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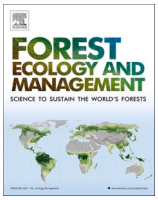

Coppice management affects leaf traits in understory species of Mediterranean oak forests

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ABSTRACT

Coppice management is returning to be a widespread silvicultural practice across European forests. However, its effects on understorey species remain poorly understood, particularly in Mediterranean woodlands. Elucidating intraspecific trait responses of these species will help to predict the interactive effects of coppicing and climate change on a relevant aspect of forest biodiversity and ecosystem functioning. We analysed leaf trait variation in ten representative herbaceous species (specialists and generalists) and the related shifts in CSR plant strategies. We compared conspecific plants from young coppice-with-standards oak stands and next high stands, across two sites in Italy. Coppicing increased the intraspecific variability of most traits and specific leaf area while reducing that of leaf area and Mg content. Both leaf area and specific leaf area were reduced, with the latter showing a significant decrease in the generalist species. Most species exhibited increased leaf dry matter content, likely due to acclimation to dryer conditions and broader temperature variations in the coppice stands. Specialists showed a reduction in leaf K and Ca concentrations whereas generalists decreased N content, thus resulting in a higher C:N ratio. Some responses appeared species-specific or shared by closely related species. Changes in trait values resulted in shifts in the CSR space towards a reduction of competitive ability and an increase of stress tolerance. Keeping forest density and closed canopies appears relevant to support the life and functions of Mediterranean understory plants, notwithstanding that the maintenance of small coppice stands may prompt phenotypic acclimation processes to ongoing global warming.

1. Introduction

Coppicing is a traditional silvicultural practice which has its roots in prehistoric times (Coles et al., 1978). In several European countries, many types of broadleaf woodlands have been continuously coppiced for centuries for the production of firewood and charcoal (Piussi and Alberti, 2015). After a general abandonment after WorldWarII, coppice management has recently gained renewed importance in Europe, and is today widely applied especially in privately owned forests (Harmer and Howe, 2003). Its widespread popularity is essentially linked to a simpler application compared to close-to-nature management types and to the quick income generated by the firewood market. Today, coppice management is applied to approximately 16 % of the productive forests in Europe, especially in the southern and eastern countries (Spinelli et al., 2021). In Italy over 42.3 % of the broadleaf and sclerophyllous forests are currently coppiced, especially those formed by oaks (*Quercus* sp.), chestnut (*Castanea sativa*), beech (*Fagus sylvatica*) hop hornbeam (*Ostrya carpinifolia*) and other broadleaves (Gasparini et al., 2022). After the pandemic, the extent of forest subject to coppicing is even increasing due to the strong demand for renewable energies and the correspondingly expanding market. Because of this, coppicing is also becoming a socially divisive issue fueling heated debates about its sustainability and compatibility with nature conservation. It is therefore important to better understand what are, and will be, the short- and long-term effects of this silvicultural practice on ecosystem functioning and forest biodiversity in the current age of climate change. This appears especially important in the Mediterranean region, where increasingly frequent and intense events of drought, heat waves, fires and windstorms are causing widespread damages to woodlands and trees (Bussotti and Pollastrini, 2017; Peñuelas and Sardans, 2021), with effects also on the understorey (Iacopetti et al., 2021).

Compared with other management forms, coppicing is an intense-

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disturbance regime causing a strong simplification of the forest structure, reduction of stand density and canopy cover, at every utilisation event (usually every 15–25 years; Duncker et al., 2012). A sudden increase of solar radiation reaching the forest floor is the main environmental effect after each utilisation (Decocq et al., 2004; Denslow, 1980). Changes in the light regime are usually associated with further changes at the stand scale in microclimate, decomposition, soil pH, nutrient availability, and others (Larcher, 2003; Zellweger et al., 2019; Meeusen et al., 2021; De Frenne, 2024; Santi et al., 2024).

Altogether, these changes are expected to have multiple influences on the entire biotic assemblage of the forest, and especially the below-canopy organisms that are adapted to live in the shade of the trees and shrubs. Among these organisms there are the plants of the understorey, a layer that contributes to over 80 % of the plant diversity of temperate forests, is involved in multiple functional processes and provides several ecosystem benefits (Gilliam, 2007; Landuyt et al., 2019). In Mediterranean forests, the understorey often includes endemic, rare and vulnerable species (Selvi et al., 2022), that are among the targets of biodiversity conservation programmes (e.g. the European Biodiversity Strategy 2030).

Despite their importance for biodiversity conservation and ecosystem functioning, however, how understorey plants are affected by the habitat changes described above is still poorly understood, especially in the Mediterranean region. In European temperate forests it has been shown that forest openness can exacerbate macroclimate change impacts on understorey plant population dynamics due to reduced temperature buffering capacity (Sanczuk et al., 2023). Other studies have highlighted that functional traits of understorey communities are also influenced by forest density and position (edge vs. interior; Govaert et al., 2024) and that openness is an important driver of plant trait responses especially in areas with wider temperature variation such as the Mediterranean (Padullés Cubino et al., 2021). Bricca et al. (2023) reported that the understory community of high beech forests show more acquisitive traits than coppice-with-standards forests, while Chelli et al. (2024) found that forest structure, along with climate and soil, significantly influences the functional diversity of some plant, leaf and seed traits. Moreover, Santi et al. (2024) found that coppicing in oak stands increases leaf dry matter content as a response to lower temperature buffering capacity and stronger solar irradiance, compared with high forest.

The above studies, however, were mostly based on plant trait values retrieved from public databases and were focused on trait responses at the whole understory level, e.g. shifts in community weighted mean or trait functional diversity driven by species turnover and/or changes in abundance. On the other hand, the role of intraspecific variation still remains poorly explored, although this is a key component of phenotypic plasticity and thus of the species acclimation capacity to different habitats and changing site conditions (Richards et al., 2010; Lemke et al., 2012; Garnier et al., 2016; Paź-Dyderska et al., 2020; Westerband et al., 2021, Govaert et al., 2024; Puglielli et al., 2024). Accordingly, we here examined the effects of management on intraspecific variation of seven leaf traits which are considered both response and effect traits affecting one or more ecosystem functions, such as nutrient cycling and productivity (Lavorel and Garnier, 2002; Suding et al., 2008; Portela et al., 2023). Moreover, trait variation is considered to affect competitive ability (C), stress tolerance (S), and adaptation to disturbance (R) of plant species and populations, thus affecting their position in the CSR ecological space (Pierce et al., 2013; Garnier et al., 2016). Despite some limits of the CSR theory (Rosado and de Mattos, 2017), this theory and its implementation based on leaf traits still provide a useful approach to describe plant responses and strategies in relation to environmental conditions (e.g. Pierce et al., 2017; Li et al., 2024; Han et al., 2024).

Accordingly, elucidating intraspecific trait variation and shifts in the CSR ecological space in understorey plants exposed to the consequences of coppicing and stand openness can provide insights into the effects of this management form on a relevant component of forest diversity and functioning. To this purpose, our study focused on ten representative herb and grass species of south European oak forests belonging to different functional types, ecological groups (e.g. specialists vs. generalists) and angiosperm clades. Species were sampled in two sites of central Italy, both including open stands currently managed as coppice-with standards and next stands managed as high forests, or unmanaged after the abandonment of coppicing for decades, under the same site conditions (altitude, soil, slope, etc.). Because of their higher density and canopy cover, the high forest stands represented a more natural habitat for the understory species and thus a suitable reference for comparison with the coppice stands. The two sites therefore provided a suitable model system to shed light on the following questions: i) what are the effects of coppicing on leaf traits of understorey plants of oak forests? ii) are the magnitude and direction of trait responses related to the species functional type and ecological group? iii) how trait variation influences the species strategies in terms of ruderal, stress-tolerant and competition capacity?

2. Materials and methods

2.1. Study sites

The study was performed in two lowland oak forests in central Italy, one in the northern and one in the southern part of Tuscany. Although these forests are located in different macroclimatic contexts, they both belong to the broad category “Thermophilous Deciduous Forests” (European Environment Agency classification, EEA 2016).

The northern forest “Bosco ai Frati” (43.5910 N, 11.1814E, altitude 250–270 m a.s.l.), is located in the Sieve river valley north of Florence; it is included in the Continental biogeographic region (EEA 2016) or Temperate Division according to Blasi et al. (2014), and is characterised by a mean annual temperature of 12.2°C and 873 mm of precipitation (weather station of Barberino di Mugello, Florence). The soil originates from sandy-clayey alluvial sediments and lignite deposits and is acidic (pH 4.14–4.69, Table 1), leached and oligotrophic. The forest is representative of the EEA type “Turkey oak, Hun-garian oak and Sessile oak forest” (type 8.2) and is dominated by deciduous oaks (*Quercus cerris* and *Q. petraea*). Main associated tree species are *Fraxinus ornus, Sorbus torminalis, S. domestica, Carpinus betulus, Acer campestre, Malus sylvestris*, while the shrub layer includes *Crataegus laevigata, C. monogyna, Cornus mas, Euonymus europaeus, Pyracantha coccinea, Ligustrum vulgare, Lonicera caprifolium*, and others that are typical of this forest habitat (Carrari et al., 2016). The herb layer is mostly composed of acidophilic species such as *Hieracium racemosum, Teucrium scorodonia, Veronica officinalis, Genista pilosa*, and others. The forest has existed since at least the early Middle-Age and is thus “ancient” sensu Peterken (1974), Hermy et al. (1999) and Wulf (2003). Managed for centuries by local monks and Franciscan friars, it was split in two parts during the last century. The privately-owned part is managed as traditional coppice-with-standards to produce firewood (logging every 18 years), whereas high forest management is applied in the public part to support nature conservation and related ecosystem services (Santi et al., 2024). This forest is incorporated in the Natura2000 network (ZPS, IT5140006) as it represents a relict fragment of the ancient plain forest of the Sieve River valley, hosting a high biodiversity including protected animal (amphibians) and plant species.

The southern forest “Aratrice” (42.9744 N,11.2142E, altitude 128 m a.s.l.) is located ca. 130 km to the southwest and is included in the Mediterranean biogeographic region (EEA 2016; Blasi et al., 2014). The climate is typically Mediterranean, with a mean annual temperature of 14.5°C and total annual precipitation of 849 mm (weather station of Roccastrada, Grosseto). The soil derives from siliceous sandstones and consists of a mix of thin and coarse Pleistocene alluvial sediments; it is moderately acidic (5.23–5.65, Table 1) and less oligotrophic than in the northern forest. Also this forest belongs to the type “Turkey oak, Hun--garian oak and Sessile oak forest” (8.2; EEA 2016), despite its more

Table 1
Geographical coordinates, age, basal area (BA), canopy cover, air temperature (maximum, Tmax and minimum, Tmin) based on in situ thermologgers, soil pH and Photosynthetic Active Radiation (PAR) for each plot (C: coppice; F: high forest) in the northern (NF) and southern forest (SF).

Site	Plot	Coordinates	Age (Years)	BA (m^2/ha)	Canopy cover (%)	Tmax (°C)	Tmin (°C)	Soil pH	PAR (μmol m^{-2})
	C1	43.98, 11.30	5	15.19	60	25.80 ± 5.95	5.87 ± 5.37	4.45 ± 0.20	1447.67
	C2	43.98, 11.30	7	15.84	65			4.14 ± 0.24	1335.67
NS	C3	43.98, 11.31	8	18.41	55			4.29 ± 0.27	1154
	F1	43.98, 11.30	60	31.88	85	23.43 ± 5.17	6.52 ± 5.20	4.69 ± 0.14	23.33
	F2	43.98, 11.31	60	33.91	90			4.45 ± 0.16	20
	F3	43.99, 11.30	60	32.66	90			4.50 ± 0.21	29.33
	C1	42.97,11.21	4	5.41	50	31.23 ± 6.88	8.98 ± 5.11	5.27 ± 0.45	1595.67
	C2	42.97,11.21	4	10.06	55			5.43 ± 0.26	1338
SF	C3	42.98,11.21	4	6.4	50			5.65 ± 0.13	1457.33
	F1	42.97,11.22	40	27.44	85	25.24 ± 4.19	10.22 ± 4.93	5.58 ± 0.49	50.67
	F2	42.97,11.22	40	25.58	85			5.41 ± 0.40	31.33
	F3	42.97,11.22	40	27.17	85			5.23 ± 0.42	75

Mediterranean and thermophilous character than the northern forest. The tree layer is dominated by *Q. cerris* with sporadic *Q. pubescens,* and frequent secondary trees such as *Fraxinus ornus, Acer campestre, Sorbus torminalis, S. domestica, Pyrus communis* and *Malus sylvestris.* The shrub layer includes *Crataegus monogyna, Ligustrum vulgare,* evergreen sclerophyllous species such as *Phillyrea latifolia, Erica arborea* and others, while numerous species like *Rubia peregrina, Brachypodium sylvaticum, Festuca heterophylla, Betonica officinalis, Crocus etruscus, Dioscorea communis,* etc. are frequent in the herb layer. The woodland is privately owned. In former times, regular coppice-with-standards management with short rotation cycles (12–15 years) was applied in all the forests of the area, but this was largely abandoned after 1945. Decades of natural forest dynamics thus allowed recovery in many sites, resulting in stands with a higher density, biomass stock, canopy cover and structural complexity. During the last two decades, however, coppicing returned massively for socio-economic reasons and most of the abandoned and aged coppice forests in private areas were again subject to utilizations for firewood production, with rotation cycles of ca. 18 years. In part of our study forest, a coppice cut was applied in winter 2018–2019, whereas other parts were not disturbed and could conserve their structural characteristics of aged forest.

2.2. Plot selection and characterisation

For plant sampling, six representative plots were established in each forest site, three in the high forest stands (high forest or long-abandoned coppice) and three in the stands subject to recent coppicing (Fig. 1). Within each forest, the selected plots had nearly identical site conditions in terms of altitude, slope aspect, inclination and soil characteristics (Table 1). This was important to exclude confounding site factors and to examine as orthogonally as possible the effects of forest management on plant traits. In both forests, plots were established in coppice-with-standards stands between 4 and 8 years old. Circular plots of 513 m^2 (Gasparini et al., 2022) were used to measure the main structural variables, such as the percentage of canopy cover, and the number and diameter of woody plants with dbh > 3 cm at 1.30 m. Basal area (m^2/ha) and canopy cover (%) were first determined for each plot as main stand structural variables; these are shown in Table 1. Basal area was ca. 15–18 m^2/ha in the coppice stands and 31–33 m^2/ha in the high forest stands of the northern forest; in the southern forest, it was ca. 5–10 and 25–27 m^2/ha, respectively.

In each forest, air temperature was measured in one coppice plot and in one high-forest plot, considering the springtime (April, March and May) of 2022 and 2023, using Lascar EasyLog EL-USB-1 thermologgers (sensitivity=0.5°C; measuring range= −35 °C - +80 °C) following the methods of Meeussen et al. (2021). The air sensor was fixed to a wood pole at 1 m from the forest floor and protected by a white plastic shield to avoid direct solar radiation. In each forest site, a total of four loggers were thus installed. After collection, data were visually checked to delete unreliable values due to overheating and uprooting. Then, daily maxima (Tmax), and minima (Tmin) were determined. As expected, (see Santi et al., 2024), temperature buffering capacity was reduced in the coppice plots: air Tmax and Tmin were respectively lower and higher in the high forest in both sites (Table 1).

Finally, eight bulk soil samples per plot were randomly gathered at 4–5 cm depth to measure pH, using an extract of 1–10 dilution of soil with deionized water and pHmetre. Soil pH was assessed for each plot, averaging the measurements from the eight replicates. Mean pH values

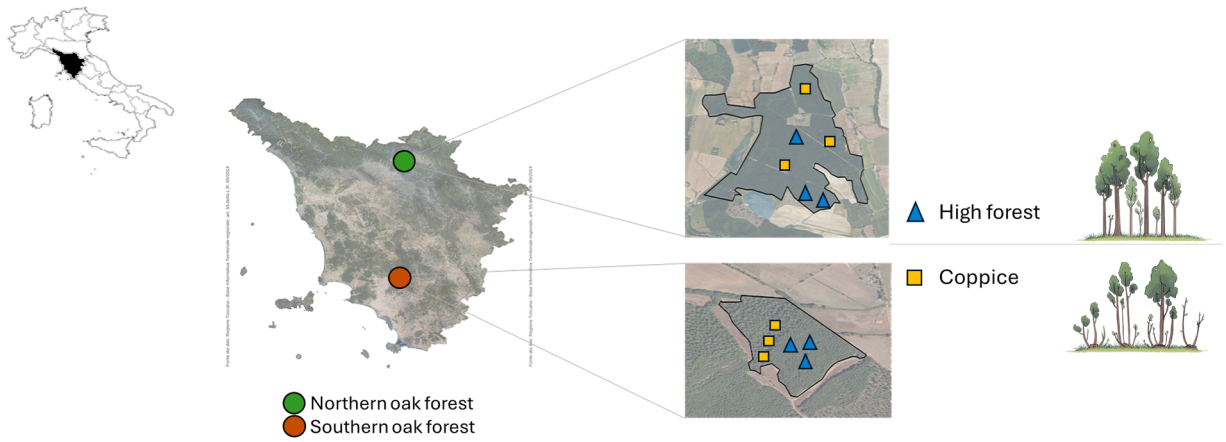

Fig. 1. Italian oak forest sites selected for this study. In both sites (northern and southern), leaf collection for trait analyses was performed in three coppice-with-standards plots (orange squares) and three plots subject to high forest management or left to natural dynamic development for a long time (blue triangles).

were lower in the high forest plots, in both forests (Table 1). Photosynthetically active radiation (PAR, μmol m^{-2}) was measured at 1.30 m above the ground at three randomly selected points in each plot using a light sensor reader (Fieldscout, Spectrum Technologies, Inc. 3415FX). PAR measurements were taken almost simultaneously in the plots of the same forest at ca. 1:00 pm. Then, the average of these measurements was determined in each study area. Mean PAR values in both forests were largely over 1000 μmol m^{-2} in the coppice plots and below 75 μmol m^{-2} in the high forest stands (Table 1).

2.3. Study species

In each of the two forest sites, we selected six understorey species that are widely distributed across different European regions and in most of the Italian territory (Pignatti et al., 2017–2019), and here frequent in various forest communities of the category "Thermophilous deciduous forests", according to Pignatti (1998). These species were frequent and usually abundant in our sites, either coppice or high forest.

The list of species with full nomenclature and main characteristics is given in Table 2. Only two of these species, *Cruciata glabra* and *Brachypodium sylvaticum,* were present in both forests due to their location in different biogeographic regions and bioclimatic contexts. The study species belong to eight angiosperms families, both monocots and dicots. Two of them are typically Mediterranean and mainly distributed in southern Europe (i.e. *Cyclamen repandum* and *Anemonoides apennina*), whereas the others are more typical of continental Europe and the Eurosiberian region, such as *Anemonoides nemorosa, Brachypodium sylvaticum, Lonicera caprifolium* and *Betonica officinalis*.

The species belong to three Raunkiaer's life-forms, geophytes, hemicryptophytes (herbaceous perennials with and without underground organs and buds, respectively) and phanerophytes (woody), and three main functional groups, e.g. herbs, graminoids (*Brachypodium*) and vines (*Lonicera*). These species also differ in their degree of specialisation for forest habitats, based on the recent classification by Heinken et al. (2022). Seven species are considered "specialists" because usually associated with forest interiors (category 1.1, six species) or with both interiors and edges (category 1.2, one species), whereas three are considered "generalists" because found in either forest or open habitats (category 2.1). Among the selected species, *A. nemorosa, V. reichenbachiana* and *B. sylvaticum* are listed as Ancient Forest Species in Hermy et al. (1999), due to their strong preference for forests with continuous existence for at least three centuries; based on our experience, *Physospermum cornubiense* and *A. apennina* are also species of this type in our region. Species Ellenberg Indicator values (T, L, C, H, R, N) after Pignatti (2001) are reported in supplementary table 1.

Information about leaf functional traits of these species is still scanty with only seven species investigated for at least one trait, based on major available trait databases. Hence this study provides first trait data for three vascular plant species that are still completely unknown (i.e. *A. apennina, C. repandum* and *P. cornubiense*).

2.4. Plant sampling

Leaf collection was performed in spring 2023, during May (southern site) and June (northern site), at the time of vegetation peak and simultaneously in the coppice and high forest stands between 8.00 and 10.30 a.m., to minimise phenological variation and optimise the comparison of trait values between the two groups of individuals for each species (Fajardo and Siefert, 2016). Difference in the sampling time period (May-June) depended on the latitudinal and macroclimatic differences between the two forest sites. Collection followed standard protocols (Kleyer et al., 2008). Within each plot, twenty healthy and fully expanded leaves for each of the six species were collected from randomly selected individuals. Normally, two leaves per individual were collected, one from the base or the lower part of the stem, and one from the middle or upper part of the stem; for those species with usually only one leaf at the time of sampling (e.g. *Physospermum cornubiense, A. nemorosa*), a single basal leaf was collected from twenty individuals. In total, 240 leaves per site were collected. Fresh leaves were carefully placed in plastic bags and stored in a refrigerated box for transportation to the laboratory.

2.5. Functional traits

We analysed ten leaf morphological and chemical traits representing response and effect traits at the same time, because dependent on environmental conditions and thus reflecting acclimation processes on one hand while influencing ecosystem processes on the other (Westoby and Wright, 2006; Violle et al., 2007; Díaz et al., 2013). The analysed morphological traits were: i) Leaf area (LA, mm^2), which is strongly related to photosynthesis rate, water and heat balance, and leaf temperature (Cornelissen et al., 2003; Falster and Westoby, 2003; Díaz et al., 2016); ii) Specific Leaf Area (SLA, m^2/kg), which is a reliable proxy of photosynthetic capacity, productivity, resource availability and light-use efficiency (Niinemets, 2001; Evans and Poorter, 2001; Wright et al., 2004; Garnier et al., 2016); iii) Leaf Dry Matter Content (LDMC, mg/g), which is negatively associated with relative growth rate and photosynthetic rate, while showing a positive correlation with nutrient retention (Cornelissen et al., 2003; Poorter and Garnier, 2007). The chemical traits were: i) leaf C content which usually exhibits a positive relationship with LDMC, lower stomatal conductance and transpiration rate (Rawat et al., 2021); ii) leaf N content, a good indicator of plant photosynthetic capacity, respiration and growth rate (Wright et al., 2004); iii) leaf C:N ratio (C:N) which is also negatively correlated with relative growth rate, photosynthetic rates, reflecting higher concentration of Rubisco and other photosynthetic proteins in the leaf (Evans and Seemann, 1989; Field and Mooney, 1986); iv) leaf P concentration that shows a positive correlation with photosynthetic rate, leaf respiration rate, and relative growth rate (Poorter and Bongers, 2006; Garnier et al., 2016; Matsuo et al., 2023); v) leaf K content, which enhances photosynthetic assimilation, regulates gas and water fluxes, and guarantees light absorption efficiency and osmotic regulation (Sardans and

Table 2
Understorey species studied in the two forest sites. *B. sylvaticum* and *C. glabra* were sampled in both the northern (NF) and southern forest (SF). Raunkiaer's life forms are after Pignatti (2001), while forest guilds are based on Heinken et al. (2022), ancient forest species (AFS) on Hermy et al. (1999) and on our expert evaluation.

Site	Species	Family	Life form	Forest guild	AFS
NF	*Physospermum cornubiense* (L.)DC.	Apiaceae	H scap	1.1	yes
NF	*Anemonoides nemorosa* (L.)Holub	Ranunculaceae	G rhiz	1.1	yes
NF	*Viola reichenbachiana* Boreau	Violaceae	H scap	1.1	yes
NF	*Lonicera caprifolium* L.	Caprifoliaceae	P lian	2.1	no
NFandSF	*Brachypodium sylvaticum* (Huds.)P.Beauv.	Poaceae	H caesp	1.2	yes
NFandSF	*Cruciata glabra* (L.)Ehrend.	Rubiaceae	H scap	2.1	no
SF	*Cyclamen repandum* Sm.	Primulaceae	G bulb	1.1	no
SF	*Anemonoides apennina* (L.) Holub	Ranuncolaceae	G rhiz	1.2	yes
SF	*Betonica officinalis* L.	Lamiaceae	H scap	1.1	no
SF	*Lonicera etrusca* Santi	Caprifoliaceae	P lian	2.1	no

Peñuelas, 2021); vi) leaf Mg content that is strictly linked to photosynthesis and the synthesis of chlorophylls (Hauer-Jákli and Tränkner, 2019); (vii) leaf Ca content which regulates water flow, stabilises the elements of membranes, and strengthens cell walls (White and Broadley, 2003; McAinsh and Pittman, 2009; Dodd et al., 2010, Gilliham et al., 2011).

Leaf area, fresh and dry weight were determined as in the LEDA protocol (Kleyer et al., 2008). Fresh weight was determined as soon as leaves were brought to the laboratory, using a precision balance (Toledo Mettler with sensitivity=0.1 mg); secondly, leaves were scanned (1653 ×2338 pixels, 200 dpi), to allow leaf area measurement using the Lafore software (Lehsten, 2005). Leaves were then stored and allowed to dry for at least two weeks at room temperature. Next, samples were further dried in the oven for 72 hours at 40°C before determining dry weight. Five leaves per species were then pooled to obtain a single sample of sufficient biomass to assess leaf nutrient concentrations with spectrophotometry; one sample per species and plot was thus used. Chemical analyses were performed through high temperature combustion at 1150 °C using an elemental analyser (Bario MACRO cube CNS, Elementar, Germany), and a SpectrAA220 spectrophotometer (Govaert et al., 2024).

2.6. Data analyses

Mean trait values and coefficients of variation were first calculated for each species in the coppice and in the high forest plots of both sites. The coefficient of variation (CV) was used as a measure of trait variability (following Schlichting and Levin, 1984; Richards et al., 2005; Portsmouth and Niinemets, 2007; Ligarreto et al., 2011; Lemke et al., 2012). We assessed the influence of forest management on CV and functional traits building linear mixed models to avoid the influence of pseudo-replication and clustering due to plot similarities. In order to study the effects of the two different management types on CV, Formulas (1) and (2) were used for morphological and chemical traits, respectively.

$$y = \text{forest management} + (1|\text{species}) + (1|\text{site:plot}) \quad (1)$$

$$y = \text{forest management} + (1|\text{species}) + (1|\text{site}) \quad (2)$$

Trait variation patterns were then examined in relation to forest management. To this purpose, we assessed the influence of coppice stands on the morphological traits of each species (response variable: functional trait, FT) using the model in Formula 3.

$$y = \text{forest management} + (1|\ \text{plot}) \quad (3)$$

Next, the possible effects of the forest site were evaluated with the first model for the two study sites, separately; this allowed us to see whether the two forest guilds had a different response to management in the two forest sites. To this purpose, we standardised the values of the traits using the *mutate_at* function in the dplyr package and then we used the following formula: morphological trait = forest management + (1| species) + (1| plot).

Position shifts in the Grime plant strategy scheme (Grime, 2001) were also assessed by calculating the CSR percentages (Competitive ability, Stress-Tolerance, Ruderality) for each species and the two ecological groups in coppice and high forest stands (coppice and high forest plots) in both study sites, using the StrateFy calculator (Pierce et al., 2017). This tool allows calculation of the CSR components of single leaf samples starting from leaf area, fresh weight and dry weight. The ggtern function in the ggtern R package was then used to plot results in the form of Grime triangles. The significance of the shifts of each species was determined with a linear mixed model using the plot as a random factor (see formula 3). Furthermore, we assessed the influence of forest management on specialists and generalists CSR components using formula 1.

Concerning the chemical traits, leaf C, N, C:N, P, K, Mg and Ca content values were standardised and log-transformed to symmetrize skewed distributions and decrease the influence of potential outliers (Hedges et al., 1999; Verheyen et al., 2012). In this case, the variation of leaf chemical traits was tested using the model in Formula (2), based on a single concentration value for each nutrient obtained by pooling the five leaves of each species. Chemical analyses could not be performed in the case of *C. glabra* due to insufficient amount of leaf tissue.

Models were built using the *lmer* function (Bates et al., 2014) in the lmer package. Model assumptions were tested by exploring the relationships between the explanatory and the response variables, and checking the error variance, independency and normality of the error distribution according to Zuur et al. (2009).

Variation of LA, SLA, LDMC were summarised and displayed using non-metric multidimensional scaling (NMDS). Trait values were standardised before calculating a squared Euclidean distance matrix. The significance of the differences between the two management forms was tested using PERMANOVA with 999 permutations (Oksanen et al., 2013) and the multivariate dispersion homogeneity test, using the beta-disper function (Warton et al., 2012). Scattergrams with ellipses were obtained with the metaMDS and ordiellipse functions, respectively. All ana-lyses were performed with R vs. 4.3.3 (R Core Team, 2021).

3. Results

3.1. Morphological traits

Means, standard deviations and CV of each trait in the two forest sites and management types are given for all species in supplementary tables 2 and 3. Model results pointed to a general increase of the coefficient of variation in the coppice plots. In fact, all traits except for LA and LDMC, showed enhanced variability in the coppice stands. However, only the CV of LA and SLA, was significantly different between the two management forms (Table 3). Model results showed that effects on LA values were very similar among the ten species in both sites (supplementary table 4). In most of them, LA was reduced in the coppice plots (p-value<0.05), although in three hemicryptophytes (*B. sylvaticum*, *B. officinalis, V. reichenbachiana*) and one phanerophyte (*L. caprifolium*) this effect was non-significant. This negative effect on LA was confirmed when analysing specialists and generalist species separately (p-value<0.01), in both study sites (Table 4, Fig. 2, supplementary table 5).

The five species with significant variation in SLA exhibited decreased values of this trait in the coppice plots, except for *P. cornubiense* (p-value<0.01); in this species, SLA was higher in the coppice plots (supplementary table 6). A similar response was observed in the geophyte *C. repandum,* though not significantly. In both forest sites, either specialists or generalists tended to reduce their SLA in the coppice plots (Table 4, Fig. 2). However, this effect was significant only for generalist species in the southern oak forest (p-value<0.1, supplementary table 5).

Based on our results, LDMC did not significantly vary when considering the two forest sites together (Table 4, Fig. 2). When analysing data from the two forests separately, LDMC of generalist species decreased in the coppice stands in the southern thermophilous forest (supplementary table 5). Looking at the species-specific responses, coppicing increased mean LDMC values (p-value<0.05) in the specialists *A. nemorosa, B. sylvaticum* and *B. officinalis* and in the generalist *L. caprifolium*, whereas this trait was decreased in the generalist *C. glabra* (p-value<0.05, supplementary table 7). Interestingly, the latter species exhibited a contrasting pattern in the two forest sites. While LDMC was significantly reduced by coppicing in the southern forest, this was increased in the northern forest.

NMDS analysis based on LA, SLA and LDMC showed relevant shifts in the ordination space related to forest management (Fig. 3). PERMANOVA tests supported significant effects of coppice in seven species, but not in one generalist (*C. glabra*), and in two specialists (*B. sylvaticum* and

Table 3
Effects of coppicing on the direction and magnitude of variation of morphological and chemical traits. Linear mixed models were built using the CV as response variable and the high forest stand as reference level. For morphological traits, species and site:plot were used as random factors, whereas for chemical traits species and site were used as random factors; *p < 0.1; * *p < 0.05; * **p < 0.01.

	Leaf Area (mm^2)	Specific Leaf Area (m^2/kg)	Leaf Dry Matter Content (mg/g)	Leaf C content	Leaf N content	Leaf C:N ratio	Leaf P content	Leaf K content	Leaf Ca content	Leaf Mg content
Coppice	−0.37 *	0.60 *	−0.07	59.67	2.85	4.70	4.35	18.43	3.890	−3.48 ***
	(0.21)	(0.37)	(0.73)	(36.97)	(3.67)	(5.13)	(2.70)	(12.28)	(2.77)	(1.64)
Intercept	3.41 ***	4.28 ***	7.50 ***	78.98	10.78	11.52 ***	6.06 ***	14.74	7.29 ***	10.03 ***
	(0.29)	(0.45)	(0.98)	(26.14)	(2.61)	(4.09)	(2.04)	(10.38)	(1.96)	(1.17)

Table 4
Slopes and intercepts of the models for each ecological group (gen: generalists, spe: specialists), using morphological traits as response variables and the high forest management type as reference level. In the linear model, species and site:plot are used as random factors (pooled data from the two forest sites). Note: *p < 0.1; * *p < 0.05; * **p < 0.01.

	Leaf Area (mm^2)		Specific Leaf Area (m^2/kg)		Leaf Dry Matter Content (mg/g)	
	gen	spe	gen	spe	gen	spe
Coppice	−0.037 ***	−0.379 ***	−0.563 *	−0.027	−0.011	0.021
	0.013	0.085	0.334	0.099	0.023	0.308
Intercept	-0.368^{***}	0.468	0.461	−0.205 *	−0.136 ***	0.081
	0.054	0.392	0.368	0.112	0.017	0.341

V. reichenbachiana). Direction of the shifts was variable depending on the species. Coppicing caused a prevalent shift towards the positive parts of the first axis (Dim. 1), although *P. cornubiense,* and *L. etrusca* showed an opposite response. All species from the coppice plots were shifted towards the negative part of the second axis (Dim. 2), with the only exception of *L. caprifolium,* which tended to move towards the positive part of it, and *A. nemorosa*, in which no shifts could be detected.

3.2. Chemical traits

Mean values, standard deviations and CV of leaf chemical traits in each species in the two management types are given in supplementary tables 2 and 8. Coefficient of variation (CV) for leaf Mg content was significantly lower in the coppice stands. Variability in the leaf concentration of the other elements analysed was instead tendentially increased, though not significantly. When pooling all ten species together, coppicing significantly decreased the leaf concentration of K and Ca (supplementary table 9). Leaf concentrations of these two elements in the specialist species were negatively affected (p-value<0.05) in the coppice plots (supplementary table 9). Nitrogen concentration was reduced in the generalists, resulting in an increase of leaf C:N ratio. In these species, coefficients of variation of P, K, Ca, and Mg were significantly different between the two forest structural types (p-value<0.01) (Table 3, supplementary table 9). In particular, the variability in P and Ca content was enhanced in the coppice stands, whereas variability in the levels of K and Mg content was negatively affected (Table 3).

3.3. CSR strategies

The competitive ability (C) of either specialist or generalist species was significantly reduced in the coppice plots. On the other hand, coppicing increased stress tolerance (S) in both groups, though this effect was strongly significant only for the specialists (p-value<0.01, Table 5). When pooling all species together, ruderality (R) was not significantly different between the two structural types but specialist and generalist species displayed opposite trends. Generalists implemented a more ruderal strategy in the high forest stands, while specialists did the same in the coppice plots (Table 5). The species-specific responses related to forest management are given in the supplementary table 10 and displayed in Fig. 4. In the coppice plots, the hemicryptophyte *P. cornubiense* and the geophytes *A. apennina* and *A. nemorosa* showed a significant decrease in their competitive capacity. Here, stress tolerance was instead significantly enhanced, except for *V. reichenbachiana, C. glabra* and *B. sylvaticum* from the northern forest. Ruderality was decreased in the coppice plots in the case of *C. repandum, L. caprifolium,* and *B. officinalis*, while *P. cornubiense* implemented this strategy more in the coppice than in the high forest (Fig. 4).

4. Discussion

4.1. Levels of intraspecific trait variability

Compared with the dense forest, the level of intraspecific variability of most traits was tendentially increased in the open coppice plots. This finding would support the stress-induced hypothesis according to which unfavourable conditions may enhance functional trait variance as a result of increased mutation and recombination rates, hence genetic variation (Hoffmann and Merilä, 1999). On the other hand, the reduced variability in LA, LDMC and leaf Mg content observed in the coppice plots appears more in line with the stress-reduced hypothesis (Valladares et al., 2007). According to the latter, phenotypic variability declines under unfavourable abiotic factors and environmental harshness due to slower reproduction, growth and low levels of competition. In late successional stages, namely in the high forest, enhanced phenotypic variation could be a mechanism promoting the competitive ability of individual plants, thus their coexistence in the community (Grime, 1986; Lepik et al., 2005; Lemke et al., 2012). Moreover, the increase in population size that usually occurs in species thriving in favourable sites (the high forest) can lead to an increase of genetic variability and to a consequent enhancement of phenotypic variability (Albert et al., 2010).

4.2. Direction of variation of morphological traits

Both generalist and specialist species displayed a significant decrease in LA in the coppice stands. The increased light intensity and evapotranspiration rates, coupled with a decrease of the forest temperature buffering capacity caused by coppicing (Chelli et al., 2023; Govaert

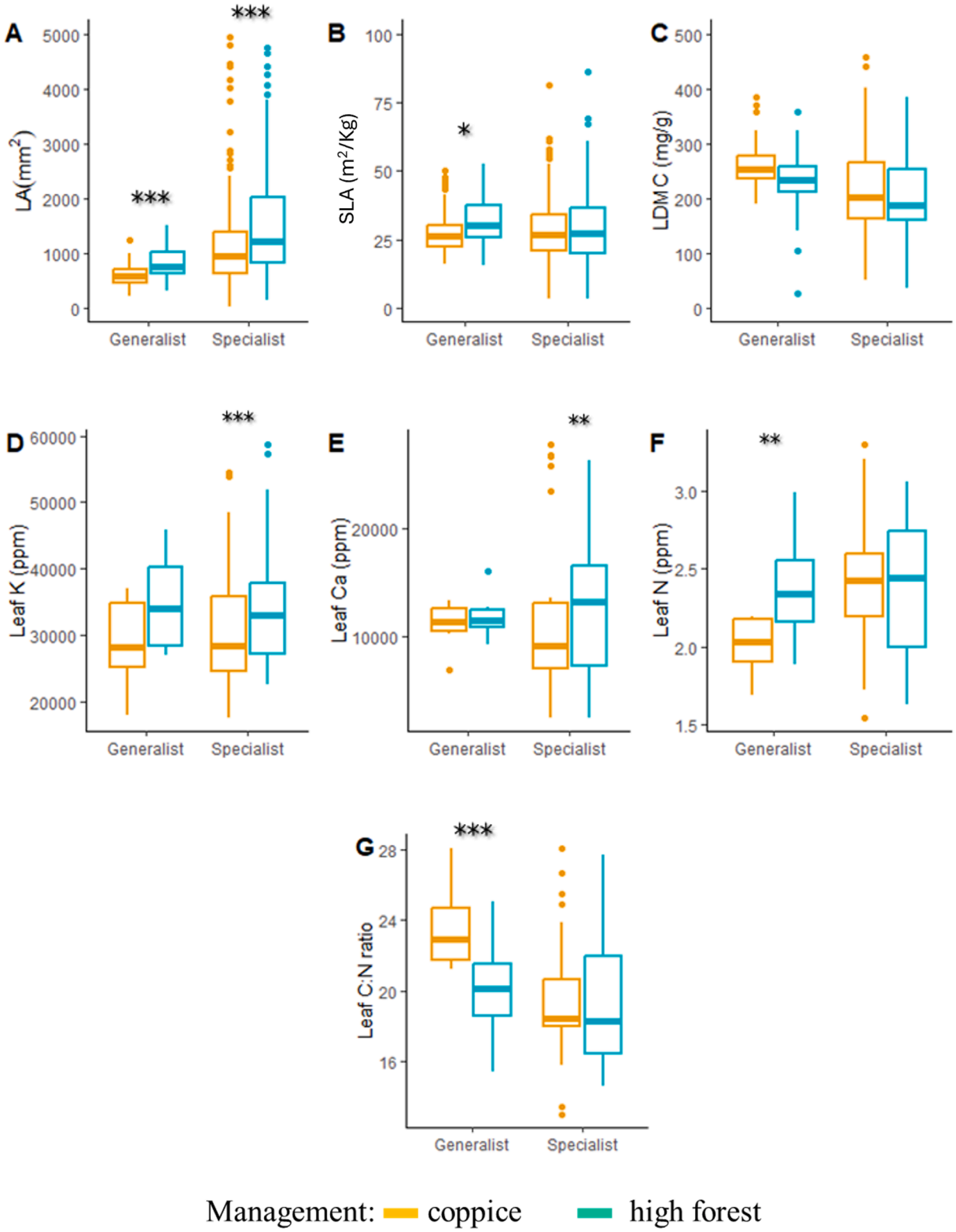

Fig. 2. Variation of morphological and chemical traits, in relation to forest management. For chemical traits, only significant variations are shown. Statistical significance was assessed with linear mixed models using the species and plot as random factors for morphological traits, and the species and site as random factors when considering chemical traits as response variables. Note: *p < 0.1; * *p < 0.05; * **p < 0.01.

et al., 2024; Santi et al., 2024) are likely factors driving this "defence" response in the warm and water-limited habitats studied here. In most cases, leaf area reduction results from decreased blade expansion to allow a more efficient control of transpiration, by limiting stomatal density and improving water use efficiency (Lamont et al., 2002; Xu and Zhou, 2008; Pérez-Ramos et al., 2013). In addition, LA reduction is a likely response to limit photo-oxidative damages with increased solar irradiance and higher temperature extremes, resulting from a lower investment of resources for primary metabolism at the advantage of secondary metabolism with defence functions (Li et al., 2024; Mathur,

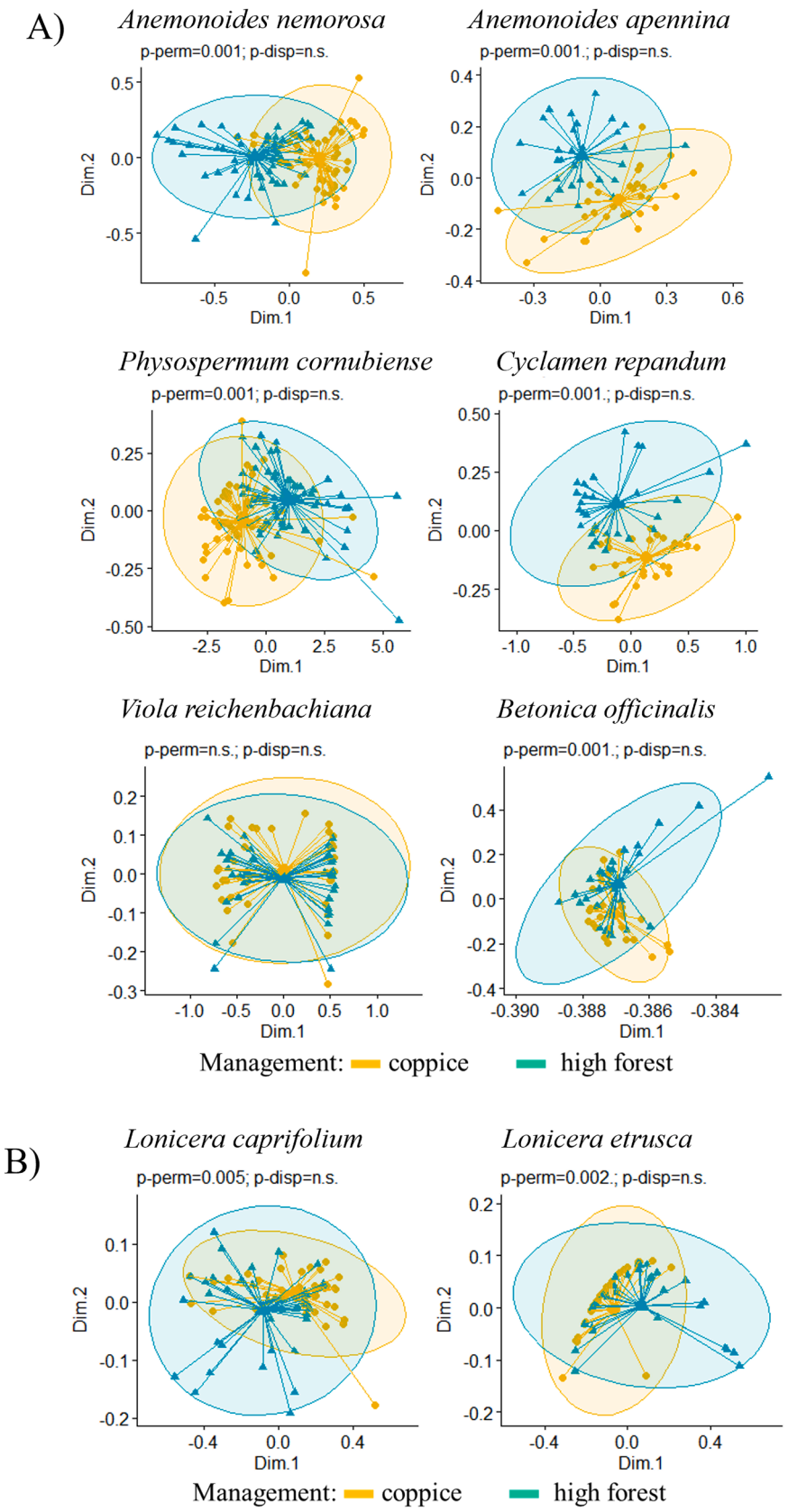

Fig. 3. NMDS species scattergrams based on LA, SLA and LDMC (squared Euclidean distance matrix) showing shifts determined by forest management for specialists (A) and generalists (B). The figure shows only the species that were significantly influenced by management (p-perm<0.05, and p-disp=n.s.).

Table 5
Percentages of Grime CSR strategies for specialist and generalist species in the coppiced plots and in the high forest plots of the two investigated forest sites. For each strategy, the significance of the shift with respect to forest management was tested with linear models using the species and site:plot as random factors; *p < 0.1; * *p < 0.05; * **p < 0.01.

Specialists				Generalists		
Strategy	Coppice	High forest	p-value	Coppice	High forest	p-value
Competitor	31.92	38.48	***	10.09	12.39	***
Stress-tolerant	20.79	15.99	***	36.57	29.48	*
Ruderal	47.29	45.53	n.s.	53.34	58.12	n.s.

2014; Wright et al., 2017). Under this circumstance, significant limitation of growth, productivity and leaf expansion occurs (Ruhland and Day, 2000).

Reduction in LA in the coppice plots was paralleled by a significant decrease in SLA in the generalist species. Hence, these showed more plasticity with regard to light intensity than the specialists, likely due to their more heliophilous character (Markesteijn et al., 2007; Garnier et al., 2016). Previous findings suggest that higher temperatures (mean, maximum and minimum) and lower soil nutrient concentrations may also have a negative effect on SLA of understory species, because plants grow smaller and have thicker leaves as a defence from higher transpiration rates (Govaert et al., 2024). In the more shady and thermally buffered conditions of the high forest, higher SLA in the generalists is associated with a decrease of leaf thickness to promote light interception, gas exchanges and leaf area expansion, through the concomitant increase in leaf N concentration, as also suggested by model slopes (Cooper and Qualls, 1967). However, the tendential increase in SLA shown in the coppice plots by the two specialists *P. cornubiense*, a hemicryptophyte in the Apiaceae family, and *C. repandum,* a bulbous geophyte in the Primulaceae family, pointed to phenotypic plasticity and the existence of species-specific responses not related to phylogenetic position, ecological group or plant functional type. In these two species, the reduction in leaf dry weight in the coppice plots was greater than the reduction in leaf area discussed above, thus resulting in an increased SLA in response to disturbance by management. The *growth-differentiation balance* hypothesis could provide an explanatory framework for this response (Herms and Mattson, 1992). In unfavourable conditions (e.g. water limitation) the rate of C assimilation could be so low that the photosynthetic carbohydrates are largely used in the respiration process. In this case, both production of structural carbohydrates for growth and of secondary metabolites for defence are strongly limited (Herms and Mattson, 1992). The divergent response of *P. cornubiense* also emerged from the NMDS analysis based on LA, SLA and LDMC, as this was the only specialist species with coppice plots samples to the left of high forest plots samples (e.g. with lower values) on the first ordination component.

Looking at LDMC, generalists showed a significant decrease of this trait in the coppice stands in the southern forest. This effect was due to the generalist *C. glabra*, which was the only species exhibiting a significant decrease of LDMC in the coppice stand in this study site. In fact, all the other species that displayed significant variation showed an increase in the value of LDMC in the coppice plots (supplementary table 7). Increase in leaf dry matter content in these species was likely the result of acclimation to stronger solar radiation involving the thickening of epidermal cuticles to prevent water loss and light oxidative stress (Yeats and Rose, 2013). Such processes potentially enhance leaf nutrient retention while decreasing relative growth rate and photosynthetic capacity, therefore implementing a more resource conservative strategy (Garnier et al., 2016). The positive effect of canopy openness due to coppicing on LDMC is in accordance with recent evidence from European forests, showing that understories increase their conservative resource use under more open canopies and in regions with higher extreme temperatures, such as the Mediterranean (Padullés Cubino et al., 2021). On the other hand, the LDMC decrease of the generalist *C. glabra* in the coppice plots of the southern oak forest is another case of divergent response, pointing to the existence of species-specific constraints affecting trait responses to habitat disturbance.

4.3. Direction of variation of chemical traits

The leaves of the forest specialist contained more Ca and K, while those of the generalists were higher in N, in line with their more ruderal and nitrophilous character (Denelle et al., 2020; Chelli et al., 2023). Our findings show that forest management can significantly affect leaf chemical traits in both groups. In the coppice plots, there was a significant reduction of Ca and K in the specialist species, while generalists responded with a decrease in leaf N content associated with a significant increase in the C:N ratio. The reduction in leaf K content could be due to a higher allocation of this nutrient in the roots to enhance water absorption capacity by osmotic adjustment (Gleeson and Tilman, 1990). A decrease in leaf N content in the generalists was associated with a decrease in SLA, supporting the general correlation between these two traits (Garnier et al., 2016). The above responses may be related to various factors, among which the negative effect of coppicing and open forest structure on soil properties especially in terms of reduced nutrient availability (e.g. Switzer and Nelson, 1973; Hansen and Baker, 1979; Ranger and Nys, 1996). Previous studies reported a significant decrease in Ca, K, N content in the soil of coppiced stands (Hölscher et al., 2001; Šrámek et al., 2015). Dryer soil conditions in the coppice plots soil could have also contributed to the decrease of leaf Ca and K content, since the cations of these two macronutrients are transported through the xylem in a transpiration-rate dependent process (Peel and Rogers, 1982). Furthermore, according to the growth allocation and the growth balance hypothesis (McCarthy and Enquist, 2007), when water is the limiting factor, resources are preferentially allocated to the parts of organs where these are most needed, namely in the roots to promote the uptake of water and other nutrients. Moreover, the higher light availability and larger temperature variations in the coppice stands may also have affected leaf N content, in association with SLA. This is in line with recent evidence from European understories that the interaction between soil properties and light availability can affect leaf N content and SLA, while temperature mostly influences the C:N ratio (Govaert et al., 2024; see also Vanneste et al., 2019).

4.4. Ecological strategies

The significant loss of competitive ability shown by generalists and specialists in the coppice stands indicates that species of both groups were able to maximise the capture and use of resources only in the low-disturbance high forest, with more buffered thermal conditions, higher nutrient and water availability. Instead, coppicing led to an enhanced stress tolerance in both groups, with the specialists exhibiting a strong (significant) response to disturbance by coppicing. Due to their higher sensitivity to changed site conditions (Gasperini et al., 2022), these species shifted to resource conservation in the coppice stands more than the generalists. This supports that stress tolerance and resource conservation tend to be implemented when temperature extremes are higher (Govaert et al., 2024), especially in warm regions to reduce heat damage and water loss (Vargas et al., 2021). Increase of stress tolerance in the specialists from the coppice stands was associated with a weak (non-significant) increase of ruderal character, while generalists shifted to this strategy more in the high forest stands, suggesting their ability for a fast resource use and rapid growth to enhance their competitive ability with specialists in rather fertile habitats (Denelle et al., 2020).

However, divergent responses occurred again in species without clear functional or phylogenetic affinities, such as *C. repandum, L. caprifolium,* and *B. officinalis,* in which ruderality decreased in the coppice plots. Moreover, *V. reichenbachiana, C. glabra* and partly *B. sylvaticum* (in

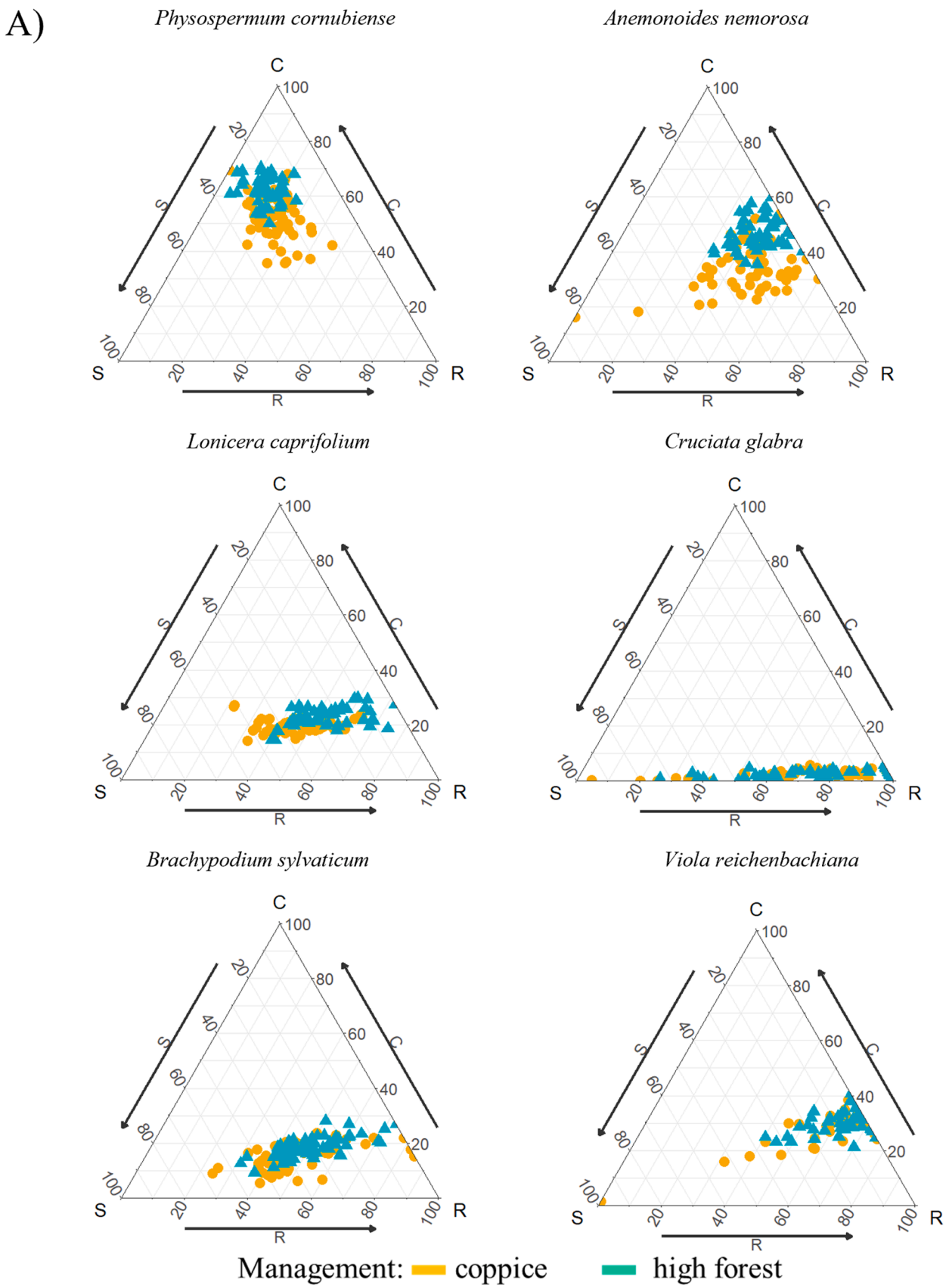

Fig. 4. CSR triangles exhibiting shifts in the ecological strategies shown by the study species in the two management forms in the northern (A) and southern oak forest (B). CSR percentages were calculated based on morphological trait values; the significance of shifts are given in supplementary table 10.

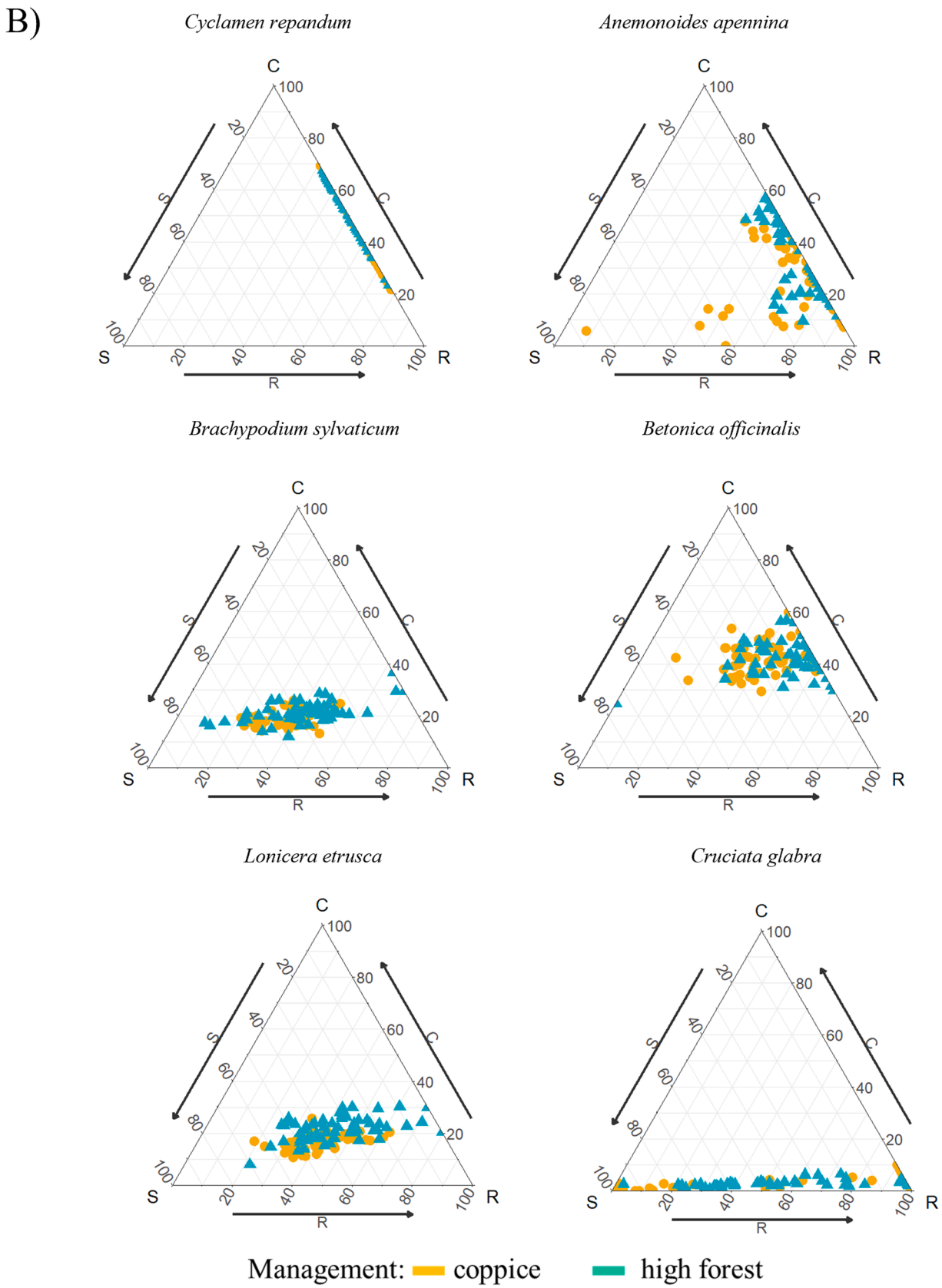

Fig. 4. (*continued*).

the northern forest) did not significantly enhance stress tolerance in the coppice plots, pointing to a lower trait plasticity in response to variation in site conditions.

5. Conclusions

This work helps to advance our understanding of the short-term

effects of coppice management on a poorly known aspect of the biodiversity of a species-rich forest ecosystem of the Mediterranean region, e.g. the intraspecific leaf trait responses of understorey species. With respect to the dense forest stands, we found an influence on either the variability or the direction of these responses, which largely depended on traits and species. Similar effects occurred in ecologically and functionally close species, while some responses appeared species-specific or determined by phylogenetic relatedness (e.g. similar responses in the two species of *Anemonoides* and *Lonicera*). Generalist and specialist species showed comparable phenotypic plasticity in the analysed traits, and partly similar responses. Overall, the level of intraspecific variability of most traits was increased in the young coppice stands, which, on one hand, may represent a positive aspect pointing to the adaptive ability of the examined species to the open forest conditions and to the enhancement of a forest diversity facet. On the other hand, the more significant and largely shared responses were a reduction in leaf area and a tendential increase in leaf dry matter content, as well as a decrease in leaf nutrient concentrations and specific leaf area in the generalist species. These negative shifts in trait values implied a reduction of competitive ability coupled with enhanced stress tolerance, due to increased environmental harshness in the open coppice stands. Adopting close-to-nature management or leaving forests to their natural dynamics towards closed-canopy structures are therefore optimal approaches for supporting the life and functions of Mediterranean understory plants, notwithstanding that the maintenance of small coppice stands in high forest landscapes may prompt phenotypic acclimation processes to ongoing global warming.

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Author contributions

Ilaria Santi and Federico Selvi conceived and designed the research and wrote the original manuscript. Ilaria Santi performed the data analyses. All authors collected data and contributed to the manuscript.

CRediT authorship contribution statement

Ilaria Santi: Writing – original draft, Formal analysis, Data curation, Conceptualization. **Marco Cabrucci:** Data curation, Writing – review & editing. **Elisa Carrari:** Writing – review & editing, Validation, Methodology, Data curation. **Cristina Gasperini:** Writing – review & editing, Investigation, Data curation. **Pieter De Frenne:** Writing – review & editing, Validation, Supervision, Methodology. **Federico Selvi:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122517.

Data availability

Data will be made available on request.

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