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Contrasting patterns of tree features, lichen, and plant diversity in managed and abandoned old-growth chestnut orchards of the northern Apennines (Italy)

Giovanna Pezzi[a], Simone Gambini[a], Fabrizio Buldrini[a]*, Fabrizio Ferretti[b], Enrico Muzzi[c], Giorgio Maresi[d], Juri Nascimbene[a]

[a] Department of Biological, Geological, and Environmental Sciences, Università di Bologna. Via Irnerio 42, 40126 Bologna, Italy (giovanna.pezzi@unibo.it, fabrizio.buldrini@unibo.it, simone.gambini2@studio.unibo.it, juri.nascimbene@unibo.it)

[b] CREA Research Centre for Forestry and Wood, v.le Santa Margherita 80, 52100 Arezzo, Italy (fabrizio.ferretti@crea.gov.it)

[c] Department of Agricultural and Food Sciences, Università di Bologna. Viale G. Fanin 44, 40127 Bologna, Italy (enrico.muzzi@unibo.it)

[d] Centre for Technology Transfer, Fondazione Edmund Mach. Via E. Mach 1, I-38010 San Michele all'Adige, TN, Italy (giorgio.maresi@fmach.it)

* Corresponding author; fabrizio.buldrini@unibo.it

Abstract

In mountain regions of southern Europe, old-growth chestnut orchards maintained by traditional management were a key component of the economic, cultural, and ecological heritage. Currently, many stands are abandoned due to decreased economic sustainability even though, according to European policies, the loss of traditionally managed old-growth chestnut orchards should be contrasted to prevent biodiversity loss. In this study, we preliminarily mapped the remnants of old-growth chestnut orchards across a region of the northern Apennines (Italy) with a strong tradition of chestnut orchard cultivation. Then, we assessed the effects of management/abandonment in terms of tree features (e.g. size, crown structure, health conditions), occurrence and abundance of target epiphytic lichens, and richness and composition of understory vegetation. Our results revealed contrasting patterns of tree features, lichen, and plant diversity in managed and abandoned old-growth chestnut orchards of the northern Apennines, supporting the view that traditional management is fundamental for the long-term maintenance of healthy veteran trees, the enhancement of epiphytic lichens related to old-growth conditions, and plant diversity. This indicates that 1000 years of 'chestnut civilization' represent a cultural heritage that benefits nature conservation, promoting a virtuous interplay between human activities and biodiversity. For this reason, policies aimed at sustaining traditional management in old-growth chestnut orchards are indispensable to avoid the degradation and loss of this habitat and its centuries-old cultural and ecological legacy.

Keywords

Castanea sativa; Chestnut diseases; Failure risk assessment; Intermediate disturbance hypothesis; *Caliciales*; *Lobaria pulmonaria*

Introduction

In mountain regions of southern Europe, including Italy, *Castanea sativa* Mill. orchards were a key component of the economic, cultural and ecological heritage. Since the early Middle Ages, chestnut orchards provided one of the main staple foods (Pitte, 1986; Conedera et al., 2004; Squatriti, 2013), and influenced the lifestyle of mountain people, leading to a phenomenon called 'chestnut civilization' (Gabrielli, 1994; Arnaud et al., 1997; Conedera et al., 2004). These anthropogenic woods modelled the landscape and were maintained by traditional management, including mowing, grazing, and tree pruning.

Although a first decline coincided with the eighteenth-century Little Ice Age, on Italian mountains the massive abandonment of many chestnut orchards occurred after the mid-20th century. After World War II, strong social-economic changes caused an exodus towards cities, provoking the loss of traditional cultivation and lifestyles (Arnaud et al., 1997; Conedera and Krebs, 2008; Bounous, 2014). Besides these social dynamics, pests and pathogens acted as disturbance factors with both direct and indirect effects, i.e. influencing perceptions and attitudes of chestnut growers towards the cultivation (Turchetti et al., 2012). In the middle of the 20th century, the spread of *Cryphonectria parasitica* (Murr.) Barr, the agent of chestnut blight, forced the abandonment of many stands, which then started to evolve as mixed woods (Mondino, 1991; Romane et al., 1995; Arnaud et al., 1997; Paci et al., 2000; Conedera et al., 2001). In Italy, since the beginning of the 20th century, chestnut orchards have decreased by about 90%, from more than 608.000 ha (Vigiani, 1908) to 60.000 ha that are currently cultivated (Bounous, 2014).

According to the conservation polices of the European Union, the loss of traditionally managed old-growth chestnut orchards should be contrasted to prevent biodiversity loss (Arnaud et al., 1997; Piussi and Pettenella, 2000). Old-growth chestnut orchards with semi-natural undergrowth are included in the list of habitats worthy of conservation according to the Council Directive 92/43/EEC. In general, their conservation is likely dependent on moderate, but relatively continuous, traditional management (e.g., Gondard et al., 2001, 2007). In this perspective, they represent a tangible expression of an intangible cultural heritage, and a tight bond between man and forest (see UNESCO Convention) that should be preserved.

Traditionally managed old-growth chestnut orchards may host species-rich plant communities (Gondard et al., 2001; Barbati and Marchetti, 2005), including species of conservation concern, such as several orchids or species related to dry grasslands, which may be threatened by abandonment. While management intensification (i.e. frequent mowing) is unlikely to occur due to the scarce economical value of this cultivation, abandonment is expected to drive major changes in plant community composition and richness (Nascimbene et al., 2014, 2016).

In old-growth chestnut orchards, the occurrence of veteran trees provides refugia to organisms that depend on this virtually missing habitat across European forests (Krebs et al., 2008). This is the case for epiphytic organisms that require long ecological continuity, in particular the forest lichen *Lobaria pulmonaria* (L.) Hoffm. In Italy, chestnut orchards are among the main habitats for this species, often hosting luxuriant populations (e.g. Matteucci et al., 2012) that were likely originated by propagules from the surrounding beech or oak forests. However, contrary to surrounding forests that may have been intensively exploited, chestnut orchards provide more suitable ecological conditions for this lichen. At the tree level, tree features (e.g. size, age, health conditions) are the main drivers for these species, while at the stand level forest management is the main driver with contrasting effects. Intensive management is usually highly detrimental, while abandonment of management leading to closed canopy stands may also negatively affect this species (Nascimbene et al., 2013a, 2013b, 2016; Brunialti et al., 2015). Besides local factors, also landscape features may influence the occurrence and abundance of this lichen, whose dispersal is mainly related to vegetative propagules over relatively short distances (Löbel et al., 2009). Due to its peculiar ecology and its easy detectability it is considered a valuable indicator of forest sites that host high lichen diversity and species of conservation concern (Nascimbene et al., 2010). Among these, species belonging to the order *Caliciales* are associated with old-growth stands characterized by long ecological continuity (Selva, 1994; Brunialti et al., 2015).

In this study, we preliminarily mapped the remnants of old-growth chestnut orchards across a region of the northern Apennines with a strong tradition of chestnut orchard cultivation. Then, we assessed the effects of management/abandonment in terms of tree features (e.g. size, crown structure, health conditions), occurrence and abundance of target epiphytic lichens (*L. pulmonaria*, *Caliciales*), and richness and composition of understory vegetation. Due to the low intensity practices applied in managed orchards, we expect trees to have different and healthier conditions compared to abandoned orchards. Moreover, we expect to find more suitable conditions for *L. pulmonaria* in managed compared to abandoned orchards, and more diverse and richer plant communities that also include species of conservation concern related to semi-open habitats. Finally, we expect that the abundance of *L. pulmonaria* could be a reliable indicator of species related to old-growth stands, as in the case of the lichens belonging to the *Caliciales*.

Materials and Methods

Study area

The study was carried out in a 1935 km^2 area that includes the chestnut belt of the Apennines between Bologna and Modena (centroid 44.2561645 N, 10.9453453 E; Fig. 1a). Its altitudinal range is about from 300 up to 1000 m a.s.l., from the deciduous *Quercus*-dominated forests to the *Fagus sylvatica* belt (Ubaldi et al., 1993). Chestnut orchards cover only 2% of this area and are closely linked to the local tradition and cultural heritage (Pezzi et al., 2019). Traditional management was carried out by regular mowing (twice or thrice a year) and pruning of trees, sometimes topped. Contrary to other Mediterranean areas, fire and *slupatura* (burn inside the trunk cavities and mechanical removal of damaged wood) were rarely used to sanitize decayed trunks (Fenaroli, 1946; Seijo et al., 2017, 2018). Burrs and pruned branches (and even leaves, when they were not used for other purposes) were generally removed, burned in single burning places with localized and controlled fires.

Thanks also to specific quality trade-marks and promotion initiatives, only *marroni* (i.e. the top quality fruits) have benefitted from a renewed interest in chestnut cultivation since the 1980s (Pezzi et al., 2017). In these forests, ink disease caused by *Phytophthora cambivora* (Petri) Buism. has been recorded since the last century and initially caused great concern about the survival of chestnut orchards due to the rapid spread of its attacks (Quattrocchi, 1938). Chestnut blight caused by *Cryphonectria parasitica* occurred for the last seventy years but has been controlled by the natural spread of hypovirulence (Turchetti et al., 2008). Asian chestnut gall wasp (*Dryocosmus kuriphilus* Yasumatsu) was first reported in 2007 and its parasitoid *Torymus sinensis* Kamijo was first released in 2010 (Vai et al., 2014).

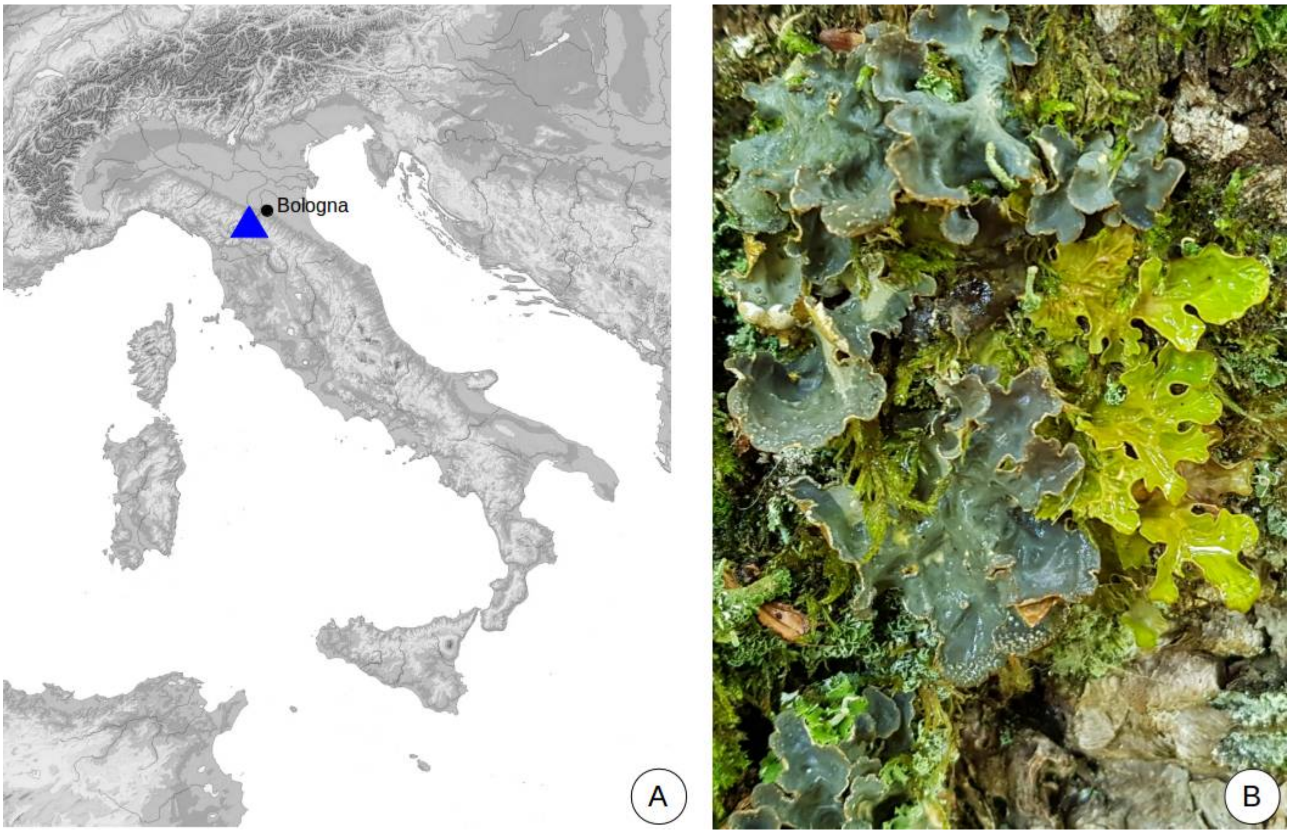


Figure 1. a) Location of the study area (blue triangle) within Italy; b) thalli of *Lobaria pulmonaria* (L.) Hoffm. (grey-green to grey-brown, on the right) and *Lobarina scrobiculata* (Scop.) Nyl. (blue-

grey, on the left) on the trunk of a veteran chestnut tree (the thalli are wet); view of an old-growth managed (c) and abandoned (d) chestnut stand. Photographs taken by G. Pezzi, July 2018 (a, b, c), and G. Maresi, July 2018 (d). [2-column fitting image, colour online only]

Sample selection

As the pattern of old-growth chestnut orchards was largely misunderstood and spatial information was almost lacking, we preliminarily conducted informal interviews to map old-growth stands within the study area (January 2017 to April 2018). We first turned to people in charge of chestnut associations, then to owners/managers and local experts. New contacts were added via snowball sampling (Hislop et al., 2004; Tongco, 2007). We stopped when no additional suitable stands were identified, or when the same stand had been previously mentioned. In total, 48 people were interviewed. These were asked to inform us of chestnut stands at least 0.2 ha wide and with a majority (> 70%) of trees with a diameter at breast height (DBH) at least of 1 m. Despite the lack of a strong correlation between diameter and age for these formations, according to the current literature a chestnut tree with a DBH of about 1 m is centuries old (Krebs et al., 2005; Temel et al., 2009). Preliminary surveys were carried out to check the congruence of the sites with the required standard. Then, each chestnut stand was mapped in QGIS 3.4 (www.qgis.org) by visual interpretation of current digital orthophotographs coupled to a forest map. Overall, 20 old-growth chestnut orchards were mapped. Their surface varied between 0.2 to 4.4 ha (Table 1), mainly with a northern aspect, at an altitude ranging between 600 and 1030 m. Slope was on average 18.3° (± 12.1°). Canopy cover was on average 82.5% (± 18.3%). 12 stands were still traditionally managed (11 through mowing, 1 through grazing) and 8 were abandoned (Fig. 1c,d). Furthermore, 17 were multi-varietal stands, while only 3 were mono-varietal stands (*marroni* stands).

The field survey was carried out in June-July 2018 to obtain information on the main tree features, on the occurrence and abundance of target epiphytic lichens (i.e. *L. pulmonaria* and *Caliciales*), and undergrowth vegetation. Each stand was sampled through an 85 m transect, along which 10 chestnut trees were selected and five 5 × 5 m vegetation plots were regularly placed.

Table 1. General features of the 20 old-growth chestnut orchards. For each examined stand, centroid coordinates are given in WGS 84 as reference system.

Stand	Lat. N (°)	Long. E (°)	Extent (ha)	Altitude (m a.s.l.)	Slope (°)	Exposure	Management
ALBE	44.23431569	10.92732514	0.35	820	30	NW	Managed
ALP2	44.13343623	10.88385259	0.40	930	10	NW	
BAL1	44.26506962	11.34018064	0.53	650	20	N	
GAGG	44.24136697	10.99360049	0.56	670	10	NE	
MALA	44.22446988	10.92814309	0.51	900	5	NE	
MART	44.21683909	11.37867011	0.57	730	40	S	
MONT	44.23195568	10.92689686	0.28	800	30	NW	
PIGH	44.22164423	10.93021957	0.20	950	5	W	
SPON	44.13549313	10.89902546	0.35	890	10	NW	
PRIA	44.27244870	11.35271828	0.72	640	20	N	
STAN	44.22920382	10.92679194	0.46	840	10	W	
TRES	44.13208347	10.90276305	0.44	940	30	NW	
ALP1	44.13327507	10.88298493	0.66	890	40	NW	Abandoned
BAL2	44.26424548	11.33968890	0.40	670	30	N	
BURC	44.10592682	10.92572239	4.06	1030	20	S	
POGG	44.10400122	10.92358048	4.39	1015	25	S	
POR1	44.13296076	11.09445196	0.55	860	0	NW	
POR2	44.13339436	11.09565897	0.57	870	5	NE	
SERR	44.21515106	11.09893862	1.60	670	10	NE	
TORR	44.32923316	11.04493297	1.04	600	15	NW	

Assessment of tree features

For each selected tree, DBH, tree height, crown insertion and size were measured (Klamkin, 1971, 1976). A measuring tape was used for diameters, while a Vertex III Haglof hypsometer was adopted to measure height and crown insertion. The visible crown extension in each of the four cardinal directions was measured by vertically looking up. Then vitality, presence of diseases, structural condition and failure risk were evaluated. Vitality was expert-based assessed on crown condition (Turchetti et al., 2012), adopting the following scale: vigorous plant, slightly suffering, suffering, declining, dead. The three main diseases of chestnut were considered in the evaluation of healthy status. Chestnut blight was assessed by counting the number of healing, healed, virulent, and intermediate cankers on the crown and trunk (see Turchetti et al., 2008). Each tree was assigned to one of the following two levels: predominance of hypovirulent (healing and healed cankers), or virulent infections. Ink disease was evaluated considering three classes: no symptoms, early symptoms (rarefied foliage and small and yellowing leaves), dead tree with completely dead crown and brown flames from collar. We also recorded old and recent attacks. Asian chestnut gall wasp (hereafter ACGW) was assessed by means of an inspection of the crown. Four levels of parasite presence were adopted: no galls observed, from 1 to 10 galls, from 11 to 100 galls, more than 100 galls (heavy infestation). When possible, up to 5 galls were collected and opened to assess the presence of the parasitoid *Torymus sinensis*, whose occurrence was recorded.

The state of preservation of the trees was assessed considering the presence of damages and structural defects (see Table 2) in different parts of the trees (crown, trunk and collar), following the indications reported by the International society of Arboriculture (Smiley et al., 2017). The level of damage and related failure risk was assessed by adapting the risk classes reported by Smiley et al. (2017): low risk (no damage); moderate risk (low level of damages, management needed); high risk (medium degree of damages, problems for tree stability and need of management); extreme risk (high degree of damages, tree stability strongly affected and few or no possibilities of management).

Table 2. Summary of structural defects considered in assigning score of damage to the single parts of the trees (crown, trunk and collar).

Tree part	Defect type
Crown	Asymmetry, dead branches, old or recent pruning wounds, other wounds, decaying wood with rot and/or cavities, fruiting bodies
Trunk	Leaning, wounds, decaying wood with rot and/or cavities (% of diameter), fruiting bodies
Collar and root	Wounds, decaying wood with rot and/or cavities (% of diameter), fruiting bodies, excavation or soil movement in the root area, soil cracking

Lichen and plant survey

On each selected tree, the surface covered by *L. pulmonaria* was assessed from the base up to the crown insertion as a proxy for its abundance. The total extent occupied by the species (hereafter abundance) was obtained as a sum of the areas of the thalli occurring on each trunk. The area of each thallus was calculated as the product of the two major axes of the thallus measured by a ruler positioned on a pole (Benesperi et al., 2018). The occurrence of all the lichen species belonging to *Caliciales* was recorded in a north-exposed 30 × 180 cm plot placed with its shorter side at the base of the trunk. In each of the five 5x5 m plots placed along the transect, the occurrence of all vascular plant species was recorded. Nomenclature of lichens follows Nimis (2016), while for plants it follows Pignatti et al. (2017-2019).

Data analysis

We used Canonical Discriminant Analysis (*candisc* package; Friendly and Fox, 2017) to test the effect of management/abandonment on tree features: DBH, crown size, crown insertion, height, vitality, structural defects and failure risk.

We tested the effect of management/abandonment, tree DBH (mean value at the stand level), and the landscape composition (500 m and 3000 m spatial extent) on abundance of *L. pulmonaria* at stand level. Multiple linear regression was performed with a stepwise AIC method for the variable selection (*vegan* package; Oksanen et al., 2019). Landscape composition (i.e. amount of beech, chestnut, and oak woods) was evaluated in 500 m and 3000 m radius circular buffers centred on the centroid of each old-growth chestnut orchard. The Forest Map (scale 1: 10000) of the Emilia-Romagna Region (available at http://ambiente.regione.emilia-romagna.it/it/parchi-natura2000/foreste/le-foreste-dellemilia-romagna/le-foreste-in-emilia-romagna) was used as a source of data for landscape analysis. Furthermore, the capability of *L. pulmonaria* abundance to predict the species richness of *Caliciales* at the stand level was tested using the Spearman's correlation coefficient.

Finally, we tested the effect of management/abandonment on plant species richness and composition. Differences in species richness between managed and abandoned stands was evaluated by Pearson's test. A Non-Metric Multidimensional Scaling (NMDS) based on Bray–Curtis dissimilarity matrix was used to display the pattern of plant species composition (*vegan* package; Oksanen et al., 2019). An Indicator Species Analysis (*indicspecies* package, ver. 1.7.8; De Cáceres 2019) was used to identify species that were overrepresented in managed and in abandoned stands (i.e. indicator species).

All the analyses were performed using R 3.6.1 for statistical computing and graphics (R Core Team, 2019).

Results

Tree features

Two hundred chestnut trees were sampled. The average DBH was 1.3 m (range: 0.7-3.0 m). The most represented diameter classes ranged between 1.00 and 1.70 m (Fig. 2); classes from 1.90 to 3.00 m prevailed in abandoned stands. The average tree height was 9.3 m (range: 4.2-16.7 m), crown insertion 3.3 m (range 1.7-6.0 m) and crown size 221 m^2 (range: 5-570 m^2).

In general, vigorous trees prevailed (Fig. 3a); only 13 dead trees were found, 12 of which in abandoned stands. The good vitality conditions were also related to low levels of damage caused by pests and diseases. Chestnut blight was recorded in 98.5% of the trees (Appendix 1), prevalently with hypovirulent infections; only single and sporadic recent virulent infections were found on the crown. Ink disease was only recorded as old attacks in 8 trees (6 of them already dead) clustered in 5 stands (3 abandoned, 2 managed). ACGW was recorded on 86 trees, with less than 10 galls per tree. Furthermore, 86% of 120 examined galls contained *T. sinensis* larvae.

However, the failure risk ranged from moderate to extreme (Fig. 3b) since all the trees showed some structural problems, mainly related to the presence of wood decay and holes caused by old pruning or other types of wound. Several trees had heavy branches with weak attachment to the trunk.

On the whole (Fig. 4), a positive and significant correlation was found between management and tree height (P = 0.000) and crown size (P = 0.014). In contrast, in abandoned stands trees showed significantly higher values of DBH, defects of the crown, trunk, and collar and failure risk (P = 0.000), while vitality was lower than in managed sites (P = 0.001).

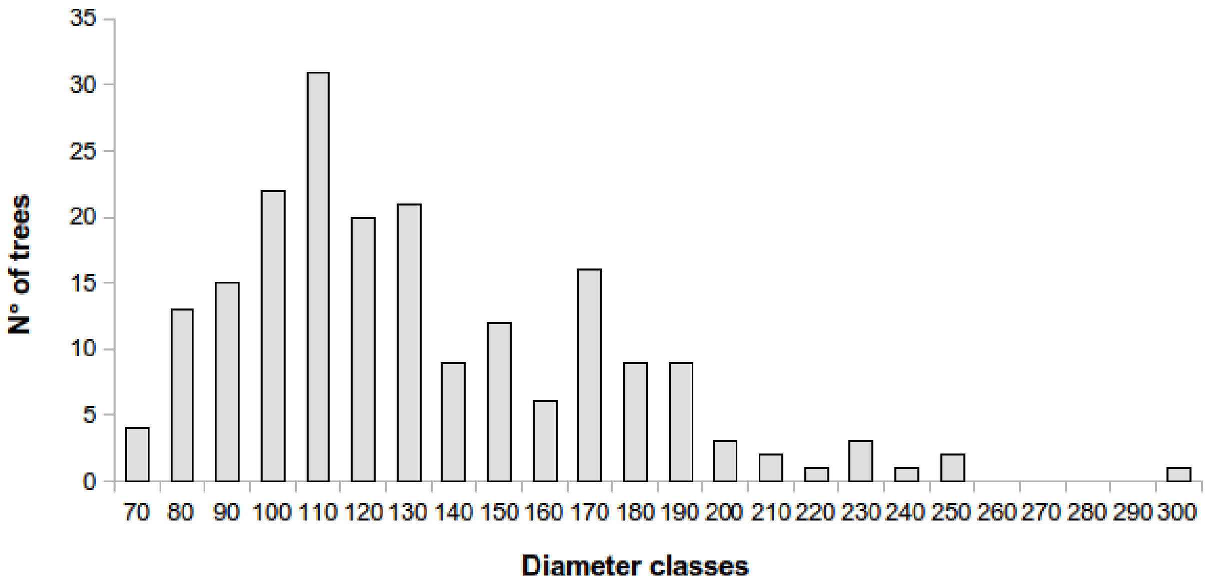


Figure 2. Frequency of the diameter classes of the 200 chestnut trees surveyed. Diameter classes are expressed in cm. [2-column fitting image]

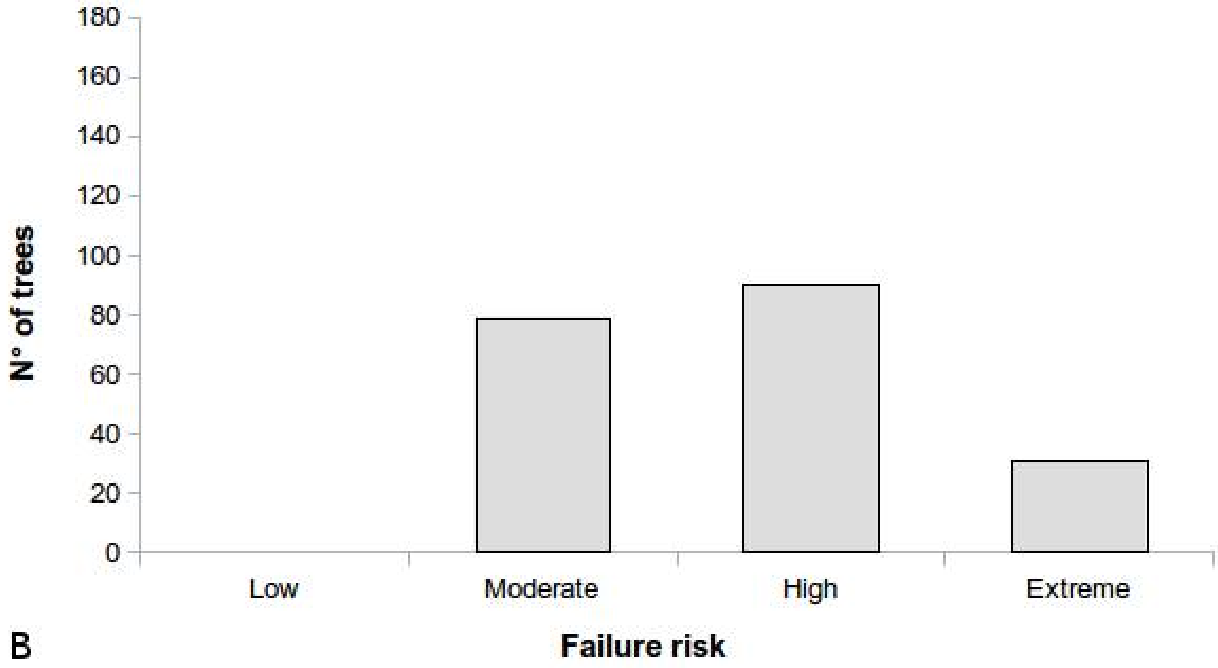
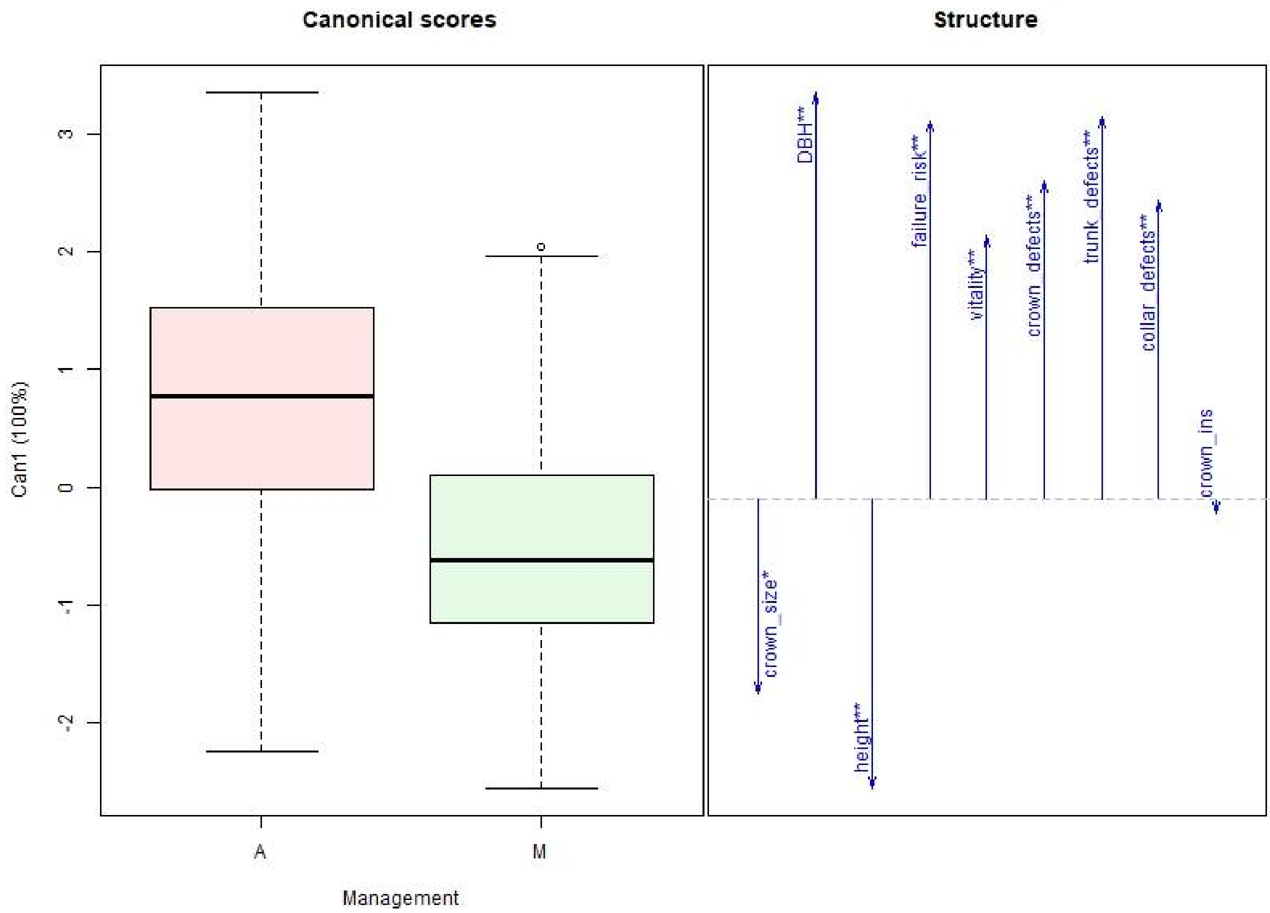


Figure 3. Pattern of vitality (a) and failure risk (b) of the 200 chestnut trees surveyed. [2-column fitting image]

Figure 4. Results of Canonical Discriminant Analysis of features measured for the sampled trees stratified under management conditions (M= Managed, A = Abandoned). Levels of significance: * $P < 0.05$, ** $P < 0.01$. [2-column fitting image; colour online only]



Target epiphytic lichens

L. pulmonaria (Fig. 1b) occurred on 38 trees (DBH = 1.32 ± 0.38 m) clustered in 11 old-growth chestnut orchards (8 managed, see Appendix 2). In two stands the species was found together with its close relative *Lobarina scrobiculata* (Scop.) Nyl. *L. pulmonaria* abundance ranged from 50 to 3800 cm² at the tree level and from 50 to 14505 cm² at the stand level. The abundance of *L. pulmonaria* was only significantly predicted by increasing beech woods in the landscape (Table 3), both at 500 m (P = 0.001) and at 3000 m (P = 0.009) buffers. In the latter model also management was significant (P = 0.029), predicting higher abundance in managed stands.

11 *Caliciales* belonging to the genera *Acolium*, *Calicium*, *Chaenotheca*, and *Chaenothecopsis* were found in 13 stands (Appendix 2). The most common were *Calicium adspersum* (17 records in 10 stands), and *C. salicinum* (12 records in 6 stands). A positive relationship was found between the

number of species belonging to *Caliciales* and the abundance of *L. pulmonaria* (ρ = 0.619, P = 0.0056).

Table 3. Regression models of factors affecting abundance of *L. pulmonaria* at stand level. Model 1 considers habitat amounts at 500 m ring buffer, while Model 2 at 3000 m. M = managed; A = abandoned.

Model		Estimate	Std. Error	t value	Pr(>|t|)
1	(Intercept)	-1.046	11.402	-0.092	0.928
	M/A	24.023	13.450	1.786	0.092
	Beech woods (500 m)	11.859	2.812	4.217	0.001
2	(Intercept)	-97.138	54.789	-1.773	0.095
	M/A	32.081	13.386	2.397	0.029
	Beech woods (3000 m)	3.422	1.162	2.946	0.009

Pattern of plant diversity

Overall, 313 plant species were found. Species richness at the stand level ranged from 32 to 106 species. Some species worthy of conservation were found among orchids: *Cephalanthera longifolia*, *C. rubra*, *Epipactis helleborine*, *Listera ovata*, *Neotinea maculata*, *Platanthera bifolia*, and *P. chlorantha*. Additional species of conservation concern, which are protected at regional level (Regional Law 24-1-1977, n. 2), were *Dianthus armeria*, *D. balbisii* and *Gentiana asclepiadea*. 40 occurrences of these species were recorded in managed stands and 20 in abandoned stands.

Managed stands had a significantly higher species richness than abandoned stands (P = 0.0014). In managed stands, species richness ranged from 72 to 106 species (average: 87.42 ± 3.42), whereas in abandoned stands it ranged from 32 to 88 species (average: 61.25 ± 6.80). The effect of management on plant communities was also confirmed by the pattern of species composition, as indicated by the NMDS plot (stress 0.096, Fig. 5). The Indicator Species Analysis revealed 22 species significantly overrepresented in managed stands and 7 in abandoned stands (Table 4). In managed stands, grassland species prevailed, whereas in abandoned stands wood and pre-forestry species prevailed.

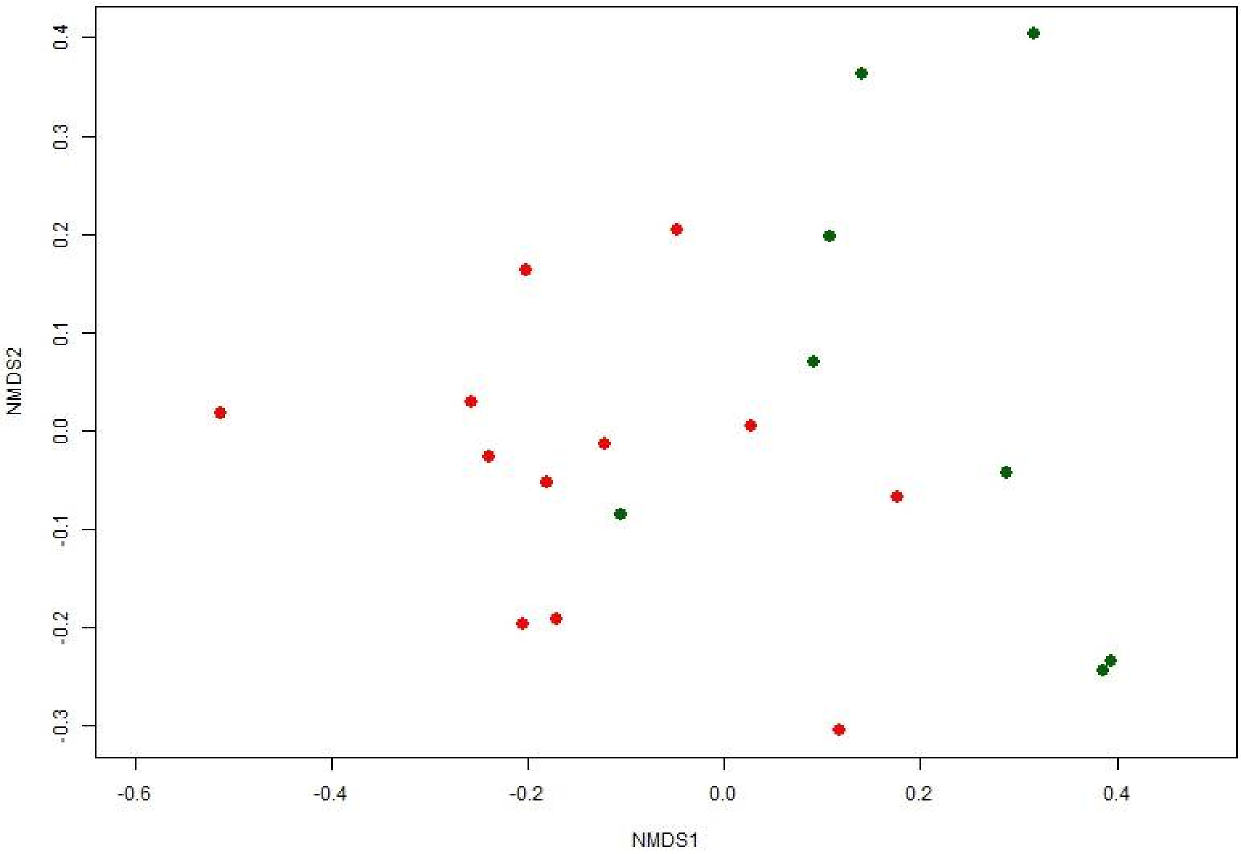


Figure 5. NMDS plot of the plant species composition pattern in managed and abandoned stands. Red dots: managed stands; green dots: abandoned stands. Stress = 0.096. [2-column fitting image; colour online only]

Table 4. List of indicator species for managed and abandoned stands. The *p*-value is also given.

Stand type	**List of species**
Managed	*Anthoxanthum odoratum* and *Lotus corniculatus* ($P < 0.01$), *Lychnis flos-cuculi*, *Holcus lanatus*, *Genista tinctoria*, *Cynosurus cristatus*, *Campanula rapunculus*, *Plantago lanceolata*, *Achillea collina*, *Trisetum flavescens*, *Danthonia decumbens*, *Polygala vulgaris*, *Aira elegantissima, Leontodon hispidus*, *Schedonorus pratensis*, *Taraxacum* gr. *officinale*, *Calluna vulgaris*, *Leucanthemum* gr. *vulgare*, *Trifolium campestre*, *Helianthemum nummularium*, *Rhinanthus alectorolophus* ($P < 0.05$)
Abandoned	*Fraxinus ornus*, *Rosa canina*, *Lactuca muralis*, *Cytisus scoparius*, *Melica uniflora*, *Abies alba*, *Teucrium scorodonia* ($P < 0.05$)

Discussion

Our results revealed contrasting patterns of tree features, lichen, and plant diversity in managed and abandoned old-growth chestnut orchards of the northern Apennines, supporting the view that traditional management is fundamental for the long-term maintenance of healthy veteran trees, the enhancement of epiphytic lichens related to old-growth conditions, and plant diversity.

Our old-growth chestnut orchards survived the three main diseases that are currently quite compatible with tree health. For example, blight damages are low, usually involving only single desiccated branches, and hypovirulence predominated as in other Italian chestnut areas (Turchetti et al., 2008). Also ink disease rarely occurs in the investigated stands, even if the disease remains as a potential risk. ACGW is present only with few galls always parasitized by *Torymus sinensis*, thus confirming the effectiveness of the biological control (Vai et al., 2014). However, in abandoned orchards these reduced damages likely accumulate over the years, producing the spectral aspect of these stands (Turchetti and Maresi, 2008). Moreover, in abandoned stands crown size, and height are lower possibly due to competition with invading trees, while crown, trunk and collar defects due to wood decay are higher. Light reduction, competition and decay are worsened by the age of the plants, producing the failure or the death of the old trees, whose main trunk is often replaced by clones of the same tree (when some roots survive) as if it were coppice. Consistently, our results indicate that in abandoned stands failure risk is significantly higher than in managed stands and overall tree vitality is lower.

In managed orchards the occurrence of veteran trees arranged in an open forest structure and the absence of shoots that cover the trunks may explain the higher abundance of the forest lichen *L. pulmonaria* (Nascimbene et al., 2013) as compared to abandoned stands, where increasing canopy closure and the decay of the more ancient trees coupled with re-sprouting of new shoots around remnant trunks may reduce habitat suitability for this large lichen. In these anthropogenic habitats, the maintenance of the most valuable species is thus related to low intensity, traditional management (Nascimbene et al., 2014). The exclusive occurrence of the declining and red-listed lichen *Lobarina scrobiculata* (Nascimbene et al., 2013c, 2016) and the higher occurrence of *Caliciales* (whose species richness is predicted by the abundance of *L. pulmonaria*) in managed orchards clearly corroborate the importance of these anthropogenic habitats for epiphyte conservation. However, our results also stress the role of landscape composition around the old-growth chestnut orchards, indicating that the abundance of *L. pulmonaria* is maximized in stands embedded in a beech forest-dominated landscape. The huge historical herbarium records, available since the first half of 19^{th} century, suggest a long lasting persistence and a higher commonness of both *L. pulmonaria* and *Lobarina scrobiculata* in our study area (Bertoloni, 1867; Saccardo and Fiori, 1894; Zanfrognini, 1902; see also Appendix 3), where they established luxuriant populations in both beech and chestnut stands (Bertoloni, 1867). In this historical scenario, old-growth beech forests may be considered the primary habitat for these lichens, while anthropogenic chestnut stands likely provided a suitable secondary habitat that allowed their survival when most beech stands were converted to coppice. Frequent disturbance in coppice stands coupled with the absence of old trees and the muffling of the trunks by the excess of shoots may have caused the rarefaction of these lichens in beech stands, while the more stable ecological conditions and the occurrence of veteran trees in old-growth chestnut orchards provided a valuable refuge. In this perspective, the effect of the landscape found in our study may reflect a historical condition in which the old-growth beech forest originally supplied propagules for the establishment of the species in old-growth chestnut orchards that currently are likely the main propagule hot-spots in the mountain forest landscape of the Northern Apennines (Matteucci et al., 2012).

The role of managed old-growth chestnut orchards for biodiversity is also confirmed for plant communities (e.g. Gondard et al., 2001, 2007; Nascimbene et al., 2014), with significantly higher species richness than in abandoned stands. Moreover, our results indicate that the abandonment of management practices (i.e. mowing and/or grazing) triggers compositional shifts that may cause the loss of several species of conservation concern, as in the case of many orchids. In general, plant communities of the managed stands host species related to open habitats (*Molino-Arrhenatheretea* Tüxen 1937 or *Festuco valesiacae-Brometea erecti* Br.-Bl. & Tüxen ex Br.-Bl. 1949), while in abandoned stands pre-forestry and woody species tend to prevail (*Laburno-Ostryion* Ubaldi 1980 and/or *Fagetalia sylvaticae* Pawłowski in Pawłowski, Sokołowski & Wallisch 1928; Ubaldi et al., 1993; Pezzi et al., 2011). Historical records (Bertoloni, 1867) corroborate the view that the floristic composition of managed stands remained almost unchanged for decades, further underlining the role of traditional management for maintaining stable ecological conditions (Tomaselli, 1989).

Conclusions

Our study supports the view that old-growth chestnut orchards are a perturbation-dependent system (Vogl, 1980; Gondard et al., 2001) whose effectiveness for biodiversity conservation depends on the maintenance of low-intensity management. In this perspective, mowing and pruning are still the most effective practices for preserving the old-growth chestnut orchard habitat and its associated biodiversity. However, pruning needs to be light and not frequent, aiming to restore a suitable architectural structure, cutting only dangerous branches and saving biodiversity niches (Zapponi et al., 2017). Topping and heavier pruning used in the past are likely the main causes of the current precarious status of the surviving trees. Moreover, also sporadic fire as a sanitation method or to burn mowed and pruned material should be avoided, since it may negatively impact on long-term soil conservation. Our results indicate that 1000 years of *chestnut civilization* represent a cultural heritage that benefits nature conservation, promoting a virtuous interplay between human activities and biodiversity. For this reason, policies aimed at sustaining traditional and even more sustainable management in old-growth chestnut orchards are indispensable to avoid the degradation and loss of this habitat and its centuries-old cultural and ecological legacy.

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CR CRediT author statement

Giovanna Pezzi, Giorgio Maresi, Fabrizio Ferretti, Simone Gambini, Fabrizio Buldrini, Juri Nascimbene: *Conceptualization, Methodology*

Giovanna Pezzi, Giorgio Maresi, Fabrizio Ferretti, Simone Gambini, Fabrizio Buldrini, Juri Nascimbene: *Data curation*

Enrico Muzzi: *Statistical Analysis*

Giovanna Pezzi, Giorgio Maresi, Juri Nascimbene: *Supervision*

Giovanna Pezzi, Giorgio Maresi, Fabrizio Ferretti, Fabrizio Buldrini, Enrico Muzzi, Juri Nascimbene: *Writing-Original draft preparation*

Giovanna Pezzi, Giorgio Maresi, Fabrizio Ferretti, Fabrizio Buldrini, Enrico Muzzi, Juri Nascimbene: *Writing-Reviewing, and Editing*