



# Vegetation and pastoral traits of wood pastures in the eastern Italian Pre-Alps

Marco Santacà<sup>a</sup>, Matteo Gecchelin<sup>b</sup>, Michele Scotton<sup>a,\*</sup>

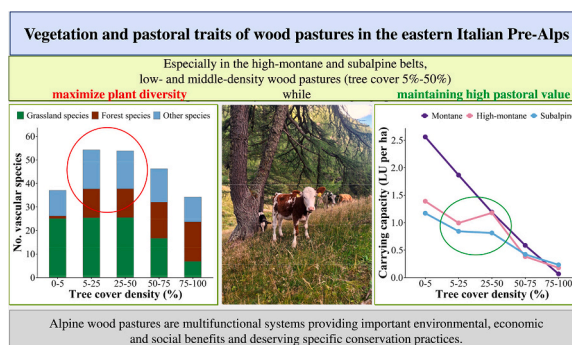
<sup>a</sup> Department of Agronomy, Food, Natural Resources, Animals and Environment, University of Padova, Viale dell'Università 16, 35020, Legnaro, PD, Italy

<sup>b</sup> Department of Land, Environment, Agriculture and Forestry, University of Padova, Viale dell'Università 16, 35020, Legnaro, PD, Italy

## HIGHLIGHTS

- From open pasture to dense wood, forest species gradually replace grassland species.
- Species richness is highest in low- and middle-density wood pastures (bell-shaped relation).
- The pastoral value decreases about linearly from open pasture to dense wood.
- In the lowest altitudinal belt, the pastoral value decreases more rapidly.
- Low- and middle-density wood pastures deserve conservation and restoration efforts.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

### Keywords:

Pastoral value  
Species richness  
Tree cover  
Vegetation  
Wood pasture

## ABSTRACT

After being long contrasted owing to alleged damages to forest regeneration, traditional semi-natural wood pastures (WPs) have recently regained interest for their biodiversity and cultural heritage. To support public policies and actual management aiming at conserving or restoring them, ground cover, vegetation and pastoral traits of Alpine WPs with increasing tree cover (TC) were studied at 99 sampling plots distributed in three altitudinal belts (montane, high montane and subalpine). In the tree-cover gradient from open pasture (TC 0%–5%: OP) and the very high-density WP (TC 75%–100%: VHDWP), the number of grassland and forest species decreased and increased, respectively, resulting in a bell-shaped relation with the highest species richness in the low- and middle-density WPs (TC 5%–25% and 25%–50%: LDWP and MDWP). In the same gradient, the pastoral value decreased linearly, particularly from the high-density WP (TC 50%–75%: HDWP). This decline occurred as the growth and abundance of grassland species significantly diminished when light availability dropped below 50% of full sun. Consequently, the herbaceous vegetation cover became less complete (more bare soil and moss cover), and the abundance of distasteful or poisonous forest species increased. Compared with OP, the decrease in pastoral value in the different WP types was particularly important in the lower altitudinal belt, especially due to the higher abundance of poisonous species. LDWP and MDWP are important for their high biodiversity and relatively high pastoral value. HDWP has lower pastoral value and species richness, but it also deserves

\* Corresponding author.

E-mail address: [michele.scotton@unipd.it](mailto:michele.scotton@unipd.it) (M. Scotton).

<https://doi.org/10.1016/j.scitotenv.2026.181422>

Received 6 September 2025; Received in revised form 30 December 2025; Accepted 16 January 2026

Available online 27 January 2026

0048-9697/© 2026 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

conservation as a source from which high-value LDWP or MDWP can be restored. The conservation and restoration of WP types should be legal and financially viable when site and livestock-utilisation requirements still exist.

## 1. Introduction

Wood pastures (WPs) are semi-natural, multifunctional ecosystems with high ecological, forage and cultural value (Königer et al., 2005; Gillet et al., 2002). In WPs, the varying tree cover (TC) creates habitats with different levels of light availability, which is favourable to species with different degrees of heliophilia. In addition, selective grazing and trampling by domestic animals contribute to the development of species-rich phytocoenoses that are unique to these WPs. Until the middle of the past century, WPs in the alpine regions contributed significantly to livestock feeding (Spatz and Weis, 1983). However, after the Second World War, wood grazing was increasingly prohibited because of the alleged damages to forest regeneration, soil compaction and increased erosion risks (Königer et al., 2005; Rösch, 1992).

Despite the surface decrease that occurred in the last decades, WPs occupy wide areas in Europe today, which, according to Plieninger et al. (2015), amount to approximately 203,000 km<sup>2</sup>, with a higher presence in the Mediterranean and Eastern European countries. Bergmeier et al. (2010) identified 24 WP types around Europe, mainly belonging to boreal, nemoral and meridional bioclimatic zones. According to Plieninger et al. (2015), WPs cover 4.7% of the Alps territory and 5.3% of the Italian countryside, and according to Mayer et al. (2003), 15% of the Swiss mountain forested area is grazed.

In the last decades, concerns about biodiversity loss have led to a rediscovery of the high nature value of WPs. Previous studies have highlighted that TC density plays a crucial role and that wood closing following grazing cessation reduces the number of habitat types, synusia and species whose presence is linked to the high WPs plant biodiversity (Gillet et al., 1999). Habitat diversity is also important for animal diversity. E.g., the European WP habitats are important for at least 37 European bird species (Bergmeier et al., 2010) and a recent study in the Swiss Jura WPs (Wider and Zemp, 2025) showed that the mixture of heterogeneous WP patches with intermediate TC density and of homogeneous patches of open pasture and dense forest allows in the best way the conservation of both specialist and generalist bird and hoverfly species. Allegations of damage to forest renovation have also been reconsidered. In Swiss WPs, the percentage of young trees damaged by wild ungulates was three times higher than that by cattle (Mayer et al., 2002). In addition to biodiversity, WPs supply numerous ecosystem services. Compared with open pastures, they are significantly more efficient in terms of carbon sequestration and retain better phosphorus in the soil (Nair et al., 2007).

The growing interest in WPs is evident from the numerous research projects funded and conducted across Europe in the recent decades. Notable examples include projects in Germany (Rupp and Michiels, 2020) and Switzerland (Mayer et al., 2003). Silvo-pastoral systems have also been included in EU agri-environmental schemes. However, WPs still suffer from insufficient recognition within the EU's environmental policy. The 1992 Habitat Directive includes only a small proportion of semi-natural WP ecosystems within the habitats listed in the Directive Annex I (Bergmeier et al., 2010; Plieninger et al., 2015), making their conservation difficult.

Previous studies on WP vegetation have highlighted the relationship between tree density and the botanical composition of the understorey. In areas with intermediate TC, plant species richness was found to be higher than that in both dense wood and open pastures, and this pattern was consistent across temperate (Rösch, 1992; Gillet et al., 1999) and boreal (Oldén, 2016) environments. However, the relationship between bird and overflies richness and tree density was found to be positive and linear (not hump-shaped) in the cited study by Wider and Zemp (2025).

A second aspect highlighted was the overlap of grassland and forest species in areas with intermediate tree density (Müller et al., 2013).

Research conducted in Austrian Tyrol reveals that the forage values of mountain WPs vary significantly in terms of production amounts and quality, depending on the wood vegetation type, especially when compared with open pastures (Spatz and Weis, 1983). According to Liss (1987), semi-natural WPs do not provide sufficient energy for cattle diets. However, temperatures in WPs are generally lower than in open pastures, leading to slower grass growth. This means that good-quality forage is often available even when the grass in open pastures has become over-mature (Mayer et al., 2004; Kallenbach et al., 2006). In addition, studies conducted in artificial agroforestry systems at lower altitudes indicate that although TC negatively affects the amount of forage yield, the grass tends to have better nutritive value. Furthermore, animal production in these systems is comparable to that of open pastures (e.g. Kallenbach et al., 2006).

This variability in the results can be largely attributed to the fact that most studies did not consider the different levels of TC. As highlighted by Spatz and Weis (1983), this factor considerably affects the amount and quality of forage production. In addition, understanding the relationship between the natural and agricultural value of WPs and TC density is crucial for EU agri-environmental policy, as it determines the level of funding allocated for the conservation management of these silvo-pastoral ecosystems.

In this study, open and WPs in calcareous Italian Pre-Alps areas were studied, with the following objectives and hypotheses:

- to analyse the vegetation types and species richness of Alpine WPs with different TC densities. It was hypothesized that the TC density would affect significantly both vegetation and species richness and that in the gradient between open pasture and dense wood plant richness would culminate at intermediate TC levels;
- to quantify the forage value and productivity of WPs compared with open pastures. In this regard, a decrease of forage value and productivity from open pasture to dense wood was expected;
- to examine how vegetation and productivity in WPs vary with different TC densities in relation to altitude, from the montane to the subalpine belt. The hypotheses were that vegetation and productivity would be negatively affected by the altitude but that the decrease from open pasture to dense wood would be proportionally less at higher altitude due to a lesser TC density of high-altitude forests.

## 2. Materials and methods

### 2.1. Study sites

The study area is located in the Asiago upland of the Venetian Pre-Alps in northeastern Italy. The dominant lithological substrata in this region are primarily calcareous, and the precipitation is relatively uniform, averaging between 1400 and 1500 mm per year. Depending on the altitude, the mean annual temperature ranges from 2 °C to 10 °C. Given the similarity of geological and climate traits to the northeastern Italian Pre-Alps, the study site can be considered a fairly representative of this region.

The main economic activities are tourism, agriculture and cattle farming. In most cases, during the vegetative period, many cattle farms transfer their animals to high-altitude summer farms, which are used for 3–4 months and include open semi-natural pastures, WPs and woodlands.

As regards the forest vegetation, the area is divided into three

altitudinal belts (ABs) (Del Favero, 2004):

- Montane belt (800–1400 m a.s.l.): In this belt, temperature is never a limiting factor for woodland vegetation, resulting in a full and regular TC. The main tree species are *Fagus sylvatica* and *Picea abies*;
- High-montane belt (1400–1650 m a.s.l.): At this altitude, temperature begins to limit the growth of broadleaved trees, leading to a regular but sparse woodland tree cover. Coniferous species thrive in this environment, with *Picea abies* being the dominant species, followed by *Abies alba*;
- Subalpine belt (1650–1900 m a.s.l.): In this belt, temperature significantly restricts the growth of coniferous trees, resulting in an often incomplete woodland TC. The main tree species here include *Picea abies* and *Larix decidua*.

In the three ABs, the types of pasture vegetation vary with altitude (Ziliotto et al., 2004):

- Montane belt: Unfertile pastures on basic soil are characterised by low-productive *Bromus erectus* vegetation (alliance *Bromion erecti* Koch 1926), whereas fertile pastures consist of *Lolium perenne*–*Cynosurus cristatus* or *Festuca rubra*–*Cynosurus cristatus* grasslands (*Cynosurion* R. Tx. 1947);
- High-montane belt: Unfertile pastures are represented by *Bromus erectus* vegetation, whereas fertile pastures are represented by *Festuca rubra*–*Cynosurus cristatus* or *Poa alpina* vegetation (*Poion alpinae* Oberd. 1950);
- Subalpine belt: Unfertile pastures comprise *Sesleria varia* grasslands (*Seslerion caeruleae* Br.-Bl. in Br.-Bl. et Jenny 1926), whereas fertile pastures are characterised by *Poa alpina* grasslands.

To examine the variation in vegetation between woodland and open pastures, study sites were selected across all three ABs following the experimental design shown in Table 1. Summer farms with different TC densities and WP vegetation were identified using digital aerial orthophotos. To this aim, canopy height models (CHMs) were processed using QGIS.org (2003). In the CHM raster, the percentage of pixels exceeding 1 m in height (TC percentage) was calculated for each 10 × 10 m quadrat within a grid superimposed on the raster image. With this analysis five pasture categories were identified: open pasture (OP; TC percentage < 5%); low-density WP (LDWP; TC percentage 5%–25%), middle-density WP (MDWP; TC percentage 25%–50%), high-density WP (HDWP; TC percentage 50%–75%) and very high-density WP (VHDWP; TC percentage > 75%). These ranges closely align with those used in the EU Rural Development Plans for subsidising WP utilisation (0%–5%, 5%–20%, 20%–50%, 50%–70% and >70%).

Three farms, including WPs with different percentages of TC, were randomly selected for each AB. On the maps, one to four sampling plots were randomly selected for each pasture category at each farm.

Next, sampling plots were established in the field based on the points obtained from the digital maps. In these plots, tree density was assessed

using fisheye photo analysis, a technique for examining plant canopies by capturing fisheye photos from the ground directed towards the zenith (Rich, 1989). Photos were taken using a Sirui lens (SKU 1984108) attached to a Samsung Galaxy A35 smartphone using an MSC-01 clip. The images were processed with the canopy-fisheye function from the R package hemisphereR (Chianucci and Macek, 2023) to determine the percentage of wood canopy openness. From this, the percentage of wood canopy closeness (WCC) was calculated as follows: 100%–percentage of canopy openness. Based on field checks, some WP plots were reclassified into a category of wood-pasture density that differed from that initially established using the CHM raster. The final sampling design included 99 plots distributed across the summer farms and ABs (Table 1).

## 2.2. Site surveying

The sampling-plot size was 100 m<sup>2</sup> (10 m × 10 m). Plots were surveyed in June–September 2024 for the following traits:

- Site traits: altitude, slope, aspect (declination from north: range 0°–360°), soil depth (measured using a graduated rod driven into the ground with five measurements averaged) and WCC (Section 2.1);
- Ground cover traits: percentage cover of bare soil and stones, mosses + lichens, herbaceous plants, shrubs, tree layers and individual vascular plant species (named according to Bartolucci et al., 2018);
- Grass height: measured using a graduated rod at five points in the plot.

## 2.3. Data analysis

The data analyses focused on the vegetation and the pastoral traits within the average plots associated with the previously mentioned WCC ranges. An analysis of the behaviour of individual species in relation to tree density will be performed in a future study.

To check whether the vegetation was significantly affected by the environmental factors considered in the experimental design (AB and WCC), permutational MANOVAs with the Vegan function Adonis2 (Oksanen et al., 2024) which is based on the principles of McArdle and Anderson (2001) were performed. As sampling plots from the same summer farm cannot be considered independent, to avoid pseudoreplication, permutations were constrained within farms (summer farm introduced as strata argument). Species abundances were log(x + 1)-transformed before the analyses. The association matrix between the plot species compositions was calculated using the Ružička dissimilarity coefficient (Ružička, 1958). The multivariate homogeneity of group dispersions assumed by the PERMANOVA performed alongside db-RDA was verified through the PERMDISP2 procedure outlined by Anderson (2006). The assumption was confirmed based on the log-transformed data. In the initial PERMANOVA, the effect of two experimental factors on vegetation was evaluated. The test included the factor AB at three levels (montane, high montane and subalpine) and the factor WCC at five levels (OP, LDWP, MDWP, HDWP and VHDWP) and their

**Table 1**

Overview of summer farms and sampling design for the study on vegetation and pastoral traits of wood pastures in the calcareous Italian Pre-Alps.

Altitudinal belt	Summer farm	Latitude (WGS 84)	Longitude (WGS 84)	Altitudinal range (m a.s.l.)	Size (ha)	Geological substratum of survey sites	No. sampling plots per farm	No. sampl. plots per altit. belt
Montane	Camprossignolo	45.818909	11.567406	1124–1256	75	Carbonate	11	33
	Melaghetto	45.873209	11.590487	1123–1311	91	Carbonate and shale	11	
	Montagna Nuova Davanti	45.831338	11.614129	1070–1327	28	Carbonate and shale	11	
High-montane	Trugole	45.923623	11.383648	1418–1561	28	Carbonate	11	33
	Campomulo	45.939496	11.551790	1504–1780	114	Carbonate	11	
	Mandrielle Vecchio Patrimonio	45.935760	11.390486	1544–1686	51	Carbonate	11	
Subalpine	Larici di Sotto	45.966125	11.418581	1533–1767	92	Carbonate	11	33
	Zebio	45.927423	11.510044	1438–1774	237	Carbonate	11	
	Quarti di Verena	45.918564	11.418722	1554–1921	141	Carbonate	11	

interaction. Given that the test results for unbalanced designs can vary depending on the order in which the main factors are introduced (Borcard et al., 2018), the test was conducted using both orders of factors. When the interaction was found to be significant at  $p \leq 0.05$ , the effects of each factor were examined separately. Subsequently, the difference between each pair of factor levels was assessed using the pairwise comparison procedure provided by the function `pairwise.adonis2()` (Bakker, 2024). To prevent an inappropriate increase in the number of incorrectly rejected null hypotheses, the false discovery rate correction was applied to the  $p$ -values (Pike, 2011).

Redundancy analysis (RDA) was used to identify the primary trends of vegetation patterns that were most correlated with environmental factors. Species abundances were  $\log(x + 1)$ -transformed before the analyses. As explanatory variables, slope, aspect, soil depth and WCC were introduced after standardisation by scaling them to zero mean and unit variance. Aspect was input as the radiation index (range 0–1), a measure that is consistent with the level of solar irradiance and can be calculated based on the declination from North, as suggested by Roberts and Cooper (1989). The significance of the explanatory variables in the RDA was assessed using permutation tests.

Information regarding the phytosociological behaviour of the 329 species found in the sampling plots was obtained from Landolt et al. (2010). The phytosociological class to which the species belonged was used to categorise the grassland and forest species into the following groups: *Molinio-arthenatheretea* (MA), fertile-grassland species; *Festuco-Brometea* (FB) and *Elyno-Seslerietea caeruleae* (ES), unfertile-grassland species; *Carpino-Fagetea* (CF), beech forest species; and *Vaccinio-Piceetea excelsae* (VP), spruce forest species. To evaluate the distance between the intermediate WP types and the two extreme types (OP and VHDWP), the dissimilarity coefficient of Ruzička was calculated between LDWP, MDWP, HDWP and VHDWP compared with OP and between OP, LDWP, MDWP and HDWP compared with VHDWP. The two values of the dissimilarity index obtained for each of the three ABs, and the main univariate vegetation traits (number and overall abundance of species belonging to the mentioned main species classes, bare soil cover, mosses + lichens cover and species richness) of the five WP types were analysed using parametric univariate analysis of variance (ANOVA). The assumptions of residual normality and variance homogeneity were checked graphically with Q-Q plots and through Levene tests, respectively. When the assumptions were not confirmed, the data were transformed using  $\log(x + 1)$ , square root or fourth root transformations. Post hoc pairwise mean comparisons were performed using the Tukey test. When no transformation could produce data consistent with the ANOVA assumptions, the comparisons were performed using the non-parametric Kruskal–Wallis test, followed by Dunn's non-parametric post hoc test ( $p$ -values adjusted using the Benjamini–Hochberg method) for the pairwise mean comparisons.

To characterise the pastoral traits of the five WP types, the following four parameters were considered: forage value (indicating forage quality and palatability), grass height (indicating grass production), pastoral value (indicating both forage quality and productivity) and carrying capacity (expressed as the number of livestock units that can be fed per unit pasture surface).

For each sampling plot, the forage value was calculated for three vegetation layers accessible to grazing animals (mosses + lichens, shrubs and herbaceous species) as the mean of the forage values of the species found in each layer, weighted by the species percentage cover. Forage values for individual species were taken from the study by Klotz et al. (2002), using a scale from 1 to 9, where 1 indicates poisonous species, 2 indicates little or no forage value and 3–9 indicate low to high levels of forage value. The forage value for each sampling plot was obtained by calculating the mean of the values from three layers, weighted by their percentage cover. The pastoral value was calculated similarly to the foraging value. The pastoral values for individual species (on a scale from 0 to 5, where 0 indicates poisonous species and 1–5 indicate low to high pastoral value) were obtained from the study by Cavallero et al.

(2007). The resulting weighted mean (scale 0–5) was then rescaled to 0–100 by multiplying by 20. According to the method described by Cosic (1987), the carrying capacity of each sampling plot was calculated from its pastoral value using the following procedure:

- The pastoral value was proportionally adjusted to account for the area covered by bare soil + stones, as non-vegetated ground does not produce forage;
- The adjusted pastoral value was then multiplied by a fragility coefficient that corresponds to the plot's inclination: 1 for inclinations  $0^\circ$ – $10^\circ$ , 0.9 for inclinations  $10^\circ$ – $30^\circ$ , 0.8 for inclinations  $30^\circ$ – $40^\circ$  and 0.65 for inclinations  $>40^\circ$ ;
- The reduced and corrected pastoral value was multiplied by an altitude coefficient and by 365. This converted the pastoral value into carrying capacity, expressed in livestock unit days per ha per year. The altitude coefficients were as follows: 0.02 for altitudes up to 1500 m a.s.l. and 0.0166 for altitudes between 1500 and 2000 m a. s.l.;
- Finally, the carrying capacity, expressed in livestock unit days per ha per year, was obtained by dividing the previous value by 115, which is the average length of the grazing season in the area.

In terms of vegetation traits, the effects of WCC and AB on pastoral traits were examined. Initially, analyses were conducted considering both factors and their interaction using the same univariate procedures as previously described. In instances where a significant interaction was found, the analysis was repeated separately for each factor.

To convey the overall trend of main vegetation patterns and pastoral traits through WP types, boxplots were created showing median, interquartile range, whiskers and individual data points.

The statistical software used was R 4.3.3 (R Core Team, 2024) with the following packages:

- `vegan` (Oksanen et al., 2024) for MANOVA and RDA, using the following functions: `vegdist` to compute Bray–Curtis indices, which were subsequently used to obtain the Ruzička dissimilarity matrix as  $D = 2 \times \text{Bray}/(1 + \text{Bray})$ , with `Bray = Bray–Curtis dissimilarity`; `betadisper` for the analysis of multivariate homogeneity of group dispersions; `permutest` to assess the significance of `betadisper` application; `adonis2` for multivariate PERMANOVAs using a distance matrix; `decostand` (method = 'standardize') to standardise environmental variables to be included in the RDA models; `rda` to perform RDA; and `anova.cca` to perform a permutation test assessing the significance of environmental variables included in RDA models;
- `stats` (R Core Team, 2024), using the following functions: `qqnorm` to assess residual normality with Q-Q plots; `aov` to perform ANOVA; `TukeyHSD` for post hoc pairwise comparisons; and `kruskal.test` to implement rank sum test;
- `car` (Fox and Weisberg, 2019) for Levene's test, using the `leveneTest` function to check for univariate variance homogeneity;
- `dunn.test` (Dinno, 2024) for pairwise comparisons after the Kruskal–Wallis test.

### 3. Results

#### 3.1. Vegetation

The PERMANOVA that assessed the effect of WCC and AB on species composition showed a significant factor interaction (Table 2). PERMANOVA performed separately for each WP type indicated that the AB level affected the vegetation in all cases (Table 2 and Annex A). The highly significant differences among ABs were due to consistent changes in the presence and abundance of species from different grassland and forest types (Annexes B–D and Table 3). The effect of WCC was always highly significant in the tests performed at each AB level (Table 2). In all cases, WP vegetation differed from OP vegetation. In the high-montane and

subalpine belts, the VHDWP vegetation differed from the other WP types and from the LDWP and MDWP vegetation in the montane belt. The vegetation of LDWP, MDWP and HDWP was always similar.

The total variation resulting from RDA was 29.3 (constrained 8.45), 24.2 (constrained 8.36) and 25.3 (constrained 8.88) in the montane, high-montane and subalpine belts, respectively. Therefore, the overall variability among the five WP types was lower in the two higher ABs.

RDA graphs (Fig. 1) showed that, in all ABs, the vegetation surveys were arranged on average along the two opposite sides of the first component in the following sequence: OP, LDWP–MDWP, HDWP and VHDWP. In all cases, this arrangement was strongly related to the variation in WCC, the main influencing site trait ( $p < 0.0001$ ).

Symbols in the graphs represent sampling plots. The abbreviations used have the following meanings: The first capital letter indicates the wood pasture type (O, open pasture; L, low-density wood pasture; M, middle-density wood pasture; H, high-density wood pasture; V, very high-density wood pasture). The second and third characters refer to summer farm locations (cr, Camporossignolo; mg, Melaghetto; mn, Montagna Nuova Davanti; tr, Trugole; mv, Mandrielle Vecchio Patrimonio; cm, Campomulo; ls, Larici di Sotto; ze, Zebio; qv, Quarti di Verena). The last character represents the code of the sampling area within the wood pasture category in the summer alp.

Soil depth was the trait most related to the second RDA component in the high-montane and subalpine belts. Areas with deeper soil (Trugole, Mandrielle Vecchio Patrimonio in the high-montane belt and Larici di Sotto in the subalpine belt) were positively associated with soil depth, whereas plots with shallower soil (Campomulo in the high-montane belt and Zebio and Quarti di Verena in the subalpine belt) were negatively associated with it.

The main aspect differentiating the WP types was the relative importance of grassland species versus forest species (Fig. 2). The observed pattern was rather similar in the three belts. Along the gradient between OP and VHDWP, the number of grassland species was high until

MDWP was included. After MDWP, the number decreased. The trait was still relatively high in HDWP but dropped to very low values in VHDWP (Fig. 2). Considering species abundance, grassland species consistently decreased from OP to MDWP and dropped to a very low level in HDWP (Fig. 2). Forest species increased progressively in both number (Fig. 2) and abundance (Fig. 2) from OP to VHDWP. The increase in species number was steep from OP to LDWP and then more gradual. The increase in species abundance was nearly linear.

In HDWP and VHDWP, the number and abundance of grassland species were lower in the montane belt, intermediate in the high-montane belt and higher in the subalpine belt. The opposite was true for forest species (Annex E). The dissimilarities between the extreme WP types (OP and VHDWP) in the montane, high-montane and subalpine belts were higher, intermediate and lower, respectively (Table 3).

A second aspect characterising the vegetation pattern was the different importance of fertile (MA) versus unfertile (FB and ES) grassland species and beech (CF) versus spruce (VP) forest species. These differences were clear, especially in the comparison among the belts. Fertile-grassland species (MA in Annex E) were dominant in the montane belt. In contrast, the importance of unfertile-grassland species (FB and ES) was similar to that of fertile-grassland species in the high-montane and subalpine belts (Annex E). However, beech forest species (CF) dominated in the montane belt, whereas they had similar importance to the spruce forest species (VP) in the high-montane and subalpine belts (Annex E).

The total number of species found in the montane, high-montane and subalpine belts was 220, 215 and 203, respectively (Annexes B–D). In all belts, the highest species richness was found in LDWP or MDWP (Table 3), where both grassland and forest species were present in the same sampling plots. Generally, this trait was relatively low in the two extreme vegetation types (OP and HDWP) and increased from both extremes towards LDWP–MDWP. In LDWP and MDWP, all grassland species and nearly all forest species occurred together in the same plots.

**Table 2**

Results of PERMANOVA on the vegetation across wood pasture types with five wood canopy closeness levels and three altitudinal belts in the eastern Italian Pre-Alps. The statistical results were essentially the same in the two-factor analysis, regardless of which variable was entered first. Therefore, only the values of the statistical parameters obtained with WCC as the first variable are shown.

Type of test	Factor tested	Degrees of freedom	Sum of squares	R <sup>2</sup>	F	P > F	Pairwise comparisons*				
Two-factor test	Wood canopy closeness (WCC)	4	5.68	0.15	5.25	0.001	–	–	–	–	–
	Altitudinal belt (AB)	2	4.92	0.13	9.09	0.001	–	–	–	–	–
One-factor tests	WCC x AB	8	3.39	0.09	1.57	0.001	–	–	–	–	–
	Altitudinal belt	2	1.21	0.24	2.40	0.001	Mountain	High-mountain	Subalpine	–	–
	AB in the open pasture	2	1.07	0.29	1.85	0.002	a	b	b	–	–
	AB in the wood-pasture 5–25% WCC	2	1.17	0.22	1.98	0.001	a	a	b	–	–
	AB in the wood-pasture 25–50% WCC	2	2.14	0.30	3.89	0.001	a	b	c	–	–
	AB in the wood-pasture 50–75% WCC	2	2.73	0.27	5.25	0.001	a	b	c	–	–
	AB in the wood-pasture 75–100% WCC	2	2.73	0.27	5.25	0.001	a	b	c	–	–
	Wood canopy closeness	4	3.39	0.29	2.84	0.001	Open pasture (OP)	Wood-pasture, 5–25% WCC (LDWP)	Wood-pasture, 25–50% WCC (MDWP)	Wood-pasture, 50–75% WCC (HDWP)	Wood-pasture, 75–100% WCC (VHDWP)
WCC in the montane belt	4	3.11	0.29	2.87	0.001	a	b	b	b	c	
WCC in the high-montane belt	4	2.53	0.27	2.61	0.001	a	b	b	b	c	
WCC in the subalpine belt	4	2.53	0.27	2.61	0.001	a	b	b	b	c	

\* In the pairwise comparison, factor levels with a common letter do not differ at  $p \leq 0.05$ .

**Table 3**Univariate vegetation traits of five wood pasture types in three altitudinal belts in the eastern Italian Pre-Alps. Means sharing a common letter do not differ at  $p \leq 0.05$ .

Altitudinal belt	Trait	P-value	Wood-pasture type (letter for the pairwise comparison)*				
			Open pasture (OP)	Wood-pasture, 5–25% WCC (LDWP)	Wood-pasture, 25–50% WCC (MDWP)	Wood-pasture, 50–75% WCC (HDWP)	Wood-pasture, 75–100% WCC (VHDWP)
Montane	Bare soil (%)	<0.001	0 b	8 ab	12 a	27 a	51 a
	Mosses and lichens (%)	n.s.	1	9	5	6	17
	Species richness (no.)	<0.001	32 bc	55 a	55 a	47 ab	32 c
	Dissimilarity coefficient Ruzička (pres.-abs.) to OP	<0.001	0.61 d	0.73 c	0.75 c	0.87 b	0.97 a
	Dissimilarity coefficient Ruzička (pres.-abs.) to HDWP	<0.001	0.97 a	0.86 b	0.86 b	0.8 d	0.78 d
	Dissimilarity coefficient Ruzička (pres.-abs.) to VHDWP	<0.001	0.93 a	0.78 bc	0.8 c	0.77 b	0.73 d
High-montane	Bare soil (%)	<0.001	0 c	4 bc	2 c	30 ab	48 a
	Mosses and lichens (%)	0.003	0 b	6 a	8 a	16 a	16 a
	Species richness (no.)	<0.001	34 b	56 a	51 a	45 a	34 b
	Dissimilarity coefficient Ruzička (pres.-abs.) to OP	<0.001	0.65 d	0.8 bc	0.77 c	0.83 b	0.94 a
	Dissimilarity coefficient Ruzička (pres.-abs.) to HDWP	<0.001	0.93 a	0.78 bc	0.8 c	0.77 b	0.73 d
	Dissimilarity coefficient Ruzička (pres.-abs.) to VHDWP	<0.001	0.93 a	0.78 bc	0.8 c	0.77 b	0.73 d
Subalpine	Bare soil (%)	<0.001	0 c	2 bc	5 bc	21 ab	33 a
	Mosses and lichens (%)	0.009	0 b	2 ab	8 ab	7 ab	18 a
	Species richness (no.)	<0.001	45 bc	52 ab	55 a	46 ab	37 c
	Dissimilarity coefficient Ruzička (pres.-abs.) to OP	<0.001	0.63 c	0.73 b	0.73 b	0.76 b	0.86 a
	Dissimilarity coefficient Ruzička (pres.-abs.) to HDWP	<0.001	0.86 a	0.73 b	0.72 b	0.69 bc	0.65 c
	Dissimilarity coefficient Ruzička (pres.-abs.) to VHDWP	<0.001	0.86 a	0.73 b	0.72 b	0.69 bc	0.65 c

\* Letter for the pairwise comparisons: means with a common letter do not differ at  $p \leq 0.05$ . WCC means Wood Canopy Closeness. Statistical test used are shown in Annex D.

Even within the 5%–50% WCC range, the maximum species richness occurred at rather different tree covers in the three belts: 45%, 40% and 10% in the montane, high-montane and subalpine belts, respectively (Annex H). Grassland species that could persist under relatively high shading conditions and contributed to species richness peaks at relatively high tree covers were mainly fertile-soil species of the classes *Molinio-Arrhenatheretea* and *Artemisietea vulgaris* in the montane belt and unfertile-soil species of the class *Elyno-Seslerietea* in the high-montane belt (Annex H). MDWP was also the WP category with the highest number of species not observed in other categories (22 species compared with 20, 8, 14 and 14 in OP, LDWP, HDWP and VHDWP, respectively). This number reached 37 in the categories of WPs with low to intermediate TC (LDWP and MDWP).

In all belts, from OP to HDWP, the percentage of ground cover by bare soil plus the mosses/lichens cover (ground not covered by vascular species) increased from approximately 0% to 51%–64% (Table 3). From OP to LDWP, the cover of mosses/lichens was similar to that of bare soil

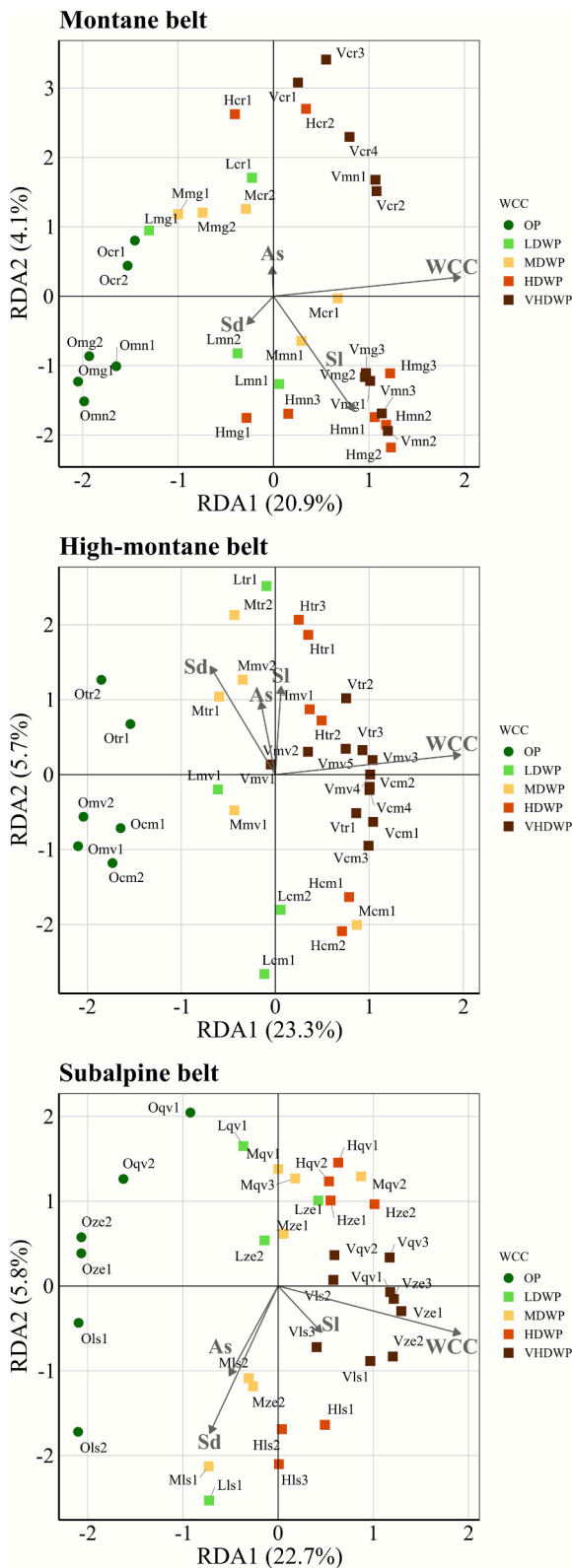
cover (0%–9%). From LDWP to VHDWP, mosses/lichens increased slightly up to approximately 18%, whereas bare soil increased more sharply, up to 33%–51%.

### 3.2. Pastoral traits

The results of the univariate two-way ANOVA on the pastoral traits (Annex I) showed that the AB effect was significant in most cases, whereas the WCC effect was always significant. The WCC  $\times$  AB interaction was significant in some cases but not in others.

The forage value of the vegetation layers accessible to grazing animals decreased from the montane belt (on average 4.1) to the subalpine belt (on average 3.6) (Table 4) and from the relatively high values of OP (5.5) and LDWP–MDWP (4.5–4.1) to the low values of the dense WP types (HDWP and VHDWP: 2.4–3.1) when averaged across ABs (Fig. 3).

The above-described pattern of forage value reflected the similar distribution of species with different forage values across the three ABs



**Fig. 1.** RDA graphs of the wood pasture vegetation surveyed in three altitudinal belts in the eastern Italian Pre-Alps. Abbreviations for wood pasture types (WCC): OP, open pasture; LDWP, low-density wood pasture; MDWP, middle-density wood pasture; HDWP, high-density wood pasture; VHDWP, very high-density wood pasture. Significance levels of the site traits in the RDA models: montane belt, WCC  $p < 0.001$ , soil depth  $p = 0.854$ , aspect  $p = 0.410$ , slope  $p = 0.079$ ; high-montane belt, WCC  $p < 0.001$ , soil depth  $p < 0.045$ , aspect  $p = 0.111$ , slope  $p = 0.158$ ; subalpine belt, WCC  $p < 0.001$ , soil depth  $p = 0.009$ , aspect  $p = 0.153$ , slope  $p = 0.346$ .

and five WP types (Annex F). From the montane belt to the subalpine belt, the abundance of intermediate- and high-value species (especially MA species) decreased. In contrast, the abundance of low-value or poisonous species (especially FB and ES species) increased. Species with high and intermediate forage values were most abundant in OP, LDWP and MDWP, whereas low-value or poisonous species were particularly abundant in HDWP and VHDWP. Poisonous species were particularly abundant in dense WPs in the montane belt. The low forage value in the denser WP types resulted from the dominance of typical herbaceous forest species, which have a mean forage value lower than that of typical grassland species (Annex J).

As with forage value, the increase in altitude and TC negatively affected grass height. The highest values (72–76 cm) were found in OP of the lowest belts, and the lowest values (21–29 cm) were found in the denser woods (Table 4). A most critical variation in the WP means of each belt was found in the transition from the montane belt to the two other belts (Table 4).

The pastoral value was affected by WCC and the WCC  $\times$  AB interaction (Annex I). As with grass height, the greatest variation among belts, averaged across WP types, occurred in the transition from the montane belt (23) to the other two belts (16–18). TC had a stronger effect on the pastoral value, which decreased on average from 32 to approximately 5 (Fig. 3). The AB  $\times$  WCC interaction also exhibited a pronounced effect (Table 4). The pastoral value showed the greatest range of variation in the montane belt: OP, LDWP and MDWP had significantly higher values than in the high-montane and subalpine belts, whereas the VHDWP value was lower than that in the other two belts. This pattern resulted from the behaviour of the species of high pastoral value, which were more abundant in OP, LDWP and MDWP of the montane belt and the behaviour of the species of low pastoral value (which also include poisonous species), which had the highest abundances in the montane belt VHDWP (Annex F).

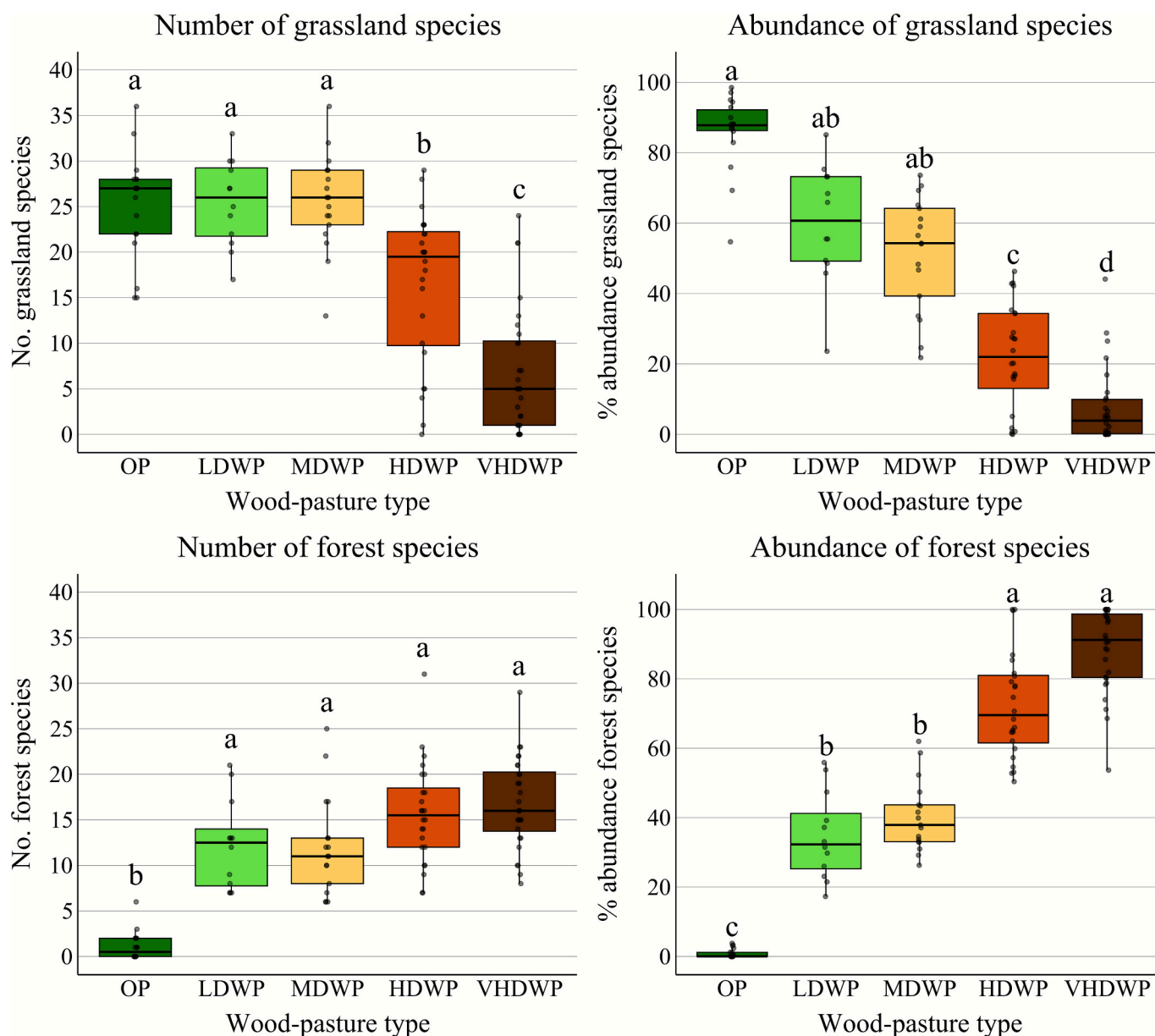
The calculated carrying capacity was in the range of 0.06–2.56 LU/ha (Table 4) and was significantly affected by WCC and the WCC  $\times$  AB interaction (Annex I). The effects of AB and WCC were similar to those observed for the pastoral value but much more pronounced, primarily due to the higher altitude of the high-montane and subalpine belts (lower value of the altitude coefficient used to convert the pastoral value into carrying capacity) and the high percentage of bare soil in the dense WP types (Table 3). The carrying capacity decreased to 65.8% and 55.5% in the high-montane and subalpine belts, respectively, compared with the carrying capacity in the montane belt (Table 4), showing a pattern similar to that observed for grass height and pastoral value (i.e., values in the high-montane and subalpine belts not very dissimilar but much lower than those in the montane belt). The WCC effect was even more important. In the AB average, compared with OP, the carrying capacity of LDWP and MDWP was 72%–62% and much lower than that of HDWP and VHDWP (27% and 9% of OP, respectively) (Fig. 3). This reduction was greatest in the montane belt (significant WCC  $\times$  AB interaction; Annex I). Compared with OP, the VHDWP carrying capacity was only 3% in the montane and 13% and 20% in the high-montane and subalpine belts, respectively (Table 4).

## 4. Discussion

### 4.1. Vegetation

In the studied WPs, AB and WCC and their interaction had a highly significant effect on vegetation.

As hypothesized, AB influenced vegetation across all types of WPs. The most important changes in the altitude gradient occurred in the high-montane belt, which, according to Ziliotto et al. (2004), marks the transition between low-altitude *Lolium perenne* or *Bromus erectus* pasture and high-altitude *Poa alpina* or *Sesleria varia* grassland. In forests, the same belt becomes limiting for mesophilous broadleaved trees, which are replaced by conifers (Del Favero, 2004). The drop in winter



**Fig. 2.** Boxplots (median, interquartile ranges, and individual data points) showing the pattern of the number and abundance of grassland and forest species in the wood pasture vegetation in three altitudinal belts in the eastern Italian Pre-Alps. Abbreviations for the wood pasture types: OP, open pasture; LDWP, low-density wood pasture; MDWP, middle-density wood pasture; HDWP, high-density wood pasture; VHDWP, very high-density wood pasture. Means sharing a common letter do not differ at  $P \leq 0.05$ . Graphs showing the patterns separately for each altitudinal belt are included in Annex G.

temperature and the increasing damage from spring frosts occurring from the high-montane belt upwards seem to be the primary factors causing this species and vegetation replacement (Klapp, 1971; Del Favero, 2004). The second important variation in the same belt was the decrease in fertile-pasture species, favouring unfertile-pasture species. This pattern was found in the western Italian Alps, where it was associated with lower management intensity at higher altitudes (Pittarello et al., 2020). More generally, this phenomenon is referred to as the 'elevation complex' (Klapp, 1971) It describes the combination of limiting pedo-climatic factors that make it difficult for high-demanding species to thrive above the montane belt.

The effect of WCC on vegetation was highly significant in all belts. This result was probably due exclusively to the different light intensities reaching the understorey in the studied WPs, as the Landolt indicator values for other possibly important factors (soil moisture and nutrients) did not differ among WP types (Annex K). Differences in species

composition due to decreasing light levels under increasing TC were the most frequently reported findings in both agroforestry (artificial) and semi-natural ecosystems. For example, in artificial shading experiments, Dodd et al. (2005) found that high shading decreased the percentage of legumes in species composition in favour of grasses. As in this study, the change in species composition occurring in semi-natural ecosystems at higher shading consisted mainly of the replacement of grassland species by woodland species. This result is consistent with that of Müller et al. (2013) in the Bavarian Alps and Sicuriello et al. (2024) in the Italian Eastern Alps, which is close to the study area. As noted by Königer et al. (2005) and confirmed by the consistently significant effect of the WCC levels on the light indicator values of grassland species (Annex K), this change is mainly a consequence of grassland species' low adaptation to low light intensity in denser woods.

In this study, the *Fagus sylvatica*-rich HDWP and VHDWP types of the montane belt were poorer in grassland species and richer in woodland

**Table 4**  
Univariate pastoral traits of five wood pasture types in three altitudinal belts in the eastern Italian Pre-Alps.

Altitudinal belt	Trait	P-value	Wood-pasture type (letter for the pairwise comparison)*					Mean
			Open pasture (OP)	Wood-pasture, 5–25% WCC (LDWP)	Wood-pasture, 25–50% WCC (MDWP)	Wood-pasture, 50–75% WCC (HDWP)	Wood-pasture, 75–100% WCC (VHDWP)	
Montane	Forage value (FV)	<0.001	5.94 a	5.65 ab	4.12 bc	3.05 cd	1.96 d	4.14
	Grass height (cm)	0.001	72 a	51 ab	72 a	54 a	21 b	54
	Pastoral value (PV) (%)	<0.001	42.9 a	35.7 a	23.5 ab	13.3 b	1.5 c	23.4
	Carrying capacity (LU per ha)	<0.001	2.56 a	1.87 ab	1.19 bc	0.54 c	0.06 d	1.24
High-montane	Forage value (FV)	0.003	5.78 a	4.18 ab	4.5 ab	3.2 b	2.7 b	4.07
	Grass height (cm)	0.001	76 a	44 abc	52 ab	35 bc	29 c	47
	Pastoral value (PV) (%)	<0.001	27.4 a	21.4 a	23.3 a	13 ab	4.8 b	18
	Carrying capacity (LU per ha)	<0.001	1.39 a	0.99 ab	1.18 a	0.38 bc	0.18 c	0.82
Subalpine	Forage value (FV)	0.007	4.8 a	3.76 ab	3.72 ab	3.11 b	2.68 b	3.61
	Grass height (cm)	<0.001	56 a	55 ab	50 ab	33 bc	25 c	44
	Pastoral value (PV) (%)	<0.001	24.4 a	17.7 ab	18.5 a	11.9 ab	8.3 b	16.1
	Carrying capacity (LU per ha)	<0.001	1.17 a	0.84 ab	0.81 ab	0.42 bc	0.23 c	0.7

\* Letter for the pairwise comparisons: means with a common letter do not differ at  $p \leq 0.05$ . WCC means Wood Canopy Closeness. Statistical test used were parametric ANOVA Kruskal-Wallis test. For details see Annex F.

species than the same WP categories in the high-montane and subalpine belts. This result, which was confirmed by the higher RDA total amount of variation among the five WP types and the higher dissimilarity Ruzička coefficient values between the extreme vegetation types, OP and VHDWP, found in the montane belt, is consistent with the hypothesis done that the vegetation difference between the extremes of the OP-VHDWP gradient is lower at higher altitude. This variation can be attributed to the greater abundance of beech trees in the montane belt, which have denser crowns than spruce trees. In contrast, the high-montane and subalpine belts are more abundant in larch, which is characterised by its open crown (Mahr, 2025). The result is consistent with the findings by Müller et al. (2013) in the Bavarian Alps, where grassland species were less abundant in the dense-crown mixed wood of the montane belt than in the more illuminated understorey of the thin-crown *Pinus sylvestris* stands.

In the OP-VHDWP tree density gradient, PERMANOVA applied with log-transformed data (reduced importance to the species abundance) revealed that the LDWP, MDWP and HDWP vegetations were not very dissimilar, particularly in the high-montane and subalpine belts. The number of grassland and forest species surveyed in these three WP types confirmed this result, as both species categories occurred together in the plant communities and were not very differently represented in the three wood densities. A very similar result was obtained by Müller et al. (2013), where low- to middle-density woods showed a similar overlap of grassland and forest species. The difference between the three WCC categories was higher in terms of species abundance, as grassland species were dominant in LDWP-MDWP and forest species were dominant in HDWP. The pattern of species overlap is related to the levels of light availability at which the C3 grassland species, which are typical of the temperate ecosystems considered here, can persist in the shaded wood understorey. Several studies (e.g., Taiz and Zeiger, 2010) have indicated that C3 plants reach light saturation at intermediate light levels, allowing them to thrive under relatively dense TC. Semchenko et al. (2012) showed that moderate shade (50% daylight) had a net facilitative effect on the average plant mass of 46 temperate grassland species.

Moreno (2008) found that an intermediate reduction in light availability of 42%–44% in the understorey can result from a TC of 16%–24%. This TC level was identified as the threshold at which the number of grassland species began to decline (Annex H).

In all ABs, the species richness exhibited an asymmetric bell-shaped pattern in the TC gradient, with the maximum occurring in the LDWP and MDWP categories (54 species in the three AB averages) and the minimum occurring at the TC extremes (34–37 species in the AB averages). The overlap of grassland and forest species resulted in the maximum richness in LDWP-MDWP, which was often observed in other WP studies from the mountains of temperate Europe (e.g. Gillet et al., 1999; Müller et al., 2013; Pomaro et al., 2013; Rupp, 2013). According to Königler et al. (2005), this higher species richness is mainly explained by greater habitat heterogeneity, resulting from site diversity (rocks, soil depth, trees of varying density, size and species and decaying wood) and grazing activity (defoliation, trampling, dunging) (Oldén, 2016). The LDWP and MDWP species richness is higher than that in OP owing to the presence of single trees or tree groups, which create shaded areas where forest species can establish. Conversely, species richness in LDWP and MDWP is higher than that in denser WP types as a consequence of more light at the soil level, the reactivation of the soil seed bank and the diaspore import by grazing and other animals (Rupp, 2013). In the present study, the highest number of species was calculated at WCC values of about 45%, 40% and 10% in the montane, high-montane and subalpine belts, respectively (Annex H). In other studies, the maximum number of species was found at lower TCs: 27% in a *Larix decidua* WP (Gillet et al., 1999), 20%–30% in the montane *Fagus sylvatica* forests of the Berchtesgaden National Park (German Alps) (Rösch, 1992) and 18%–25% in the Bavarian submontane *Pinus sylvestris* and high-montane mixed forests (Müller et al., 2013). Tree cover levels determining maximum species richness more similar to those of the WPs studied here were found in the same geographical area by Pomaro et al. (2013) on the carbonate montane *Fagus sylvatica*, high-montane *Picea excelsa* and subalpine *Larix decidua* sites (approximately 42%, 32% and 5%, respectively). Maybe, the different latitude can explain this difference.

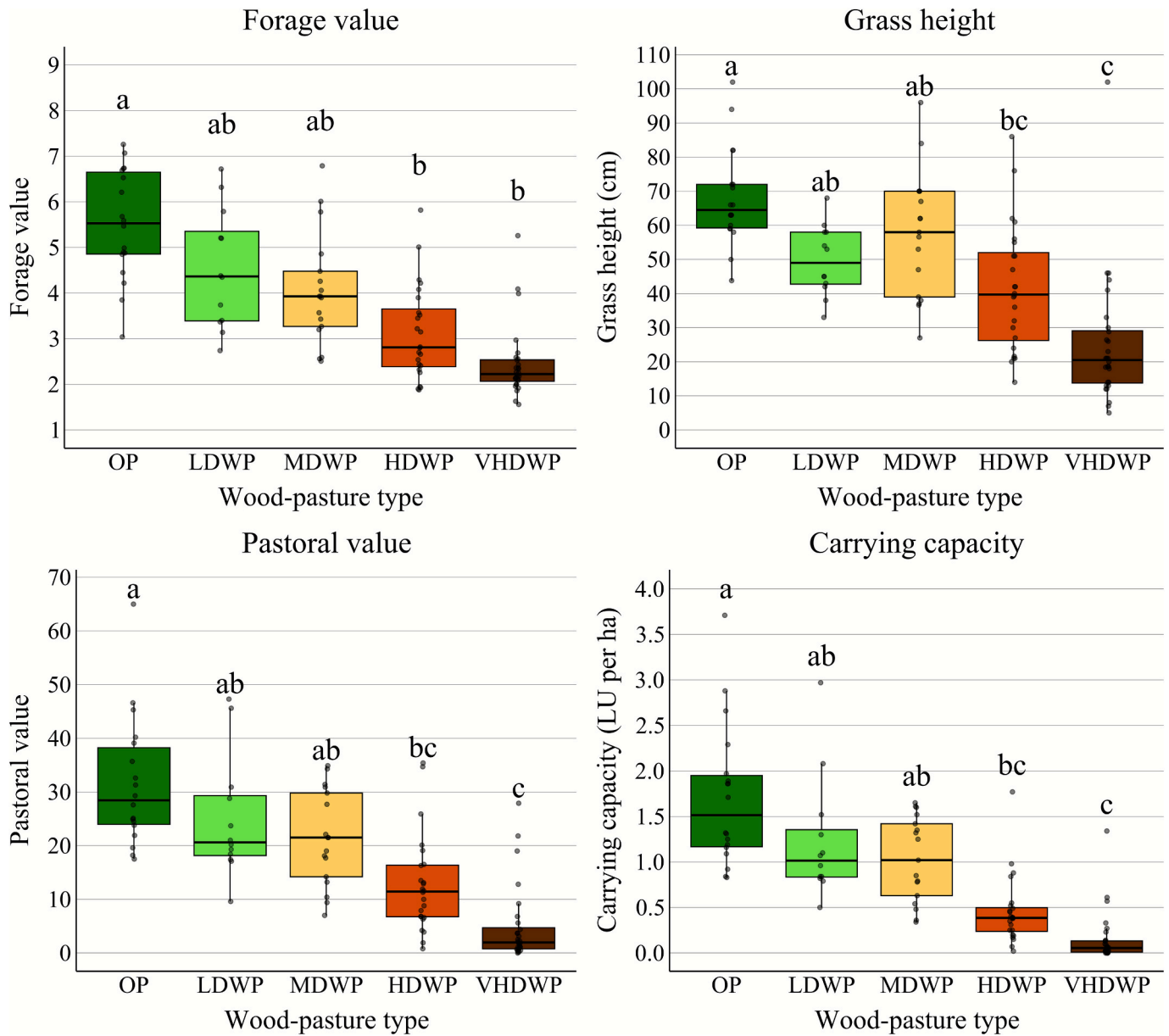


Fig. 3. Boxplots (median, interquartile ranges, and individual data points) showing the pattern of the forage value, grass height, pastoral value and carrying capacity of five wood pasture types (OP, open pasture; LDWP, low-density wood pasture; MDWP, middle-density wood pasture; HDWP, high-density wood pasture; VHDWP, very high-density wood pasture) in three altitudinal belts in the eastern Italian Pre-Alps. Means sharing a common letter do not differ at  $P \leq 0.05$ .

The sites studied by Gillet et al. (1999), Rösch (1992) and Müller et al. (2013) are at higher latitude (north of the Alps) and therefore less enlightened than those considered here and by Pornaro et al. (2013) located south of the Alps. The understory brightness level which limits the species growth could be reached at lower TC north of the Alps. With regard to the difference found among ABs, it is difficult to explain the late species-richness culmination found in the high-montane belt, where the *Elyno-Seslerietea* species responsible for this result did not show a particularly high competitiveness under shade conditions (mean Landolt light indicator index = 3.73). In contrast, for the montane belt, one possible explanation is that the fertile-soil herbaceous species, which were very numerous in this belt, had a higher tolerance to shade, as indicated by their relatively low mean value of the Landolt light indicator index values (3 and 3.52 for *Artemisietea vulgaris* and *Molinio-Arrhenatheretea* species, respectively, vs 3.75 for *Festuco-Brometea* species; data not shown).

#### 4.2. The pastoral traits

The forage value decreased significantly from the montane belt to the subalpine belt and from OP to VHDWP. These results confirm the hypotheses done with regard to the negative relationship between WP productivity and altitude or TC density. The decrease due to AB (-15%, from 4.2 to 3.6) was mainly a consequence of the low abundance of high-forage-value MA grassland species and high abundance of low-forage-value FB and ES grassland species at higher altitudes. However, the different proportions of CF and VP species in the three belts also contributed to the pattern, as CF species, which are characteristic of the montane belt, had a higher forage value than VP species, which were more prevalent in the subalpine belt. The only exception to this pattern occurred in VHDWP, where the forage value in the montane belt was lower than in the two other belts due to the particularly high proportion of poisonous species.

The forage value decrease due to the increase in TC was much higher

(−46%, from OP to VHDWP in the average of the three belts). The decrease was a consequence of the progressive reduction in grassland species (higher value) in favour of the forest species (lower value), but also to grassland species surveyed under the TC having mean forage value lower than those present in open pastures. A reduction in forage value due to increased TC has often been found in studies on WPs (Königer et al., 2005). For example, in the Karwendel Mountains (Austrian Alps), the forage value ranged between 5.3 (open pasture) and 2.3 (VHDWP) (values rescaled from the −1 to 8 range used by Spatz to the 1–9 range used by Klotz) (Spatz and Weis, 1983). In WPs, species not eaten by animals (e.g. poisonous, thorny, aromatic, unpleasant, prickly grasses, high-size ferns and mosses) can spread (Königer et al., 2005), perhaps also because shepherds do not combat weeds with the same intensity as in open pastures. In the areas studied, the main uneaten species were many poisonous forbs and ferns (e.g. *Cardamine trifolia*, *Helleborus viridis*, *Jacobaea alpina*, *Senecio cacaliaster*, *Senecio nemorensis*, *Trollius europaeus*, *Veratrum album*, *Athyrium filix-foemina*, *Dryopteris dilatata* and *Dryopteris filix-mas*). Similarly, many poisonous species were surveyed in the woods studied by Sicuriello et al. (2024). According to Bergmeier et al. (2010), at the European scale, species more or less exclusive to pastoral woodland are poisonous or distasteful herbs and can have an important role in tree regeneration through protecting young plants from herbivore uptake (Rupp, 2013).

Forage-value indices are based only on the species identity and do not consider other factors that can affect the forage quality. Some authors have found that forage digestibility was higher (with protein and fibre contents being higher and lower, respectively) in WPs than in open pastures (Mayer et al., 2003; Rösch, 1992; Kallenbach et al., 2006), although the forage content in some mineral nutrients (sodium and phosphorous) was deficient (Rösch, 1992). Another important positive trait of the WP forage is that shaded plants tend to flower later and therefore have higher protein content at the time when the open pasture species are already mature. This extends the period of good-quality forage availability (Mayer et al., 2004; Kallenbach et al., 2006). Furthermore, Mayer et al. (2005) found that, even when the herbage quantity provided by WPs was quite small, the ability of animals to select sufficiently digestible plants can result in feed of a quality high enough to meet livestock requirements.

Forage height, which is usually well correlated with forage production (Klapp, 1971), was affected by WCC. The decrease due to TC was 64% (from 68 cm in OP to 27 cm in VHDWP). In the average of the WP types, the decrease due to AB was less and not significant (−18.2% from the montane belt to the subalpine belt).

The pastoral values calculated for OP were in the range reported for fertile pastures in the western Alps (Cavallero et al., 2007), decreasing by 33% from the montane belt (approximately 43) to the subalpine belt (approximately 24). The decrease due to TC was much greater, reaching 87% (from 31.6 in OP to 5 in VHDWP). These reductions exceeded those found for both forage value and forage height because they reflected the combined decreases caused by both factors.

The carrying capacity values were even more negatively affected by AB and WCC, as additional factors came into play, namely altitude, inclination and the portion of the ground not covered by vegetation. The 45% decrease calculated from the montane belt to the subalpine belt was mainly due to altitude, although inclination also had some effect (increasing from 12° to 15°), whereas the portion of vegetation-free ground (bare soil plus stones) was similar across the three belts (18%–22%). In contrast, the decrease due to WCC was much greater (in the AB average, −91% from OP to VHDWP), as the relatively high proportion of vegetation-free ground in HDWP and VHDWP (approximately 36% and 61%, respectively) had a strong impact on productivity. However, in the high-montane and subalpine belts, the VHDWP carrying capacity decreased less than in the montane belt, maintaining values of approximately 0.18 and 0.23 LU/ha, respectively, compared with only 0.07 LU/ha in the montane belt. This outcome of the study is consistent with the initial hypothesis that at higher altitude the decrease of the WP

productivity due to the TC increase would be proportionally less than at lower altitude.

Many agroforestry researchers have studied the effect of TC on the production of the plants cultivated in the understorey. Studies analysing the effect of different TC levels on forage production (Power et al., 2001; Silva-Pando et al., 2002; Dodd et al., 2005; Devkota et al., 1998) found results that can be compared with those obtained here (Annex L). The cited studies come from New Zealand or the oceanic Spain, where the temperate, rainy climate and the type of grassland species (cool-season C3 species) are not very different from those in our study. The variability of the results shown in Annex L is rather high owing to the differences in the understorey and overstorey considered. However, the curves generally show a linear decrease in forage production, amounting to 24%–48% at a TC of 25% and to 40%–68% at a TC of 50%. The curves of the WPs studied here fall within these ranges but tend to occupy a higher position (relatively low percentage reduction) with TC up to 25% and a lower position (relatively high percentage reduction) at higher TC. This is probably due to the observed worsening of the species composition occurring in semi-natural WPs as TC increases. This aspect seems to differentiate semi-natural WPs, where the species composition can change depending on wood density, from artificial agroforestry systems, where the sown herbaceous understorey remains the same at all wood densities.

#### 4.3. Implications for planning and management

In recent years, grazed woods were in most cases excluded from both territorial planning and real utilisation. Re-proposing wood grazing would mean performing opportune planning studies and appropriate concrete actions. As for planning, the most important aspect is identifying suitable areas at the regional and local levels. Wood surfaces with TC less than 75% and close to active summer farms could be identified with the aid of orthophotos and CHM maps and the information on the distribution of the still active summer farms. Local planning by technicians should check the suitability of identified surfaces especially by field-checking the presence of grassland species in the wood understorey and the proximity/accessibility to the close summer farms. With reference to the EU agri-environmental measures, the identified surfaces could be proposed for inclusion in the list of the “Established local practices in case of permanent grassland” which are eligible for financial support.

Concrete actions of grazed wood recovery can be implemented only where enough grassland species are present in the wood understorey and could include:

- the reactivation of grazing with suitable times, animal type and stocking. Using hardy cattle breeds that primarily feed on raw forages is particularly important. A significant risk of WP abandonment arises from the use of highly productive, heavy cattle breeds which typically require a large amount of concentrate feed, making them neither well suited nor inclined to grazing in wooded areas;
- the reduction of the abundance of distasteful (thorny or poisonous) species to intermediate levels able to allow both a correct animal feeding and the protection of young trees necessary for the regeneration of the tree layer;
- the creation of surfaces with different tree cover density also by cutting trees in case of too high density and reducing the abundance of nitrophilous and distasteful species establishing at the cut areas.

## 5. Conclusions

Recent studies have highlighted the environmental and pastoral value of WPs, leading the scientific community and technicians to recognise it after decades of disavowal. In some cases, this has induced public administrations to extend financial support to these ecosystems within the rural development plans. This study aimed to evaluate the

biodiversity and agricultural importance of WP in relation to the tree-cover level, as this is a crucial aspect differentiating the wood-pasture types and the wood density is often used to weigh the amount of financial contribution from public funds.

This study confirmed the high biodiversity value highlighted in other studies. In addition to being richer in mosses, which are usually absent in open grassland vegetation, WPs contain more vascular species than open pastures and dense woods. In this study, approximately 11% of the surveyed species (37 out of 329) were present under intermediate tree covers (LDWP and MDWP) but not in open pastures and dense forests. The high number of microsites due to the presence of individual or groups of trees and shrubs within grassland areas explains most of this biodiversity. However, an important reason is that grazing among trees and shrubs is more difficult and occurs more extensively than in open pastures. Furthermore, agricultural practices for grassland improvement (e.g. fertilisation and removal of weeds and grazing residues) are complicated to perform and are usually not implemented. Based on these considerations, WPs may be considered refuge areas for extensive grassland species, which often disappear in more intensively managed open pastures.

In more detail, the study found that WPs with up to 50% TC support the highest number of species and have a significant abundance of grassland species and therefore high pastoral value. Biodiversity remains important in areas with 50%–75% tree cover; however, the abundance of grassland species decreases, and the proportion of bare soil, mosses and lichens is higher.

Based on these findings, it is strongly recommended that WPs receive greater support at the EU regulatory level, e.g. with better recognition in the Habitat Directive and enhanced subsidies within the agricultural and nature conservation policy.

Practical conservation and restoration of WPs is possible and may be easy in many alpine summer pastures which often include traditionally WP surfaces which are used when forage production in open pastures is insufficient. Supporting the maintenance and recovery of WPs would, however, involve providing financial assistance especially to shepherds who practice wood grazing with suited cattle breeds, in easily accessible areas that have been grazed in the past and where diverse grassland species still exist.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2026.181422>.

#### CRedit authorship contribution statement

**Marco Santacà:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Matteo Gecchelin:** Investigation, Formal analysis. **Michele Scotton:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization.

#### Funding

The research was funded by the European Union Next-Generation EU (Piano nazionale di ripresa e resilienza (PNRR)—Mission 4 Component 2 (Investment 1.4—D.D. 1032 17/06/2022, CN00000022—Project Agri-tech, Spoke 7 Task 7.1.2., CUP C93C22002790001 and Investment 1.5—D.D. 1058 23/06/2022, ECS.00000043—Consortium iNEST, Interconnected Nord-Est Innovation Ecosystem—Spoke 1, Research Topic 2, CUP I43C22000250006)). The views and opinions expressed are solely those of the authors and do not necessarily reflect those of the European Union, nor can they be held responsible for them.

#### Declaration of competing interest

Authors have no competing interests to declare.

#### Data availability

The data are included in the supplementary material

#### References

- Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62, 245–253.
- Bakker, J.D., 2024. Applied multivariate statistics in R. Available at <https://uw.pressbooks.pub/appliedmultivariatestatistics>. (Accessed 3 January 2025).
- Bartolucci, F., Peruzzi, L., Galasso, G., Albano, A., Alessandrini, A., Ardenghi, N.M.G., Astuti, G., Bacchetta, G., Ballelli, S., Banfi, E., Barberis, G., Bernardo, L., Bouvet, D., Bovio, M., Cecchi, L., Di Pietro, R., Domina, G., Fascetti, S., Fenu, G., Festi, F., Foggi, B., Gallo, L., Gottschlich, G., Gubellini, L., Iamónico, D., Iberite, M., Jiménez-Mejías, P., Lattanzi, E., Marchetti, D., Martinetto, E., Masin, R.R., Medagli, P., Passalacqua, N.G., Peccenini, S., Pennesi, R., Pierini, B., Poldini, L., Prosser, F., Raimondo, F.M., Roma-Marzio, F., Rosati, L., Santangelo, A., Scoppola, A., Scortegagna, S., Selvaggi, A., Selvi, F., Soldano, A., Stinca, A., Wagensommer, R.P., Wilhelm, T., Conti, F., 2018. An updated checklist of the vascular flora native to Italy. *Plant Biosystems* 152 (2), 179–303.
- Bergmeier, E., Petermann, J., Schröder, E., 2010. Geobotanical survey of wood-pasture habitats in Europe: diversity, threats and conservation. *Biodivers. Conserv.* 19, 2995–3014.
- Borcard, D., Gillet, F., Legendre, P., 2018. *Numerical Ecology With R*. Springer, second edition. Springer.
- Cavallero, A., Aceto, P., Gorlier, A., Lombardi, G., Lonati, M., Martinasso, B., Tagliatori, C., 2007. *I tipi pastorali delle Alpi piemontesi*. Alberto Perdisa Editore, Bologna (467 pp.).
- Chianucci, F., Macek, M., 2023. hemispher: An R package for fisheye canopy image analysis. *Agric. For. Meteorol.* <https://doi.org/10.1016/j.agrformet.2023.109470>.
- Cosic, Ph., 1987. Une méthode de diagnostic pastoral: de la composition de la végétation à la charge animale à préconiser. In: *Bornard A. e Dubost M. (curatori). Exploitation de pelouses et landes subalpines par des bovins et des ovins. Compte-rendu de recherche No 211*. Cemagref.
- Del Favero, R., 2004. *I boschi delle regioni alpine italiane*. Cleup, Padova (ISBN 88-7178-891-5).
- Devkota, N.R., Kemp, P.D., Valentine, I., Hodgson, J., 1998. Performance of perennial ryegrass and cocksfoot cultivars under tree shade. *Proceedings Agronomy Society of New Zealand* 28, 129–135.
- Dinno, A., 2024. dunn.test: Dunn's Test of Multiple Comparisons Using Rank Sums. R package version 1.3.6. <https://CRAN.R-project.org/package=dunn.test>.
- Dodd, M.B., McGowan, A.W., Power, I.L., Thorrold, B.S., 2005. Effects of variation in shade level, shade duration and light quality on perennial pastures. *N. Z. J. Agric. Res.* 48 (4), 531–543.
- Fox, J., Weisberg, S., 2019. *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. <https://www.john-fox.ca/Companion/>.
- Gillet, F., Murisier, B., Buttler, A., Gallandat, J.D., Gobat, J.M., 1999. Influence of tree cover on the diversity of herbaceous communities in subalpine wooded pastures. *Appl. Veg. Sci.* 2, 47–54.
- Gillet, F., Besson, O., Gobat, J.-M., 2002. PATUMOD: a compartment model of vegetation dynamics in wooded pastures. *Ecol. Model.* 147, 267–290.
- Kallenbach, R.L., Kerley, M.S., Bishop-Hurley, G.J., 2006. Cumulative forage production, forage quality and livestock performance from an annual ryegrass and cereal rye mixture in a Pine–Walnut Silvopasture. *Agroforestry Systems* 66, 43–53.
- Klapp, E., 1971. *Wiesen und Weiden*, 4. Auflage. Paul Parey, Berlin.
- Klotz, S., Kühn, I., Durka, W., 2002. BIOLFLOR - Eine Datenbank zu biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde* \*38\*: 1-333. (Bundesamt für Bonn, Bundesamt für Naturschutz). Indicator value for grassland species. Available at <https://www.ufz.de/index.php?en=38567> (accessed 09.07.2023).
- Königer, L., Schleicher, A., Mosandl, R., 2005. Die Waldweide im Bergwald des nördl. Alpenraums: Interessenkonflikte, wissenschaftliche Erkenntnisse und Konfliktlösungsansätze. *Jahrbuch des Vereins zum Schutz der Bergwelt (München)*, 70. Jahrgang, pp. 151–175.
- Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmli, W., Nobis, M., Rudmann-Maurer, K., Schweingruber, F.H., Theurillat, J.-P., Urmi, E., Vust, M., Wohlgenuth, T., 2010. *Flora indicativa. Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. Ecological indicators values and biological attributes of the flora of Switzerland and the Alps (2nd ed.)*. Editions des Conservatoire et Jardin botaniques de la Ville de Genève Haupt Verlag, Bern - Stuttgart - Wien.
- Liss, B., 1987. *Versuche zur Waldweide. Der Einfluß auf Verjüngung, Bodenvegetation und Boden im Bergmischwald unter Berücksichtigung der Einwirkung des Schalenwildes*. Dissertation an der LMU, München.
- Mahr, S., 2025. *European larch, Larix decidua*. <https://hort.extension.wisc.edu/articles/european-larch-larix-decidua/> (accessed on 15/6/2025).
- Mayer, A.C., Stöckli, V., Konold, W., Estermann, B.L., Kreuzer, M., 2002. Effects of grazing cattle on subalpine forests. In: *Bottarin, R., Tappeiner, U. (Eds.), Interdisciplinary Mountain Research*. Blackwell Verlag GmbH, Berlin, Wien, pp. 208–218.
- Mayer, A.C., Stöckli, V., Konold, W., Kreuzer, M., 2003. Hat die Waldweide eine Zukunft? Ein interdisziplinäres Projekt in den Alpen. *Schweiz. Z. Forstwes.* 154 (5), 169–174.

- Mayer, A.C., Stöckli, V., Gotsch, N., Konold, W., Kreuzer, M., 2004. Waldweide im Alpenraum. Neubewertung einer traditionellen Mehrfachnutzung. Schweizerische Zeitschrift für Forstwesen 155 (2), 38–44.
- Mayer, A.C., Stöckli, V., Huovinen, C., Konold, W., Estermann, B.L., Kreuzer, M., 2005. Herbage selection by cattle on sub-alpine wood pastures. For. Ecol. Manage. 181, 39–50.
- McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297.
- Moreno, G., 2008. Response of understorey forage to multiple tree effects in Iberian dehesas. Agric. Ecosyst. Environ. 123, 239–244.
- Müller, M., Faas, J., Pfadenhauer, J., 2013. Einfluss der Überschirmung auf die Vegetation von Almweiden in den Bayerischen Alpen Influence of the tree canopy cover on the ground vegetation of wooded mountain pastures in the Bavarian Alps. Anliegen Natur 5, 12–24.
- Nair, V.D., Haile, S.G., Michel, G.-A., Nair, P.K., 2007. Environmental quality improvement of agricultural lands through silvopasture in southeastern united states. Scientia Agricola (Piracicaba, Braz.) 64 (5), 513–519.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., Fitz John, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlenn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2024. vegan: community ecology package. R package version 2.6–8. <https://CRAN.R-project.org/package=vegan>.
- Oldén, A., 2016. Plant biodiversity in boreal wood-pastures. Impacts of grazing and abandonment. In: Jyväskylä Studies in Biological and Environmental Science. University of Jyväskylä, p. 318.
- Pike, N., 2011. Using false discovery rates for multiple comparisons in ecology and evolution. Methods Ecol. Evol. 2 (3), 278–282.
- Pittarello, M., Lonati, M., Ravetto Enri, S., Lombardi, G., 2020. Environmental factors and management intensity affect in different ways plant diversity and pastoral value of alpine pastures. Ecol. Indic. 115, 106429.
- Plieninger, T., Hartel, T., Martin-Lopez, B., Beaufoy, G., Bergmeier, E., Kirby, K., Montero, M.J., Moreno, G., Oteros-Rozas, Uytvanck, J.V., 2015. Wood-pastures of Europe: geographic coverage, social-ecological values, conservation management, and policy implications. Biol. Conserv. 190, 70–79.
- Pornaro, C., Schneider, M.K., Macolino, S., 2013. Plant species loss due to forest succession in Alpine pastures depends on site conditions and observation scale. Biol. Conserv. 161, 213–222.
- Power, I.L., Dodd, M.B., Thorrold, B.S., 2001. Deciduous or evergreen: does it make a difference to understorey pasture yield and riparian zone management? Proceedings of the New Zealand Grassland Association 63, 121–125.
- QGIS.org, 2003. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.org>.
- R Core Team, 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rich, P.M., 1989. A manual for analysis of hemispherical canopy photography. In: Los Alamos National Laboratory Report LA-11733-M.
- Roberts, D.W., Cooper, S.V., 1989. Concepts and techniques of vegetation mapping. In: Land Classifications Based on Vegetation: Applications for Resource Management. USDA Forest Service GTR INT-257, Ogden, UT, pp. 90–96.
- Rösch, K., 1992. Einfluß der Beweidung auf die Vegetation des Bergwaldes. Nationalpark Berchtesgaden, Forschungsbericht, p. 26.
- Rupp, M., 2013. Beweidete lichte Wälder in Baden-Württemberg: Genese, Vegetation, Struktur, Management. Inaugural-Dissertation zur Erlangung der Doktorwürde der Fakultät für Umwelt und Natürliche Ressourcen der Albert-Ludwigs-Universität Freiburg i. Brsg.
- Rupp, M., Michiels, H.-G., 2020. Waldweide im Waldnaturschutz Wood pasture in forest nature conservation. Standort.wald 51, 153–172.
- Ružicka, M., 1958. Anwendung mathematisch-statistischer Methoden in Geobotanik (Synthetische Bearbeitung von Aufnahmen). Biologia (Bratisl.) 13, 647–661.
- Semchenko, M., Lepik, M., Götzenberger, L., Zobel, K., 2012. Positive effect of shade on plant growth: amelioration of stress or active regulation of growth rate? J. Ecol. 100, 459–466.
- Sicuriello, F., Ferretti, F., Colangelo, P., De Cinti, B., 2024. Compositional and ecological diversity of Cansiglio forest (Friuli Venezia Giulia, Italy). Vegetation Classification and Survey 5, 225–236.
- Silva-Pando, F.J., Gonzalez-Hernandez, M.P., Rozados-Lorenzo, M.J., 2002. Pasture production in a silvopastoral system in relation with microclimate variables in the Atlantic coast of Spain. Agrofor. Syst. 56, 203–211.
- Spatz, G., Weis, G.B., 1983. Der Futterertrag der Waldweide Vortrag gehalten am 8. Juli 1982 im Kloster Irsee Kaufbeuren anlässlich des Fachseminars "Waldweide und Naturschutz". Ber. ANL 7, 174–178.
- Taiz, L., Zeiger, E., 2010. Plant Physiology, 5th edition. Sinauer Associates Inc., Sunderland. (782 pp.).
- Wider, S., Zemp, D.C., 2025. Bird and hoverfly communities are impacted by vegetation heterogeneity in wood-pastures in the Swiss Jura. Biodivers. Conserv. 34, 2139–2162.
- Ziliotto, U., Scotton, M., Da Ronch, F., 2004. I pascoli alpini: aspetti ecologici e vegetazionali. Quaderni Sozooalpi 1, 11–26.