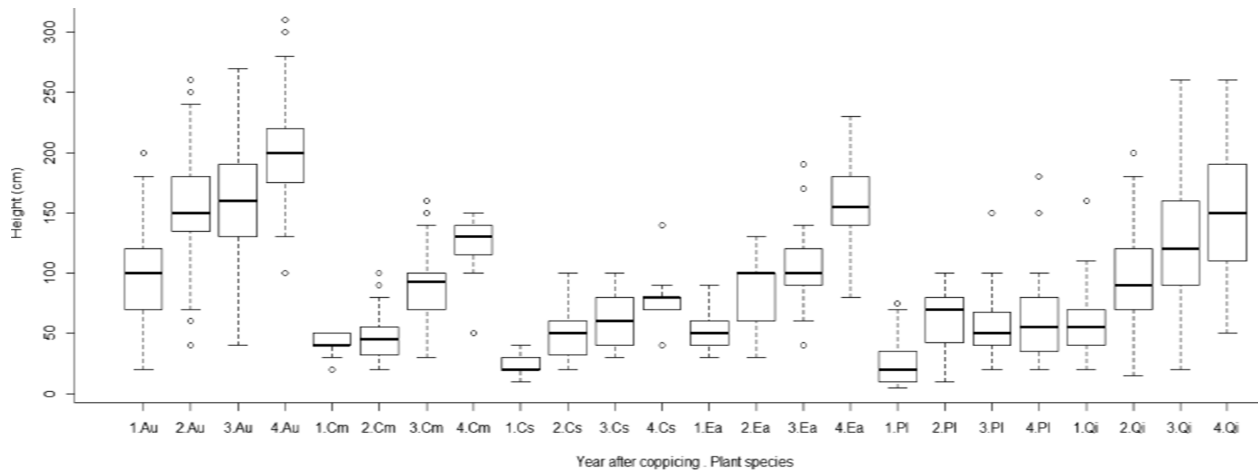


Figure 3 – Plant height increases with time from coppicing (1, 2, 3, 4 years), depending on species: *Arbutus unedo* (Au), *Cistus monspeliensis* (Cm), *Cistus salvifolius* (Cs), *Erica arborea* (Ea), *Phyllirea latifolia* (Pl), *Quercus ilex* (Qi).

slope= -0.017 ± 0.004 (SE), $p(>|z|) < 0.001$; Qi: slope= -0.013 ± 0.001 , $p(>|z|) < 0.001$); b) decreases with years from coppicing, *YfC* (Pl: slope= -0.975 ± 0.137 , $p(>|z|) < 0.001$; Qi: slope= -0.641 ± 0.069 , $p(>|z|) < 0.001$); c) decreases or increases with the density of unpalatable plants, *Du* (Pl: slope= -0.066 ± 0.015 , $p(>|z|) < 0.001$; Qi: slope= 0.024 ± 0.009 , $p(>|z|) = 0.01$), d) increases or decreases with the density of palatable plants, *Dp* (Pl: slope= 0.087 ± 0.026 , $p(>|z|) < 0.001$; Qi: slope= -0.087 ± 0.011 , $p(>|z|) < 0.001$), and e) increase with wild boar rooting activity, *WB* (only Qi: slope= 0.763 ± 0.293 , $p(>|z|) = 0.009$).

Table 2 and 3 show model selection results (AICc), pseudo R-squared (Cribari-Neto and Zeileis, 2009), and parameter estimates for each univariate model and the null, for Pl and Qi respectively. The significant correlations above are supported by the model selection based on AICc, and by Likelihood ratio tests between null and univariate models (see Supplemental S3). The effect of wild boar rooting on browsing probability (*WB*), which weakly appears within the Qi data, and the contrasting effects of density of palatable (*Dp*) and unpalatable species (*Du*), need to be further assessed with multivariate analysis. The strong negative correlation between *Du* and *Dp* (Spearman correlation= -0.707) warns also about possible effects of collinearity (Mac Nally, 2000; Dormann et al., 2013), suggesting caution in interpreting results. Among other covariates, highest correlations were found between *H* and *YfC* in both Pl (Spearman correlation, $r=0.483$)

and Qi ($r=0.599$) data sets. Such values are below the “rule of thumb” threshold of $|r| > 0.7$ that warns about high risk of collinearity problems in data analysis (Dormann et al., 2013). Patterns of the less controversial effects of time from coppicing (*YfC*) and plant height (*H*) on browsing probability of shoots are shown in Fig. 4 and 5 respectively.

Multiple regressions

Table 2 presents model selection results, pseudo R-squared, and parameter estimates of the multiple regression models run on the proportion of browsed shoots of *Phyllirea latifolia* coppices. The exclusion of *WB* and *Dp* from the general model (4^{th}) resulted in small AICc improvements (see 2^{nd} and 3^{rd} model respectively), while excluding *H*, *Du*, and *YfC* resulted in increased AICc values (see 5^{th} , 6^{th} , and 8^{th} model respectively). Therefore, the best model retains the variables *H*, *Du* and *YfC*. Note that the effect of *Dp*, which appeared to be clearly supported by the univariate model, reduces its importance (and magnitude) in multivariate models when also *Du* is present. Likelihood ratio tests between the general multiple regression model (4^{th}) and the first three models, with rather similar AICc values, do not show any significant difference between models, i.e. the most parsimonious should be retained. The table shows also parameter estimates, which have stable signs and magnitudes over the models. Consistently with the univariate analysis, the effects of plant height (*H*), density of unpalatable plants (*Du*), and years from coppicing (*YfC*), on browsing probability of shoots of green olive tree coppices are negative. All cov-

Table 2 – Variables affecting browsing probability of shoots on the Green olive tree, *Phyllirea latifolia* (n=95). Legend: Ps. R^2 =pseudo R squared (betareg); AICc=corrected Akaike Information Criterion; $\Delta AICc$ =difference between the AICc of the model and that of the best model selected (1^{st}); w=Akaike weight; K=number of model parameters; Int.=intercept; Slope parameters: *Du*=density of unpalatable plants; *H*=plant height; *YfC*=years from coppicing; *WB*=wild boar rooting; *Dp*=density of palatable plants. Model averaging: estimates of parameters obtained with a weighted mean across models (see Methods).

Rank	Model structure	Model diagnostics					Parameter estimates					
		Ps. R^2	AICc	$\Delta AICc$	w	K	Int.	Du	H	YfC	WB	Dp
1	<i>Du+H+YfC</i>	0.58	-333.8475	0.0000	0.2981	11	5.5274	-0.0980	-0.0091	-1.0640		
2	<i>Du+H+YfC+Dp</i>	0.59	-333.6377	0.2098	0.2684	12	4.7704	-0.0885	-0.0083	-1.0631		0.0421
3	<i>Du+H+YfC+WB</i>	0.58	-333.1924	0.6551	0.2148	12	5.0325	-0.0954	-0.0096	-1.0521	0.7610	
4	<i>Du+H+YfC+WB+Dp</i>	0.59	-332.4830	1.3645	0.1507	13	4.4147	-0.0874	-0.0088	-1.0561	0.6635	0.0386
5	<i>Du+YfC+WB+Dp</i>	0.57	-330.8929	2.9546	0.0680	12	4.1324	-0.0858		-1.1505	0.5613	0.0441
6	<i>H+YfC+WB+Dp</i>	0.52	-310.1599	23.6876	0.0000	12	1.4256		-0.0073	-0.9048	0.8599	0.0813
7	<i>YfC</i>	0.41	-302.3567	31.4908	0.0000	12	2.7435			-0.9750		
8	<i>Du+H+WB+Dp</i>	0.35	-293.0980	40.7495	0.0000	9	1.4177	-0.0632	-0.0164		0.8687	0.0340
9	<i>H</i>	0.24	-280.9459	52.9016	0.0000	9	1.1710		-0.0170			
10	<i>Du</i>	0.19	-279.1593	54.6882	0.0000	9	1.6087	-0.0663				
11	<i>Dp</i>	0.16	-274.4556	59.3919	0.0000	9	-0.9113					0.0869
12	<i>WB</i>	0.00	-265.3998	68.4477	0.0000	9	-0.2039				0.7806	
13	Null		-266.5380	67.3095	0.0000	8	0.2606					
Model averaging:							4.9553	-0.0925	-0.0083	-1.0659	0.3016	0.0201

Table 3 – Variables affecting browsing probability of shoots on Holm oaks, *Quercus ilex* (n=327). Legend: Ps. R^2 =pseudo R squared (β_{areg}); AICc=corrected Akaike Information Criterion; ΔAICc =difference between the AICc of the model and that of the best model selected (1^{st}); w=Akaike weight; K=number of model parameters; Int.=intercept; Slope parameters: Du=density of unpalatable plants; H=plant height; YfC=years from coppicing; WB=wild boar rooting; Dp=density of palatable plants. Model averaging: estimates of parameters obtained with a weighted mean across models (see Methods).

Rank	Model structure	Model diagnostics					Parameter estimates					
		Ps. R^2	AICc	ΔAICc	w	K	Int.	Du	H	YfC	WB	Dp
1	Du+H+YfC+Dp	0.33	-587.4307	0.0000	0.7224	12	3.2558	-0.0374	-0.0082	-0.4195		-0.0753
2	Du+H+YfC+WB+Dp	0.33	-585.4897	1.9410	0.2737	13	3.1240	-0.0361	-0.0081	-0.4162	0.1488	-0.0746
3	H+YfC+WB+Dp	0.30	-577.0046	10.4261	0.0039	12	1.8727		-0.0081	-0.3247	0.3843	-0.0595
4	Du+H+WB+Dp	0.26	-564.9889	22.4418	0.0000	12	2.0339	-0.0181	-0.0120		0.2729	-0.0739
5	Du+YfC+WB+Dp	0.30	-561.3010	26.1297	0.0000	12	1.6860	-0.0366		-0.6480	0.2046	-0.0808
6	Du+H+YfC+WB	0.29	-553.6604	33.7703	0.0000	12	1.4256	-0.0133	-0.0088	-0.4156	0.3179	
7	H	0.22	-536.2060	51.2247	0.0000	9	0.9779		-0.0130			
8	YfC	0.22	-528.2631	59.1676	0.0000	9	1.2748			-0.6407		
9	Dp	0.10	-495.9915	91.4392	0.0000	9	0.7676					-0.0876
10	Du	0.00	-454.6119	132.8188	0.0000	9	-0.8498	0.0243				
11	WB	0.01	-453.7764	133.6543	0.0000	9	-0.8663				0.7632	
12	Null		-451.0415	136.3892	0.0000	8	-0.3889					
Model averaging:							3.2143	-0.0369	-0.0082	-0.4182	0.0422	-0.0750

ariates retained in the best model are also significant with $p(>|z|)<0.001$ (see Supplemental S4).

Table 3 presents model selection results and parameter estimates of the multiple regression modes run on the proportion of browsed shoots of *Quercus ilex* coppices. The exclusion of WB from the general model

(ranked 2nd) resulted in a reduction of the AICc value (see 1st model). Excluding Du, YfC, H, and Dp resulted in a progressively more consistent increase of AICc values, providing strong support for the effect of such covariates (see 3rd, 4th, 5th, and 6th model respectively). Differently from the univariate analysis, multiple regressions exclude the effect of the covariate WB (very weak, see also the very low pseudo R-squared of model 11). The table shows also parameter estimates, which in one case show inconsistency: the effect of Du is negative across all multivariate models, while in the univariate model (10th) is positive. Considering the strong negative correlation found between Du and Dp, Du may capture and be affected by the stronger effect of Dp when this last is absent from the analysis. When the two density covariates are analysed together, their effect is consistent all over the models and always negative. Therefore, the effects of plant height (H), density of unpalatable plants (Du), years from coppicing (YfC), and palatable plants (Dp) on browsing probability of shoots of Holm oak coppices (Qi) are negative. All covariates retained in the best model are significant with $p(>|z|)<0.001$ (see Supplemental S5).

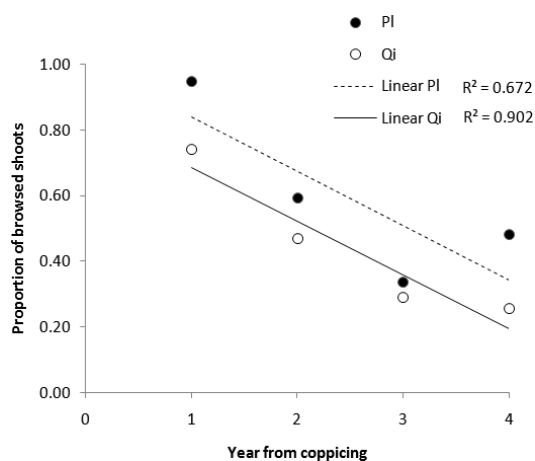


Figure 4 – Proportion of browsed shoots of *Phyllirea latifolia* (PI) and *Quercus ilex* (Qi) decreases with the number of years from coppicing (linear regression on averages per year from coppicing).

Discussion

This study shows that red deer browsing on resprouters of common trees and shrubs of the Mediterranean Holm oak forest can be affected by plant features (identity and plant height), time (years from coppicing), and spatial context (density of palatable and unpalatable woody plants at the patch level). The negative effects of plant height and time could be related to the increasing size and abundance of resources that reduces feeding impact on single plants, whereas the effect of plant identity and density suggests that the Corsican red deer makes foraging decisions based on relative palatability and abundance of plants (Bee et al., 2009).

Compared to other ungulates, red deer are opportunistic foragers having a mixed diet that can adapt to a wide type of browse, depending on environmental contexts (Bugalho and Milne, 2003; Storms et al., 2008). Nevertheless, studies of feeding selectivity show that when red deer have choice they select the most preferred plants (Bee et al., 2009; Perea et al., 2014). In a system with low density of browsers and relative high abundance of browse, we have shown that the Corsican red deer is highly selective. High levels of browsing were found on Holm oaks (*Quercus ilex*) the main tree present in the study site, and Green olive trees (*Phillyrea latifolia*), which tends to be highly preferred by deer (Massei et al., 2000; Focardi and Tinelli, 2005), and absent from heavily browsed sites (Chaideftou et al., 2009). Relative palatability of the two plant species confirms previous studies showing intermediate and high browsing impacts on Holm oaks and Green olives respectively, with Holm oaks generally showing more resistance due to higher phenolics contents, and development of thorny leaves in

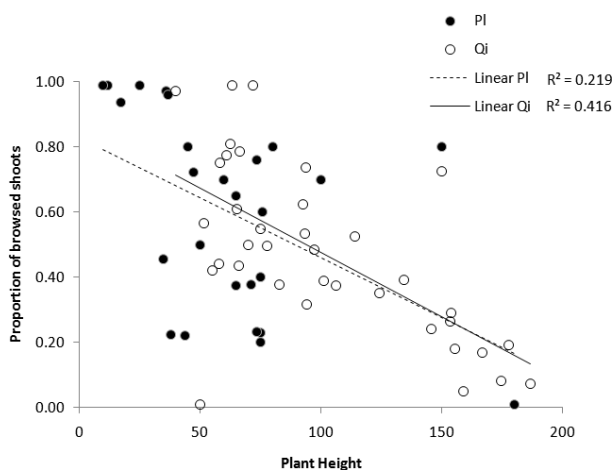


Figure 5 – Proportion of browsed shoots of *Phyllirea latifolia* (PI) and *Quercus ilex* (Qi), decreases with plant height (linear regression on averages per transect).

response to browsing (Massei et al., 2000; Focardi and Tinelli, 2005). Early-successional shrubs such as strawberry trees (*Arbutus unedo*), tree heaths (*Erica arborea*) and rockroses (*Cistus* spp.) were very seldom browsed. Data relative to plant density and heights suggest that the most abundant resource found in the system is by far the strawberry tree (*Arbutus unedo*), which is nevertheless the least browsed species. Considering that browsing rates were not related to relative abundance, differences in browsing probability could be explained by different quality among species (e.g. astringency due to phenolics contents). However, strawberry trees, and occasionally tree heaths and rockroses (*Cistus salvifolius*), have been found to be regularly browsed by red deer in other Mediterranean systems (Maillard, 1994; Fernández-Olalla et al., 2006; Martínez, 2009; Perea et al., 2014). Considering that conclusions about diet composition drawn in a particular study area will rarely be relevant to other areas (Storms et al., 2008), this fact should not surprise. Indeed, Corsican red deer feeding selectivity was already discussed to vary in different environmental contexts (Maillard, 1994). The very low browsing probability observed on the strawberry tree could be due to the fact that, differently from previous studies (Maillard, 1994; Fernández-Olalla et al., 2006; Perea et al., 2014), we investigated browsing on vegetative regeneration of coppiced plants, which have greater availability of vigorous suckers and young leaves than uncut plants. Young leaves of strawberry trees are highly astringent (Ouki et al., 2002), and could be generally avoided by red deer in the presence of other abundant and relatively more palatable resources such as Holm oak suckers. Interestingly, leaf age did not affect phenolics content in Holm oaks (Massei et al., 2000), suggesting that young leaves of Holm oak suckers could be less resistant to browsing than those of Strawberry tree suckers. This scenario could be also similar to previous studies, where faster growth and higher tannin contents of Chestnut coppices, compared to Turkey oak coppices, were suspected to be responsible of lower level of browsing on Chestnuts (Cutini et al., 2011). Possibly, different responses of plants to browsing and coppicing could explain differences in observed feeding selectivity patterns. Indeed, resprouting after severe disturbances in the presence of large herbivores is a well-known evolutionary scenario experienced by Mediterranean plants (Blondel and Aronson, 1999; Bengtsson et al., 2000), and different resistance mechanisms within the persistence niche of woody plants could be expected (Bond and Midgley, 2001). From the animal perspective, it should be acknowledged that red deer could change its selective feeding depending on season (Storms et al., 2008), drought (Bugalho and Milne, 2003), and population density (Bee et al., 2009), i.e. depending on the contexts where they browse. In practice, as red deer selectivity can vary across dimensions that can be rarely addressed by single studies, long term and extensive monitoring could be very useful to deepen understanding about variation of species-specific browsing probability of plants through space and time.

Within this context of relative palatability, we showed that the density of unpalatable plants negatively affected browsing probability of Holm oak and Green olive tree suckers. Consistently with the repelling-plant scenario of associational resistance (Barbosa et al., 2009; Bee et al., 2009), vigorous resprouting of unpalatable shrubs could provide shelters for palatable plants by reducing the feeding interest of red deer for the patch. Considering that the effect emerged at the spatial scale of transects (50 m²), which are smaller than Corsican red deer home ranges (Lovari et al., 2007), results suggest that animals make foraging decisions by moving from low quality to high quality patches (Bee et al., 2009) within coppiced stands. This role of unpalatable shrubs against herbivory on vegetative regeneration of palatable trees is also consistent with ecological theory (Bruno et al., 2003), where superior plant competitors that are more susceptible to herbivory can be facilitated by the association with early successional resistant neighbours. On the other hand, unpalatable resprouters that are displaced by superior competitors could enlarge their realized persistence niche (Bond and Midgley, 2001) in time and space, if browsing is intense enough to affect growth and survival of palatable superior competitors (Perea et al., 2014). If this scenario is correct, the positive role of unpalatable nurse plants on seedling survival, discussed for reforestation techniques

(Gómez-Aparicio et al., 2004, 2008), could be extended to manage vegetative regeneration of coppices. Ideally, plans of sustainable coppicing in areas with protected browsers could select stands with high densities of unpalatable resprouters, and favour coexistence with main trees by establishing intermediate rotation lengths (Shea et al., 2004; Sjölund and Jump, 2013) that fulfil the regeneration and persistence requirements of unpalatable species, as well as of the palatable trees, in the presence of sustainable levels of browsing. The Strawberry tree, which is in fact widespread in highly disturbed Mediterranean environments and has value for firewood and timber production (Quevedo et al., 2013), emerges as a very interesting species for the resistance of Mediterranean forests to browsing and other environmental stressors such as drought (see also Richard et al., 2009).

We also showed that the density of palatable plants negatively affected browsing probability of Holm oak coppices, with some weak evidence about positive effects on Green olive trees. These contrasting patterns could be explained by the relative palatability and abundance of the two species. The increasing abundance of palatable woody plants may attract browser to higher quality patches, resulting in associational susceptibility due to resource concentration (Frid and Turkington, 2001; Barbosa et al., 2009). However, if plant resources are abundant the feeding impact on single focal plants could be reduced in higher density patches, which is coherent with the “attractant-decoy hypothesis” (Frid and Turkington, 2001; Herfindal et al., 2015). This seems to be the case of Holm oak suckers that, considering relative abundance and average height, are by far the most abundant palatable resource within patches. On the opposite, shoots of the most preferred, rarer, and smaller Green olive trees could be more easily detected by red deer when palatable resources are concentrated (see Frid and Turkington, 2001 for an interesting case on lupines with squirrels), thus increasing browsing probability in high quality patches. However, disentangling such complex mechanisms underlying the relation between plant densities, relative palatability, and browsing probability goes beyond the scope of this correlative study. More focused observations performed at appropriated spatial scales (e.g. Herfindal et al., 2015), and direct observations of red deer feeding behaviour are needed to deepen understanding about browsing processes, and to properly assess behavioural mechanisms.

Finally, browsing probability on palatable plants clearly decreased with years from coppicing and increasing plant height. After coppicing, plant suckers start to grow and, if levels of browsing are not too high, reach heights (and biomasses) that progressively reduces the impact of feeding on single shoots. Apart from plant size, there are other mechanisms that could result in a reduction of browsing probability with time, such as reduction of leaf size, development of thorny leaves, and increased phenolics content (Massei et al., 2000; Focardi and Tinelli, 2005), which cannot be assessed here. From a practical standpoint the marked reduction of browsing probability through time support the management hypothesis about transitory effects of browsers on resprouters, based on previous studies on similar systems (Focardi and Tinelli, 2005; Lovari et al., 2007). Although high red deer densities may threaten woody plant diversity by forcing vegetation dynamics towards early successional stages (Perea et al., 2014), it seems that in the investigated coppice system deer impact is low enough, and coppice management appear to be compatible with red deer and habitat conservation. However, considering that transitory browsing pressure on growing coppices could result in long term effects on tree growth (Chianucci et al., 2015), forest management plans and monitoring should be also focussed at assessing variations of optimal rotation length due to slower growth of plants under browsing impact.

Conclusions

The attempt to model variation of browsing probability through space and time, by using information gathered within a simple and focussed monitoring program (Lindenmayer and Likens, 2010) developed within limited resources devoted to research activities (Cagnacci et al., 2013), was useful to learn about the interaction between browsers, woody plants, and forest management. In general, considering that the brows-

ing outcome depends on the interaction between animals and plants within changing ecological contexts (Owen-Smith, 2014), forest managers could monitor through space and time browsing rates with economic and informative methods (see also Frerker et al., 2013), measuring main factors thought to affect feeding behaviour of browsers. Such information should be gathered not only to quantify browsing pressure on vegetative regeneration of plants, as generally requested in mandatory monitoring plans, but more fundamentally to improve the biological understanding underlying management decisions (Nichols and Williams, 2006; Lindenmayer et al., 2008).

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Supplemental S1 Data.

Supplemental S2 Species analysis.

Supplemental S3 Univariate regressions.

Supplemental S4 Green olive trees.

Supplemental S5 Holm oaks.