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Temperate coppice forests in north-western Italy are resilient to wild ungulate browsing in the short to medium term

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ABSTRACT

In southern European temperate forests, coppicing is a traditional form of forest management that shaped the present cultural landscape, providing multiple ecosystem services. Roe deer densities have been growing notably during the last decades mainly due to the abandonment of rural areas, changes in human land use and restocking.

The impact of roe deer on coppice forests can affect the resprouting and, in turn, compromise the products and ecosystem services provided by these forests. During coppicing, stems are cut down close to the ground, where the growing shoots are exposed to deer browsing, especially during the early years following cutting.

In this study, using a browsing exclusion experiment, we investigated the impact of browsing on temperate mountain hardwood coppice forests in the western Italian Alps over a period of eleven years following coppicing.

We found that the impact of browsing was highest in the first two years following coppicing, with Quercus pubescens and Castanea sativa being the most affected tree species. The height of shoots was the variable that showed the biggest difference between fenced and unfenced areas. A significant negative effect of browsing on shoot height was found at the beginning of the experiment, with shoots growing in unfenced area showing the lowest height increments. After the third year, when the browsing intensity diminished, we observed the opposite trend, with shoots growing in unfenced areas showing higher height increments compared with fenced areas. A similar trend was observed also for the diameter of shoots over the course of the experiment. Eleven years after coppicing, however, the structural characteristics of the natural regeneration converged at all sites and in both fenced and unfenced areas.

This study shows that coppice forests are resilient to browsing and are capable to recover growth loss within a few years after browsing has naturally diminished and stopped. The research conducted also points out the importance of medium- to long-term monitoring to assess post-disturbance dynamics and evaluate implications for management.

1. Introduction

The browsing of tree regeneration by wild ungulates is a growing concern and critical challenge for the management of many temperate and boreal forests (Brang, 2017; Côté et al., 2004; Motta, 1996), especially considering the increasing ungulate abundance in different regions over the past decades (Apollonio et al., 2010; Carpio et al., 2021; Deinet et al., 2013). High-density populations of large ungulates are now widespread in Europe (Carpio et al., 2021). The impact and the perception of overabundance is higher where there are high densities of ungulates, e.g. as in protected areas (van Beeck Calkoen et al., 2020).

However, at the continental scale the problem is seen as one of the main limiting factors both for the application of a close-to-nature silviculture and for the conservation of biodiversity (Larsen et al., 2022).

Ungulate browsing in forest can often determine growth reduction and delay (Ammer, 1996; Hidding et al., 2012; Kupferschmid and Bugmann, 2008), cause mortality of tree seedlings and saplings (Vandenberghe et al., 2008) and fine roots (Ruess et al., 1998), alter inter-specific competition patterns (e.g. D'Aprile et al., 2020; Lorentzen Kolstad et al., 2018), thus hampering the recruitment into the forest canopy and the local persistence of particularly palatable species (Baker et al., 1997; Didion et al., 2009; Motta, 2003). In the long term, repeated

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and severe browsing can determine substantial changes in the composition and structure of forests (Champagne et al., 2021; Côté et al., 2004; Gill, 1992), potentially contributing to arrested succession (Thrippleton et al., 2018), and thereby reduce the forest ecological stability (Larsen, 1995), with implications for the susceptibility to subsequent disturbances. Browsing may interact with other disturbances and extreme climatic events and amplify their effects on the ecosystem (Conedera et al., 2017; Hobbs, 1996; Staver et al., 2009), further hindering the provision of multiple forest ecosystem services.

Although the impact of ungulate browsing on tree regeneration is documented in high forests, there is little information about the longer-term effects on regeneration, subcanopy and canopy layers in coppice forests (Chianucci et al., 2015). Coppice forests are stands that mainly regenerate by vegetative means, with new individuals originating mostly from shoots on living stumps capable of sprouting (i.e. stools) and root suckers, and are normally grown on short rotations (Buckley, 2020; Ciancio and Nocentini, 2004; Unrau et al., 2018). Coppice in Italy is the most important silvicultural system (coppices and high forests occupy 42.3 and 41.9% of the total forest cover, respectively) and is mainly spread in private and broadleaf forests where it amounts to more than 50% of the forested areas (Gasparini et al., 2021). In Europe coppiced forests cover more than 20 million ha, representing about 10% of the continental forest cover (Bartlett et al., 2018; Cutini et al., 2019; Unrau et al., 2018).

In most of temperate mountain forests of southern Europe coppicing is a traditional and widespread form of management that shaped a cultural landscape and provided wood and other ecosystem services for centuries (Agnoletti et al., 2022; Angelstam et al., 2021). This management partially lost interest in the 20th century when the request for its main wood products, i.e. firewood and wood charcoal, sharply declined following the availability of fossil fuels. In the last decades, instead, the coppice management showed renewed interest for its cultural importance and its rehabilitation regarding its ecological functions and the provision of numerous ecosystem services (Cutini et al., 2021; Johann, 2021). For instance, the heterogeneous landscape determined by different structures and patterns of full light and shadows in coppice forests provides beneficial conditions for many endangered plant and animal species (Gondard et al., 2006; Vacik et al., 2009), whose conservation is strictly related to the traditional management (Mairota et al., 2016); the high stem density and cover maintained via active coppicing can provide effective protection against soil erosion and rockfall (Buckley et al., 2018; Scheidl et al., 2020; Vergani et al., 2017); carbon sequestration and the substitution effect of wood products obtained from coppice forests could also support the mitigation of climate change (Prada et al., 2016), and the production of bioenergy by coppice forests in the Mediterranean region could play a role in reducing emissions from fossil fuels (Ruiz-Peinado et al., 2017; Vacchiano et al., 2017). However, the presence of ungulates feeding on palatable species sensitive to browsing that are often found in these stands, such as *Corylus avellana* and *Quercus* spp. (Augustine and McNaughton, 1998; Didion et al., 2009), may impede sufficient natural resprouting (Pyttel et al., 2013) and, in conjunction with climate change, extreme climatic events and disturbances, compromise the future provision of ecosystem services and ecological functions offered by these forests.

Here, we provide an evaluation of the medium-term effect of roe deer (*Capreolus capreolus* L.) browsing on coppice forest dynamics, taking advantage of a browsing exclusion experiment established in 2002 in temperate mountain coppice forests in the western Italian Alps. The specific objectives of this study were:

1. To quantify the browsing pressure over eleven years following coppicing on different forest species; we hypothesized that browsing pressure would be highest for the most palatable species and in the early years after coppicing but decrease over time.

2. To evaluate the effect of browsing on post-coppicing forest dynamics; we hypothesized that unfenced areas would show a retarded development compared with fenced areas excluded from browsing.

2. Material and methods

2.1. Study sites

The present study was conducted in the Bormida valley, Italy (44°27′N, 8°19′E; Fig. 1A and 1B). This valley extends over 53.582 ha in the sub-montane and montane belts at the border between Ligurian Alps and Apennines. Forests cover ca. 80% of the land, are dominated by hardwoods, and are mainly managed as coppices. Sweet chestnut (*Castanea sativa* Mill.) is the most common species in the area, accounting for more than 50% of total forest cover. European beech (*Fagus sylvatica* L.) is more common at higher elevations, while manna ash (*Fraxinus ornus* L.) occupies warmer exposures. Other tree species are mainly found in local xeric soil patches or on warmer exposures and include oak (*Quercus* spp.), Scots pine (*Pinus sylvestris* L.), and European hop-hornbeam (*Ostrya carpinifolia* Scop.). Favourable habitat conditions with high forest cover and low-intensity agriculture, and the absence of a deep and continuous winter forest cover, make of the Bormida valley a suitable environment for wild ungulates, with roe deer and wild board (*Sus scrofa* L.) being the most common species. The latter, however, isn't a threat to trees since wild boards don't directly feed on them (Giovannini, 1991). The roe deer density is very high (greater than 15 individuals 100 ha^{-1}) in the whole Liguria Region and reaches 25 individuals 100 ha^{-1} in the Bormida valley (Carnevali et al., 2009), with ungulates causing increasing damage to agricultural crops and forestry, worsening at the same time the 'perception' of the natural environment, with negative repercussions also on tourism (GAL Valli Savonesi, report 2017). The two sites selected for this study represent the main forest types, elevational range, and management history of the Bormida valley. The sites are characterized by a mountain temperate climate, with 2–3 months of summer aridity (Finke et al., 2001). Total annual precipitation is approximately 1000–1100 mm (maximum in April and November, and minimum in July-August). Mean annual temperature is 13–15 °C (maximum in July-August and minimum in January) (Finke et al., 2001). The forest composition before coppicing was dominated by sweet chestnut at Sorgenti (hereafter called *SORG*), while was a mixed manna ash–downy oak (*Quercus pubescens* Willd.) forest at Benentini (hereafter called *BENE*). Shoots had mean diameter at breast height (DBH, 1.3 m height) of 6–9 cm, and height of 10–16 m, while trees originated from seed were larger in *SORG* (Table 1). Total stand basal area had similar values at the two sites (Table 1).

2.2. Browsing exclusion experimental design

A portion of forest characterized by homogeneous structure and composition over at least one hectare was identified at each of the two study sites. These stands were coppiced in fall 2002. Two 500 m^2 permanent plots (i.e. browsing treatments) were established after coppicing at each site (Fig. 1C). The first plot was a deer exclosure (hereafter called fenced) surrounded by a 2.4 m height wire fence maintained through regular inspections (Fig. 1D); the second plot, adjacent to the exclosure, was a control (hereafter called unfenced) unprotected from herbivore browsing (Giovannini et al., 1992). A total of four permanent research units were established across the study sites (2 fenced × 2 unfenced controls).

2.3. Data collection following coppicing

In each browsing treatment data related to stools, shoots, and browsing were repeatedly collected during and at the end of the growing season from 2003 to 2013 (see Table A.1 for the complete list of sampling dates). Species, origin, number of stools with shoots, number of
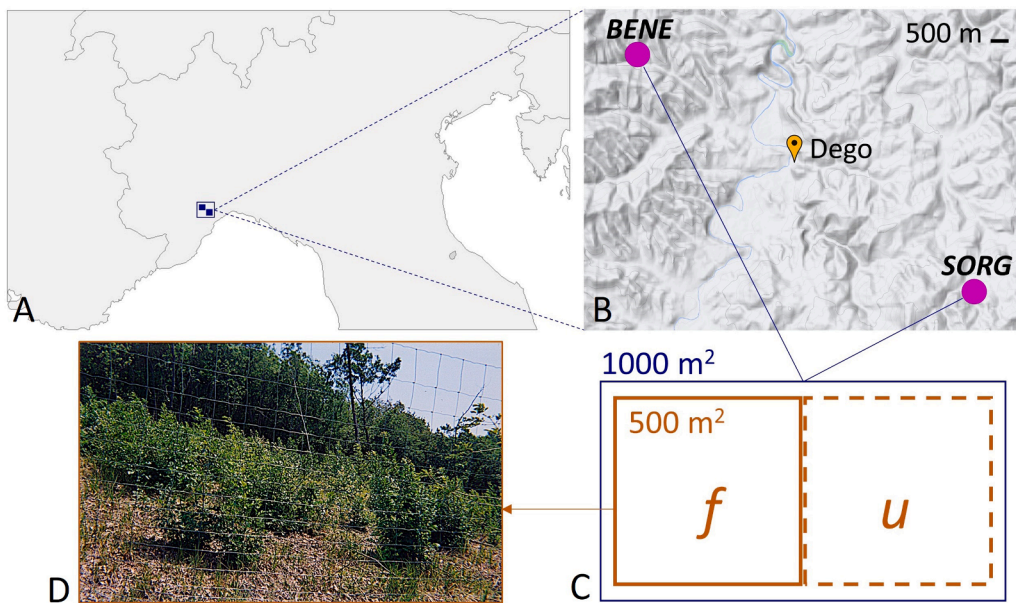
Fig. 1. Location of the study sites in Val Bormida (A, B); magenta dots denote the two study sites *BENE* and *SORG*. Terrain data used to create the map were obtained from Maps.co (My Maps Inc.). Browsing exclusion experiment design (C) showing the two 500 m² permanent plots established at each site (*f*, fenced and *u*, unfenced). Example of wire fence used to enclose the fenced plots (D). Photo: Fabio Meloni. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Pre-coppicing (reference year 2002) mean values and standard errors (SE) for the two study sites (*BENE* = Benentini, *SORG* = Sorgenti). Pre-coppicing data were collected in temporary circular plots of 12 m radius. Stems = number of stems DBH greater than 4 cm; Main forest type = species identifying the main forest type; FROR, QUPU, CASA, FASY, OSCA, PISY = proportion of manna ash, downy oak, sweet chestnut, European beech, European hop-hornbeam, Scots pine expressed as percentage of basal area; H me_{sh} = height of an average shoot; DBH me_{sh} = mean DBH of shoots; DBH me_{tr} = mean DBH of trees; BA tot = total stand basal area.

	Unit	*BENE*	*SORG*
Elevation	m a.s.l.	450	660
Aspect	degrees	180	0
Slope	degrees	25	17
Main forest type	species	OSCA-FROR	CASA
Stems	stems/ha	7140	2233
FROR	%	53.5	
QUPU	%	46.0	
OSCA*	%	0.5	
CASA	%		82.0
FASY	%		17.0
PISY	%		1.0
H me_{sh}	m	10	16
DBH me_{sh}	cm ± SE	6.3 ± 0.2	9.0 ± 0.5
DBH me_{tr}	cm ± SE	6.7 ± 0.3	18.3 ± 4.5
BA tot	m²/ha	27.8	25.1

*Note: only one stool of OSCA was found at *BENE*.

shoots per stool, status of the shoots (living or dead), diameter at the base of the highest shoot per stool, height of the highest shoot per stool, mean height of the stool, and any sign of browsing were recorded for all individuals in the plot. Browsing damage was classified according to a four-class system based on the percentage of browsed shoots per stool

Table 2

Classification of browsing damage based on the percentage of browsed shoots on each stool.

Damage class	Damage	Percentage of damaged shoots
Class 0	No damage	0
Class 1	Slight damage	< 33%
Class 2	Medium damage	33–66%
Class 3	Heavy damage	greater than 66%
Class 4	Dead	–

(Table 2).

2.4. Data analysis

In order to assess forest changes related to deer browsing, forest composition and structure sampled between 2003 and 2013 were compared for the two browsing treatments (i.e. fenced and unfenced) at each site.

A browsing intensity index (Cutini et al., 2011) was used to evaluate the browsing damage in each unfenced plot. The index identifies the average damage class for each species recorded in the plot, and it is calculated by averaging the browsing damage values of all measured stools (see Table 2 for the classification of browsing damage).

To compare the growth and number of shoots from fenced and unfenced plots with different initial heights, diameters and number of shoots per stool, a relative change (RC) index was computed as follows:

$$\text{RC} = \frac{V_t - V_{t-1}}{V_{t-1}} \times 100$$

where *V* is the considered variable (height, diameter, number of shoots), $_t$ is the current inventory date, and $_{t-1}$ is the previous inventory date.

To compare the effect of browsing on the different tree species growing at the study sites, species were classified as 'preferred' and 'secondary' based on the browsing damage experienced. At each site, the tree species recording the highest browsing damage (i.e. highest browsing intensity index value) was defined as 'preferred species', while the tree species characterized by the lowest browsing damage (i.e. lowest browsing intensity index value) was classified as 'secondary species'. In support of this classification, a null model comparison approach was adopted to verify that browsing damage was not random but dependent on species (see Appendix A.1 for details).

The correlation structure of variables and the identification of key factors driving the differences between browsing treatments were explored with Principal Component Analysis (PCA) using the *stats* (R Core Team, 2013) and *factoextra* (Kassambara and Mundt, 2017) R packages. Successional vectors (Austin, 1977) were then used to visualize the temporal trajectory of each sample unit in relation to the others from the beginning of the measurements in 2003 until the last inventory in 2013. For the years when multiple inventories were conducted (i.e. 2003, 2004 and 2005, see Table A.1 for the complete list of sampling dates), we used the mean values of all measurements for that specific

calendar year.

The potential effect of temporal autocorrelation related to the repeated measurements was evaluated with linear mixed-effect modelling with and without temporal autocorrelation. Maximum height and number of shoots per stool were selected for this test due to the completeness of observations over sequential measurements. Linear mixed-effect models included inventory date, browsing treatment (two levels: fenced vs. unfenced, with fenced as the reference level) and their interaction as fixed effects. Stools nested within sites were considered as a random effect. The temporal autocorrelation was evaluated by adding a within-group autocorrelation structure of order 1 with the function *corAR1* of the *nlme* R package (Pinheiro et al., 2017).

The effect size of browsing was assessed by the coefficient of the mixed-effect models (Bose et al., 2021; Forrester, 2019). The magnitude (i.e. effect size) and direction (i.e. positive or negative effect of browsing) of the relative change in height of the highest shoot per stool, mean height of the stool, diameter at the base of the highest shoot per stool and number of shoots per stool over time were evaluated in response to browsing. Each variable was modelled as a function of treatment (two levels: fenced vs. unfenced, with fenced as the reference level). Stools nested within sites were considered as a random effect. The linear mixed-effect modelling was performed separately for each inventory date using the *nlme* R package (Pinheiro et al., 2017).

Predictors in all models were scaled and centred to improve interpretability and allow for the direct comparison of the regression coefficients (Schielzeth, 2010). The assumptions of normality and variance homogeneity of residuals were visually verified with the *sjPlot* R package (Lüdecke, 2021).

All analyses were performed in the statistical computing software R (version 4.0.1, R Core Team, 2020).

3. Results

3.1. Browsing damage

Downy oak was the most damaged (preferred) species at *BENE*, while manna ash (secondary species) was only marginally (<10% of damaged shoots) and slightly impacted by browsing (Fig. 2, left panels). Sweet chestnut (preferred species) and European beech (secondary species) shoots at *SORG* were similarly impacted by roe deer and experienced similar browsing severity patterns (Fig. 2, right panels). At both sites, the proportion of browsed shoots and the intensity of browsing were highest in the first two years following coppicing, then dropped in the third year. Slight damage was recorded until eight years after coppicing on 10% of the downy oak shoots at *BENE*, and for five years on < 25% of shoots of both sweet chestnut and European beech at *SORG* (Fig. 2). Mortality of stools in unfenced plots was recorded from seven years following coppicing (<1% of stools affected) at *BENE*, and from two years after coppicing (4% of stools) at *SORG*. At both sites, the proportion of browsed shoots and the browsing intensity increased in late summer and fall (Fig. 2).

3.2. Effect of deer browsing on coppice vegetation

Principal component analysis of natural regeneration structure related to browsing damage and treatment (fenced and unfenced) from the first (2003) to the last (2013) inventory date is shown in Fig. 3 (see Fig. A.1 for the complete series of measurements). The first (PC1) and second (PC2) components accounted for 39.4% and 16.7% of the total variation, respectively. Shoots of both preferred and secondary species were more abundant in 2003 than 2013. The total number of shoots per stool was negatively correlated with the maximum height for preferred
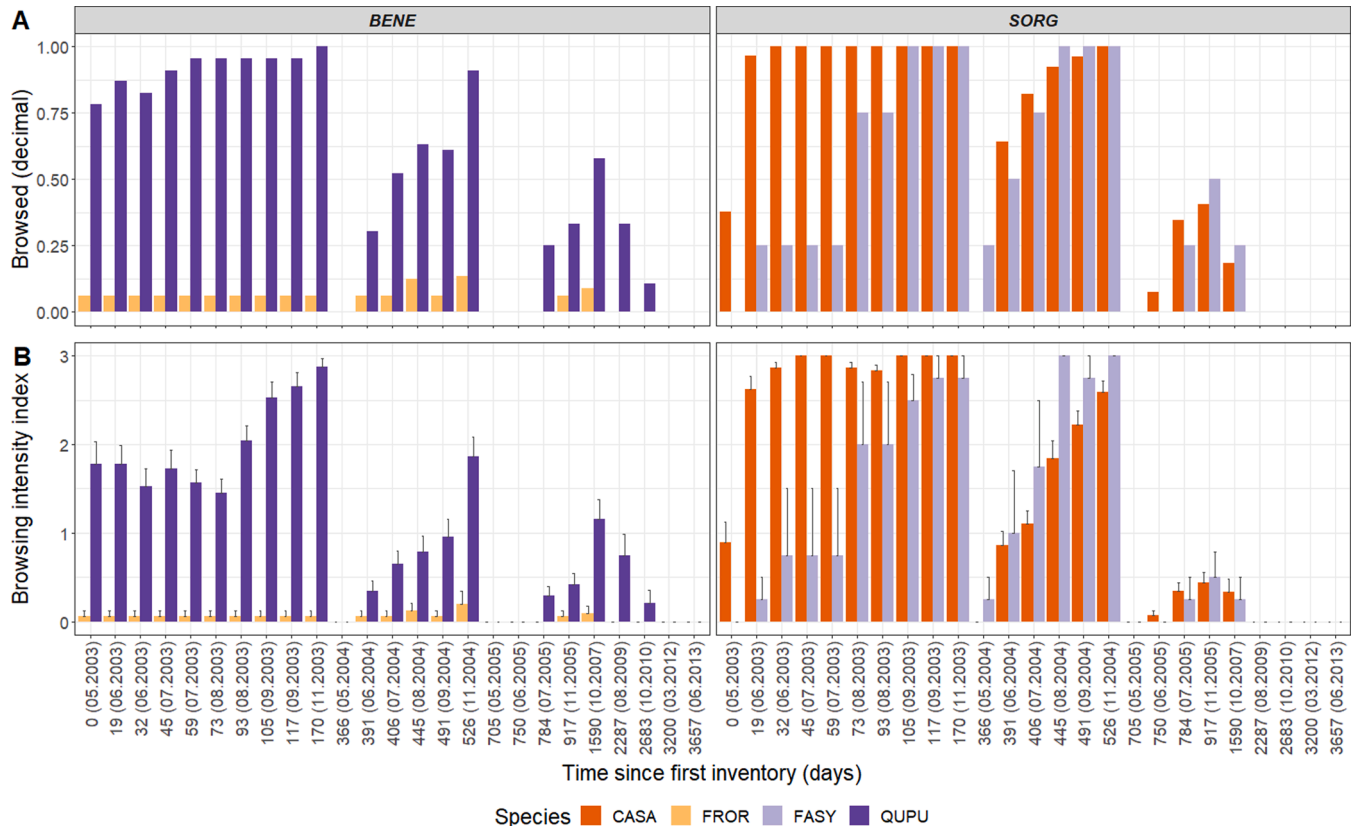

Fig. 2. Percentage of browsed shoots (A; percentage expressed as a decimal) and mean browsing intensity index (B; damage class 0–3, Table 2) for unfenced plots at *BENE* and *SORG* for eleven years after coppicing. CASA = sweet chestnut, FASY = European beech, FROR = manna ash, QUPU = downy oak. Month and year of measurement are reported in brackets. Error bars in B represent standard error of the mean.
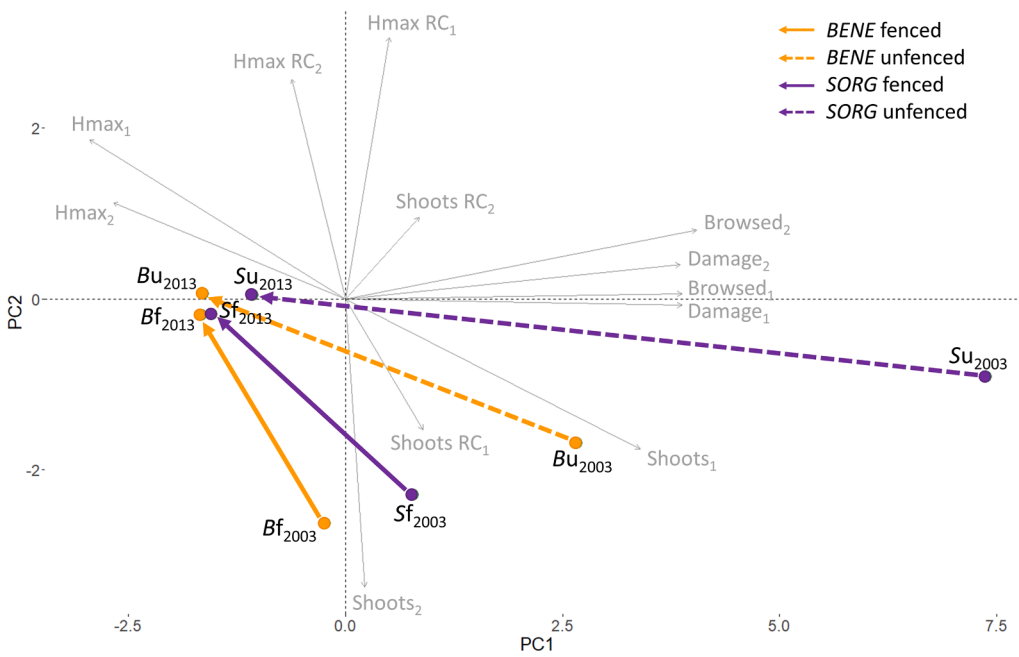
Fig. 3. Principal component analysis (PCA) of natural regeneration structure related to browsing damage and treatment (f = fenced and u = unfenced) from the first (2003) to the last (2013) inventory date at *BENE (B)* and *SORG (S)*. The first (PC1) and second (PC2) components accounted for 39.4% and 16.7% of the total variation, respectively. Browsed = percentage of browsed shoots; Damage = browsing damage; Hmax = height of the highest shoot per stool; Shoots = number of shoots per stool; RC = relative change; 1 = preferred species; 2 = secondary species. The complete series of inventory measurements over time is reported in Fig. A.1.

species, which reached similar values at all sites in both fenced and unfenced plots. For both preferred and secondary species browsing damage and percentage of browsed shoots per stool were highest towards the beginning of the experiment and negatively correlated with shoot height. Successional vectors highlighted the convergence of regeneration structure to similar characteristics over the eleven years following coppicing and the establishment of the browsing experiment in 2003, at all sites and in both browsing treatments (fenced and
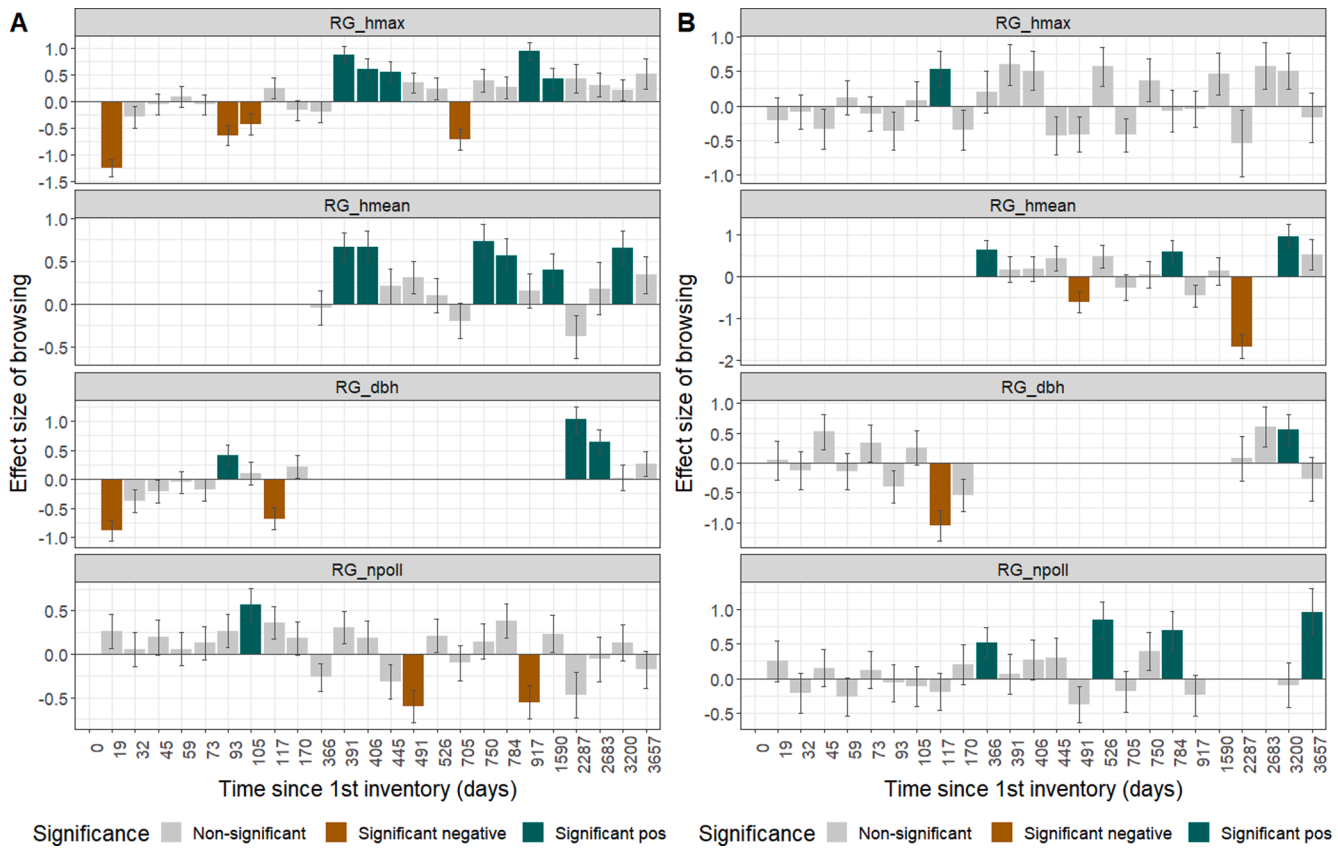

Fig. 4. Effect size (i.e. coefficient of the mixed-effect model) of browsing on the relative change of height of the highest shoot per stool (RC hmax), mean height of the stool (RC hmean), diameter at the base of the highest shoot per stool (RC diam) and number of shoots per stool (RC shoots) for preferred (A) and secondary (B) species over time. Error bars represent standard errors. Model results are provided in Tables A.4 and A.5. The analysis was performed separately for each year and species group (preferred and secondary).

unfenced).

The effect of temporal autocorrelation due to repeated measurements in the dataset analysed in this study was very small in terms of direction (positive or negative effect), effect size (magnitude of responses) and statistical significance (p-values; Tables A.2 and A.3).

The effect of browsing was mainly visible during the period of higher browsing intensity (i.e. bigger damage), after browsing diminished, and in particular for preferred species (Fig. 4, Tables A.4 and A.5). Compared with fenced areas, browsing significantly reduced the height increments at the beginning of the experiment in unfenced areas, particularly for the preferred species (Fig. 4A). When the browsing pressure naturally diminished (i.e. lower browsing severity recorded), the effect was inverted. Shoots of preferred species growing in unfenced plots generally had higher height increments compared with shoots on stools excluded from browsing. Diameter increments showed a similar trend, while the effect of browsing on the number of shoots per stool did not follow a particular pattern, although the number of shoots per stool of secondary species benefitted from growing in unfenced areas in the medium term (Fig. 4B).

3.3. Forest structure eleven years after coppicing in fenced and unfenced plots

Forest structure and environmental data collected at *BENE* and *SORG* in 2013, eleven years after coppicing, are summarized in Table 3. At that time, the main differences between fenced and unfenced plots were found both in the structure and composition of the stand, with fenced plots generally showing larger contribution of preferred species, higher stem density, and larger and taller shoots (Table 3). The shoot diameter distributions of fenced and unfenced plots at *BENE* had identical data distribution (Mann-Whitney-Wilcoxon test, p-value = 0.806), while they significantly differed at *SORG* (Mann-Whitney-Wilcoxon test, p-value = 0.006), with larger shoots in the fenced plot (Fig. 5).

4. Discussion

Based on a browsing exclusion experiment in mixed temperate coppice forests in the western Italian Alps, we examined the effect of browsing on forest structure, growth and composition during eleven years following coppicing, and evaluated the related trends in forest dynamics. The dynamics observed in this study are relevant for temperate hardwood coppice forests with elevated roe deer populations in the region. Moreover, the adopted monitoring period covers about half of a rotation period (traditionally 20–25 years) and offers a robust perspective of the post-coppicing re-establishment. The soils, elevational range, climate conditions, forest types and management history at the two sites are characteristic of temperate hardwood coppice forests

within the Bormida valley, and of sub-montane and montane coppice forests growing at the border between Ligurian Alps and Apennines. This study is one of the few browsing exclusion experiments in coppice forests that has been remeasured several (twenty-five) times over more than a decade, allowing for a better understanding of browsing impacts on the full range of stand age structure.

4.1. Browsing impact

The impact of roe deer on the studied coppice forests was mainly related to the animals feeding on shoots. Downy oak at *BENE* and sweet chestnut at *SORG* were the two species most affected by browsing. The foraging selectivity, and thus the higher palatability of the preferred species, was probably one of the determinants of the higher damage recorded. In fact, oaks are considered palatable, while other species such as beech are normally less affected by browsing (Augustine and McNaughton, 1998; Bianchi et al., 2014; Cutini et al., 2011). The preference and browsing pressure on palatable tree species, however, must be considered also in relation to other factors, such as ungulate density and presence of alternative forage sources. In fact, under high animal densities and increasing browsing pressure, also less palatable species can be heavily impacted by ungulate browsing (Borowski et al., 2021; Motta, 1996). High roe deer densities could explain why beech at *SORG* was initially also highly affected by browsing. However, other factors may have contributed to the observed patterns. The beech stools recorded at *SORG* were large and, thus, probably old. The age of the stools is a determining factor for its resprouting capacity. Older stools produce a lower number of less vigorous shoots (Ciancio and Nocentini, 2004), which could amplify the impact of browsing.

Shoots become rapidly available after coppicing, grow fast, and represent a favoured deer forage source compared with saplings originated from seeds (Moore and Johnson, 1967). The repeated browsing of the shoots at *BENE* and *SORG* caused an increase in the period of exposure to the disturbance and a further decrease in shoot growth, with the stool investing additional resources to produce new shoots. The main growth axis of the browsed shoots underwent continuous deviations with the loss of apical dominance and led to a distinctive cushion shape of the stool (Fig. 6).

We found that deer browsing rapidly inhibited shoot growth and decreased stool survival compared with fenced plots (0% of mortality recorded), with mortality of the stools recorded in the years following coppicing and the beginning of browsing. Our findings support similar patterns of reduced growth and survival observed for *Quercus petraea* in central France (Mårell et al., 2018), northern hardwood species in Michigan (Willis et al., 2021) and in temperate woodlands (Gill and Beardall, 2001).

In this study, the browsing impact decreased progressively after the
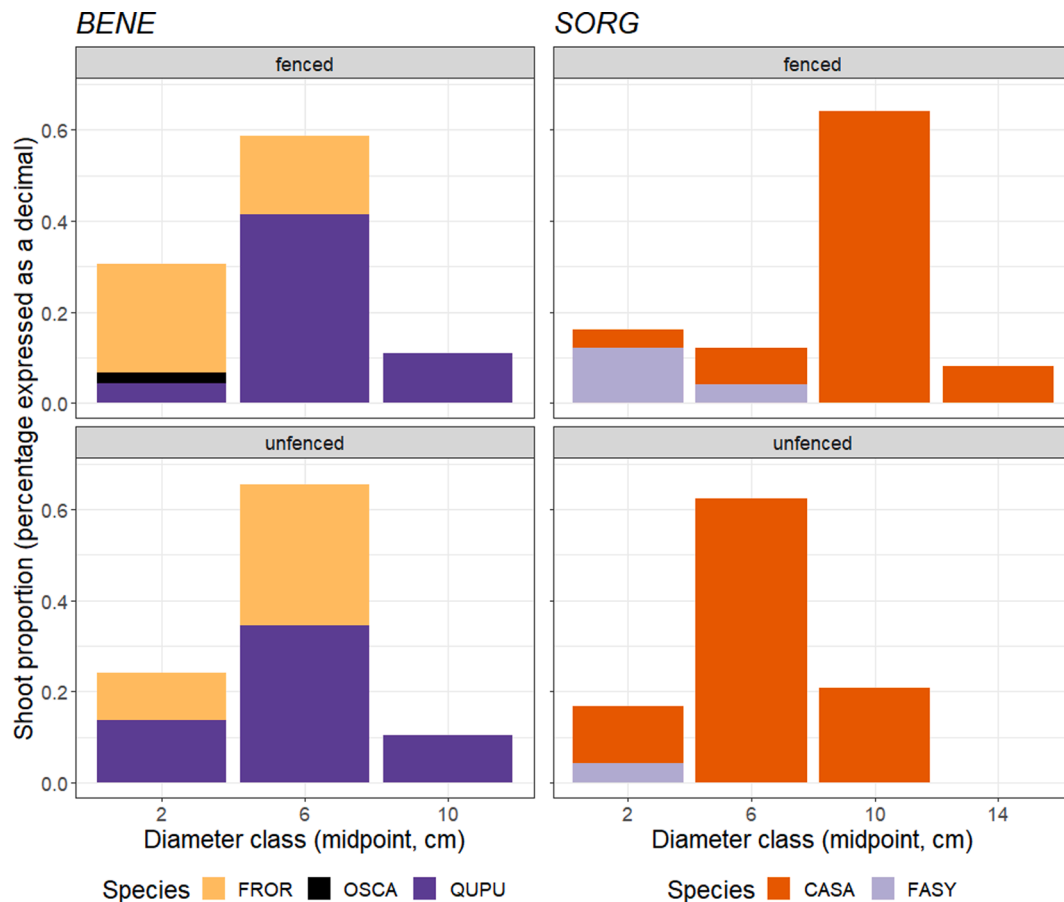
Table 3
Post-coppicing (reference year 2013) mean values, standard errors (SE) and percent difference (d$_r$, %) for the two study sites (*BENE* = Benentini, *SORG* = Sorgenti) for fenced and unfenced plots. Stems = number of stems; CASA, FASY, FROR, OSCA, QUPU = ratio of sweet chestnut, European beech, manna ash, European hophornbeam, and downy oak expressed as percentage of shoots; H me$_{sh}$ = mean height of shoots; H max$_{sh}$ = mean maximum height of shoots; Diam me$_{sh}$ = mean diameter of shoots.

	Unit	BENE			SORG		
		fenced	unfenced	d$_r$ (%)	fenced	unfenced	d$_r$ (%)
Stems	stems/ha	4840	3320	37	3400	2960	14
FROR	%	61	73	18			
QUPU	%	26	27	4			
OSCA*	%	13					
CASA	%				81	97	18
FASY	%				19	3	145
H me$_{sh}$	m ± SE	3.6 ± 0.1	3.5 ± 0.3	1	5.4 ± 0.5	4.7 ± 0.4	18
H max$_{sh}$	m ± SE	4.4 ± 0.1	4.3 ± 0.3	2	6.4 ± 0.5	3.5 ± 0.2	60
Diam me$_{sh}$	cm ± SE	5.5 ± 0.3	5.4 ± 0.3	3	8.3 ± 0.7	6.2 ± 0.5	30

*Note: only one stool of OSCA was found at *BENE*. In this case, thus, differences in the presence of the species between fenced and unfenced areas were not related to browsing.

BENE

Fig. 5. Shoot diameter distribution for the study sites (*BENE* = Benentini, *SORG* = Sorgenti) in fenced and unfenced plots eleven years after coppicing (year 2013). CASA = sweet chestnut, FASY = European beech, FROR = manna ash, OSCA = European hop-hornbeam, QUPU = downy oak.

Fig. 6. Example of downy oak stool showing a cushion shape following the repeated browsing of the shoots in the early years following coppicing. Photo: Fabio Meloni.

second year following coppicing. The lower canopy cover and the lusher coppice regrowth found during the first years after harvesting may be reasons why deer browsing was more pronounced at the beginning of our period of observations (Joys et al., 2004). As shown in previous studies, young succulent shoots are particularly attractive for deer in the first years after coppicing (Moore and Johnson, 1967). Over the years, instead, light limitations may disfavour the growth of light demanding species (Bryant and Chapin, 1986), thus affecting the forage availability. Changes in leaf structure and biochemical factors like plant secondary

metabolites, also in response to repeated browsing and plant regrowth, may affect the attractiveness of the shoots making them less palatable (Bryant and Chapin, 1986; Duncan and Poppi, 2008). Increased phenolic concentrations, and thus induced resistance, have been observed as a reaction to herbivore damage in fast-growing deciduous plants (Nykänen and Koricheva, 2004). Additionally, fast growing species, often found in coppice forests, grow beyond the critical deer browsing height of approximately 2 m (Walters et al., 2020) in a few years (the shoots of sweet chestnut and manna ash at our study sites recorded a mean height of ca. 2 m 1–2 years after coppicing). Over time, the canopy cover heterogeneity and forest edges decrease and also the movement of the ungulates may be impeded by the higher stem density and canopy cover observed in coppice forests a few years following harvesting. Different studies observed that clumped forest patches with little edge may be less attractive to roe deer (Hewison et al., 2001), and the presence of scattered large deadwood pieces may protect the regeneration processes and act as a deterrent to ungulate browsing (e.g. Bottero et al., 2013; Hall Defrees et al., 2021; Leverkus et al., 2021).

Finally, we observed a seasonal trend in browsing, with increased browsing in late summer and fall. This trend could be related to changes in the diet and activity patterns of the animals. Forbs and bramble are favoured forage sources for roe deer, and are preferred during the beginning and the central part of the growing season (Barančeková et al., 2010; De Jong et al., 1995; Storms et al., 2008), explaining why the woody plants at *BENE* and *SORG* recorded increasing browsing damages at the end of the growing season. Activity patterns of roe deer show remarkable daily to season variation in temperate forests in the Apennines, with animals choosing feeding places closed to areas with forest cover when they perceive hunting risk (Pagon et al., 2013). The hunting season in the study region is normally open between mid-

September and January (source: hunting calendar of the Liguria Region), supporting the hypothesis that a higher presence of animals benefitting from the cover offered by the forest in this period may be contributing to the increased browsing damage we observed in late summer and fall.

4.2. Effect of deer browsing on coppice vegetation and dynamics over time

The impact of deer browsing was strong in the early years following coppicing, causing significant differences in growth and number of shoots per stool between fenced and unfenced areas. Over time, however, the regeneration in fenced and unfenced plots converged to a similar structure. The capacity of the browsed stands to return to conditions similar to the non-browsed ones suggests that these coppice forests may be resilient to browsing during the rotation period.

Following the probable loss of photosynthetic area and an incomplete resource compensation (Nykänen and Koricheva, 2004), shoot growth at *BENE* and *SORG* was negatively affected by browsing in the short term, whilst after browsing diminished the remaining shoots possibly benefitted from less competition from other shoots. We found a positive effect of browsing on growth (i.e. the relative growth in unfenced areas compared with fenced areas) in the years following coppicing, suggesting that deer browsing in unfenced plots could have acted as a natural thinning agent. In fact, stem density eleven years after coppicing was higher in fenced plots. Dense coppice forests may face problems of vitality and stability, with high competition and reduced vitality, which can lead to a higher amount of biomass and, in turn, increase the risk of forest fires (Ruiz-Peinado et al., 2017) and lower the resistance to drought (Domingo et al., 2020). However, browsing significantly affected the shoot diameter distribution at *SORG* compared with the fenced area, with smaller mean diameter and a lack of shoots in the larger diameter classes. This could lead to a lengthening of the coppice rotation period, lower productivity and less valuable assortments due to technological defects (e.g. as reported for *Pinus sylvestris*, Bergqvist et al., 2013; and *Betula* spp., Härkönen et al., 2009). Although wood quality is not a relevant issue in coppice forests managed for firewood, the repeated stress and the altered growth could affect, in the long term, the stability of the stools.

The study sites are characterized by a high roe deer density, among the highest observed in Italy (Carnevali et al., 2009). The local decline in wood exploitation might have further exacerbated the browsing impact on the studied coppice forests. In fact, coppiced areas with young stools are locally relatively rare, creating attractive foraging patches for ungulates and thus potentially leading to high browsing damage (Kuijper et al., 2009). The fact that the coppiced stools were able to regenerate and recover eleven years after the forest cut, even if with lower tree densities and average diameter, is an important indicator of resilience of coppice forests to browsing.

Even if within one coppice rotation coppiced forests have the capacity to recover, long-term trends (e.g. higher mortality caused by increased stress of the stools over several rotations in addition to repeated browsing) remain to be verified. Older stools repeatedly browsed may also lose their regeneration ability (Ruiz-Peinado et al., 2017). Additionally, climate change, extreme climatic events and increasing disturbances may amplify the magnitude and the long-term negative effects of browsing on coppice forests, resulting in weakened individuals that may be more susceptible to pests and pathogens (Wood et al., 2018), with negative repercussions on forest ecosystem services and ecological functions.

5. Conclusions

This study showed that coppice forests are resilient to browsing in the medium term and are capable to recover within a few years. In coppice stands the resprouting of stools can provide sufficient regeneration even for more palatable species and in presence of high roe deer

densities. Such an experiment also indicates the importance of medium- to long-term monitoring to assess post-disturbance dynamics and evaluate implications for management.

Understanding the long-term impact of roe deer browsing in coppice forests, however, requires more insights regarding climate change, extreme climatic events and increasing disturbances, which can affect the resilience of coppice forests and make them more susceptible to pests and pathogens. Even if coppice forests show the potential to recover within one rotation, their long-term resilience following repeated browsing and weakening of the stools still needs to be evaluated. This is of particular importance also in light of the widespread presence of high-density populations of large ungulates in Europe, which may increase pressure on forest ecosystems.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120484.

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