



Sweet chestnut forests under black locust invasion threat and different management: An assessment of stand structure and biodiversity

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ABSTRACT

Sweet chestnut forests in Europe are impacted by management abandonment, non-native species invasions and diseases, among other factors. Understanding the effects of these factors is crucial for forecasting future biodiversity changes, as well as proposing appropriate planning and management strategies. We studied sweet chestnut (*Castanea sativa* Mill.) and black locust (*Robinia pseudoacacia* L.) dominated forests within three hilly landscapes (Euganean hills, Montello, and Berici hills) of north-eastern Italy. We surveyed 25 paired sweet chestnut and black locust dominated plots of 100 m² representing coppice or over-aged stands. We collected and analysed data related to vascular plant composition and richness, soil physical features (moisture content, shear strength and penetration resistance), ammonia-oxidising archaea in the soil, and stand structure features. Composition of vascular plants differed significantly between the two forest types, without the influence of management regime. Soil characteristics did not change comparing forest types, management regimes and their interaction, except for soil moisture that was higher in coppice forests. Ammonia-oxidising archaea abundance was lower in sweet chestnut stands. Sweet chestnut and black locust forests have a similar stand structure. The management regime played a role in determining mean diameter, number of stems and deadwood volume. We suggest adopting a heterogeneous array of silviculture practices to achieve the highest variety of forest structures and plant composition in Mediterranean hilly landscapes, coupled with management practices aimed at black locust control.

1. Introduction

Current occurrence, structure and composition of European forests is the result of a long history of human management (Johann, 2004; Kaplan et al., 2009). In particular, sweet chestnut (*Castanea sativa* Mill.) forest distribution and characteristics have been modified by millennia of traditional cultivation, starting from Ancient Greeks, across Romans up to the Middle Ages, when it reached the so-called 'golden age' in Western Europe (Conedera et al., 2004a). This ancient relationship with

traditional human activities makes it hard to trace the sweet chestnut original range and to separate management effects to describe its ecology (Tinner et al., 2000). The decline of the traditional cultivation in Europe started in the early 17th century mainly due to natural (e.g. climatic variation during the Little Ice Age) and social drivers, like the improvement of agriculture cultivation techniques and the rise of the industrial revolution (Conedera et al., 2004a). Industrial demand first caused the progressive over-use of sweet chestnut for charcoal and extraction of tannins, and then the progressive abandonment of forest

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stands, due to changes in industrial production methods. Moreover, the 19th century was marked by the spread of sweet chestnut major diseases, e.g. ink disease, caused by *Phytophthora cinnamomi* Rands, and chestnut blight, caused by *Cryphonectria parasitica* (Murrill) M.E. Barr (Vannini and Vettrai, 2001). Despite the decline of the species, current distribution of sweet chestnut forest in Europe covers an area of >2.5 million hectares (Conedera et al., 2016). Almost 90% of the area is concentrated in a few countries (e.g. France and Italy) with the longest tradition of sweet chestnut cultivation (Conedera et al., 2004b).

Sweet chestnut forests have a long history of management with the application of several silvicultural systems, traditionally coppicing (Manetti et al., 2017; 2020). The most common practices are single coppice (rotation ages between 10 and 20 years) and coppice with standards; but rotation ages as well as number of standards varies between regions (see summary in Manetti et al., 2022) and with changing regulations. However, in many parts of Europe, such as the northwest of Spain, many coppice stands are no longer managed or their rotation periods have been increased (Prada et al., 2020). Indeed, coppicing has shown strong decline in the last decades all over Europe and over-aging, which leads to high forest, may filter out certain plant species (Buckley, 2020) and increase the occurrence of others.

This historical trajectory reflects the great variability of local and regional patterns of stand structure and ecological dynamics of sweet chestnut forests. Current sweet chestnut forests differ (e.g. in growth, stand structure and ecological stability) according to site factors (e.g. elevation, slope and type of soil, Álvarez-Álvarez et al., 2010; Conedera et al., 2021), landscape features (Díaz-Varela et al., 2011), and current and past silvicultural treatments (e.g. Rubio and Escudero, 2003; Marcolin et al., 2020). Indeed, the application of coppicing practices can be influenced by specific environmental conditions and societal needs and, in turn, can shape sweet chestnut forest features (Fabbio, 2016). For example, physical and biological soil characteristics of sweet chestnut forests can be impacted by forestry operations; however, these are not evident after a certain time since the last intervention (Venanzi et al., 2016). Furthermore, several critical issues have been reported for sweet chestnut stands that are no longer managed; for example, changes in carbon use efficiency, slope stability and forest habitat conditions (e.g. Mairota et al., 2016a,b; Vergani et al., 2017; Pérez-Girón et al., 2020).

Sweet chestnut forests have been strongly favoured by humans and, therefore, in many cases, are found where potentially different forest vegetation should be expected. Current biodiversity assemblage can significantly differ with the great variety of sweet chestnut stands (Gondard and Romane, 2005; Pezzi et al., 2011); for example, moving from a mean of 4.5 to 29.7 plant species two years after a simple coppice cut (Gondard and Romane, 2005). In particular, different management regimes correspond to different forest stand structures and, consequently, to different biodiversity assemblages (Gondard et al., 2006; Mattioli et al., 2016; Parisi et al., 2020). Indeed, in the absence of forest management, sweet chestnut may become outcompeted by other species (see Zlatanov et al., 2013). The value of sweet chestnut stands for biodiversity has been recognised by the European Union, which declared both chestnut-dominated forests and long-established chestnut plantations with semi-natural undergrowth, relevant habitats (habitat type: *Castanea sativa* woods, code 9260) for biodiversity conservation (Habitat Directive 92/43/EEC). Indeed, many studies have shown these forests' hold high ecological importance in supporting a wide variety of flora and fauna of conservation interest (e.g. Broome et al., 2011; Guitián et al., 2012; Parisi et al., 2020; Pezzi et al., 2020). Furthermore, the conservation condition of this forest habitat type can be impacted by forestry (Campagnaro et al., 2018a).

Sweet chestnut forests are vulnerable to different non-native tree invasions; for example the wide-spread black locust (*Robinia pseudoacacia* L.) has been reported to threaten these forests through competition and substitution (Benespero et al., 2012; Campagnaro et al., 2018b; 2022) and having different impacts such as reducing native biodiversity and degrading the forest habitat (Lazzaro et al., 2020). Rural and forest

landscapes have witnessed, on the one hand, losses of sweet chestnut forests and, on the other, increase of black locust forests (Bertacchi and Onnis, 2004). Black locust can invade sweet chestnut forests (Benespero et al., 2012) and can outcompete sweet chestnut trees when colonizing abandoned agricultural lands (Sitzia et al., 2012). Furthermore, chestnut blight is considered one important factor favouring the spread of black locust in the early 20th century (Motta et al., 2009). Indeed, important changes in the distribution of these two forest types are expected in the light of future climate scenarios (Kleinbauer et al., 2010; Camenen et al., 2016; Conedera et al., 2021; Puchałka et al., 2021).

Specific research has highlighted reduced plant species richness and a diverse composition when comparing black locust and native forests also dominated by sweet chestnut (Benespero et al., 2012). However, the effects of black locust invasion on native plant communities are still debated, as contrasting results in terms of changes to diversity and composition were found in different studies (e.g. Vítková et al., 2017; Sitzia et al., 2018). Moreover, the compositional variability in invaded sites could thus be driven by changes in environmental and habitat characteristics rather than by the presence of the non-native species *per se* (Campagnaro et al., 2018c). Indeed, this nitrogen-fixing tree can affect the forest soil nitrogen cycle (Cierjacks et al., 2013). Even if microbial communities are essential components of biogeochemical cycles (Falkowski et al., 2008) and represent the vast majority of the earth's biodiversity (Wardle, 2002), different authors have pointed out that the consequences of microbial community structure changes on ecosystem functions and structure deserves more extensive studies (Sherri and Blackwood, 2015; Medina-Villar et al., 2016). Land use changes and anthropogenic disturbances like silviculture can have a significant role on non-native species invasion and on soil biota (Zhong and Makeschin, 2006; Burton et al., 2010; Medina-Villar et al., 2016).

Soil is a fundamental element of forest ecosystems and, therefore, it can provide important information on the impacts of non-native species and management regimes. Among soil microorganisms, a good indicator of soil processes and in particular those related to nitrogen cycles is represented by ammonia-oxidising archaea (AOA) (Leininger et al., 2006; Stevanato et al., 2016). However, they are often overlooked when assessing impacts of black locust on soil cycles (i.e. only few studies on bacterial communities; e.g. Lazzaro et al., 2018) and forest operations. Furthermore, soil physical attributes can provide useful information on the impact of harvesting operations.

This study aims to shed new light on the effects of different management regime intensities on sweet chestnut forests as well as on the differences with forests dominated by the invasive non-native tree black locust. We therefore used an integrative approach comparing vascular plant diversity, soil physical characteristics, ammonia-oxidising archaea in the soil, and stand structure between the two forest types (i.e. one dominated by sweet chestnut and the other by black locust) under different management regimes (i.e. stands managed through coppice systems and stands where management can be considered abandoned as the stands are over-aged compared to usual rotation ages). We hypothesise: (i) a diverse vascular plant richness and composition between the two forest types with management regimes playing a role in shaping these attributes; (ii) a lower ammonia-oxidising archaea abundance under sweet chestnut forests because of the influence of black locust on soil nitrogen cycle; (iii) no differences in soil characteristics (based on the relatively long time since last intervention); (iv) similar stand structure between forest types but different between their management regimes.

2. Methods

2.1. Study area

The study area was the foothills of the Eastern Alps in Italy including the Euganean hills (45° 18' N, 11° 42' E) in the province of Padova, the Montello (45° 49' N, 12° 7' E) in the province of Treviso, and the Berici

hills (45° 26' N, 11° 32' E) in the province of Vicenza (all part of the Veneto region). The study was conducted within the Natura 2000 network that is a system of protected areas within the European Union according to two Nature Directives (79/409/EEC, repealed by 2009/147/EC, and 92/43/EEC).

The Euganean hills cover about 15,000 ha and form a complex landscape that is considered a biodiversity hotspot. They are of volcanic origin and are an isolated hilly system surrounded by the alluvial plain between the Adige and Bacchiglione rivers. The highest hill, Monte Venda, is just over 600 m a.s.l. Both sweet chestnut and black locust trees form widespread forests and were particularly favoured by silviculture and environmental conditions (Sitzia et al., 2010). These hills are part of the Special Protection Area (SPA) and Special Area of Conservation (SAC) “Colli Euganei - Monte Lozzo - Monte Ricco” (Natura 2000 site code: IT3260017).

The Montello is a relatively large (6,000 ha) morainic hill on the northern Venetian plain, lapped to the north and east by the Piave River. It is of very modest height with a mean of 200 m. a.s.l. (maximum of 369 m a.s.l.). In this area silviculture practices, i.e. coppicing for firewood production, have favoured over time both sweet chestnut and black locust forests (Nascimbene et al., 2015). This hill is part of the SAC “Montello” (Natura 2000 site code: IT3240004).

The Berici hills (16,500 ha) are located on the floodplain near the city of Vicenza and their highest peak is 445 m a.s.l. (Monte Lungo). Among the most common forest categories, sweet chestnut forests are relatively common in deep and humid soils; whereas the distribution of black locust forests is relatively limited (Tasinazzo and Fiorentin, 2000). The area is part of the SAC “Colli Berici” (Natura 2000 site code: IT3220037).

In the Veneto region sweet chestnut occurs from 400 m to about 1,000–1,200 m a.s.l. (Masutti and Battisti, 2007). The “*Castanea sativa* woods” habitat type 9260 in Veneto is widespread on the foothills of the Alps, up to the outermost edge of the Dolomites. In the Euganean area and the Montello hills, included within the rural landscape framework, it is mainly found on slopes facing north or east. On these slopes and in deep soil stands with cooler conditions and greater water availability, sweet chestnut forests are populated by species characteristic of mesophilic forests. It is possible to find sweet chestnut forests on south-facing slopes where chestnut trees are associated with markedly thermophilic species.

Today, however, black locust is an important element of the north-eastern pre-Alpine Italian landscape. It is among the most common and abundant invasive non-native plants (Dainese et al., 2014). For example, black locust is the most frequent type of forest in the Euganean Hills, covering 2,080 ha (Sitzia et al., 2010), and in Montello. Black locust frequently occurs in the basal part of the hills and has invaded former grasslands, pastures or forests dominated by native species. Black locust can commonly be found within sweet chestnut and oak stands. Indeed, its presence in sweet chestnut forests is linked to disturbances or degraded conditions (Susmel and Famiglietti, 1968).

2.2. Sampling design and data collection

Comparing nearby invaded and not invaded sites is a commonly applied method to investigate effects of non-native species invasion (Vanderhoeven et al., 2005; Hejda et al., 2009). This approach, as indicated by Walker and Smith (1997), is a proxy to measure impacts driven by an invasive species when a before-after-control-impact design cannot be applied. We used the paired comparison method on sweet chestnut and black locust stands to compare plant communities, soil characteristics, and stand structure of the two different forest types. This paired sampling method was already applied for seeking black locust impacts on several forest types (Sitzia et al., 2012, 2018, 2021; Trentanovi et al., 2013).

A preliminary identification of sweet chestnut and black locust stands was carried out in the GIS environment (QGIS Development

Team, 2018) using the available forest type, habitat type, and forest management maps. These two former maps differentiate patches of forest based on forest type; whereas, the latter provides information on their management and are part of Forest Reorganization Plans (Trentanovi et al., 2018). This information was checked and confirmed in the field. Sweet chestnut and black locust stands of the same pair were chosen within a 700 m radius. The maximum distance between stands of the same pair was respected to obtain comparable stands in terms of land-use type and disturbance regime. A minimum distance of 1 km was set between plots of different pairs to avoid spatial autocorrelation effects. Plots were located at least five metres from stand boundaries to avoid the margin effect. We surveyed 25 pairs of sweet chestnut and black locust stands (Fig. 1). Each plot is a square of 100 m² as suggested by Viciani and Lasen (2016) for vegetation surveys in sweet chestnut forests. Analysis of the basal area contribution of sweet chestnut (mean = 85%) and black locust (mean = 92%) to the stand confirmed the differentiation in the two forest types.

Both forest types are commonly managed as coppices but, especially in recent decades and for sweet chestnut forests, there is a trend towards increasing rotation ages and ceasing management. In the study area, the common practice and regional forestry regulations result in applying a coppice with standards system with a variable number of standards depending on the forest type.

Therefore, stands were assigned to two management regime categories: managed, when the stand was considered to be under a coppice (with standards) system (see Burley et al., 2004); and abandoned, i.e. over-aged (see Harmer and Howe, 2003), when stand age exceeded normal rotation period (hereafter, we call the two management regimes: coppice vs. over-aged). Marcolin et al. (2020) defined sweet chestnut stands with ages > 25 years as over-aged. This age limit was confirmed by the ordinary rotation ages applied in hilly areas of Veneto (e.g. Andrich and Abramo, 2001) and are higher than the prescribed coppicing age for the Veneto region (Regione del Veneto, 2020). Similarly black locust over-aged stands were those > 20 years with reference to the ordinary rotation ages (e.g. Andrich and Abramo, 2001) and are higher than the prescribed minimum coppicing age (Regione del Veneto, 2020). We therefore surveyed 24 coppice (sweet chestnut = 13; black locust = 11) and 26 over-aged stands (sweet chestnut = 12; black locust = 14) (Fig. 1).

Within each plot, all trees (diameter at breast height (DBH) ≥ 5 cm) were identified at species level. Their DBH and height were recorded with the use of a tree caliper and an electronic hypsometer (Vertex IV-360 and Transponder T3). Vegetation surveys were conducted within the squared plot and each vascular species was identified and assigned to a cover class according to the Braun-Blanquet (1964) phytosociological approach. Cover class refers to stand layers that are defined on the basis of plant height as follows: ground layer – species ≤ 1 m tall; shrub layer – species between 1 and 5 m tall; tree layer – species ≥ 5 m tall.

In each stand, three increment cores were collected from representative trees, the largest ones. The number of rings was counted in the laboratory with CATRAS® program (Computer Aided Tree-Ring Analysis System) (Aniol, 1983). We recorded length and diameter for all snags (diameter ≥ 3 cm), length and minimum and maximum diameter for logs and stumps.

Three soil samples were collected in each plot to study differences in the abundance of ammonia-oxidising archaea (henceforth abbreviated as AOA) community mainly related to nitrogen-fixation activities. The abundance of AOA is correlated to their activity (Lu et al., 2015). Soil samples were taken from three representative spots within each stand. A soil corer of 1.5 cm diameter and 10 cm depth was used, litter was removed, and hollows avoided. After collection, tubes were kept open to let samples dry out at room temperature for 10–15 days. Dry soil samples were crushed, stones and other particles removed. Total DNA was extracted from an amount of 0.4 g of dried soil using the Qiagen DNeasy PowerSoil kit as described by the manufacturer's protocol. The extracted DNA was quantified with a Qubit 3.0 fluorimeter (Thermo Fisher

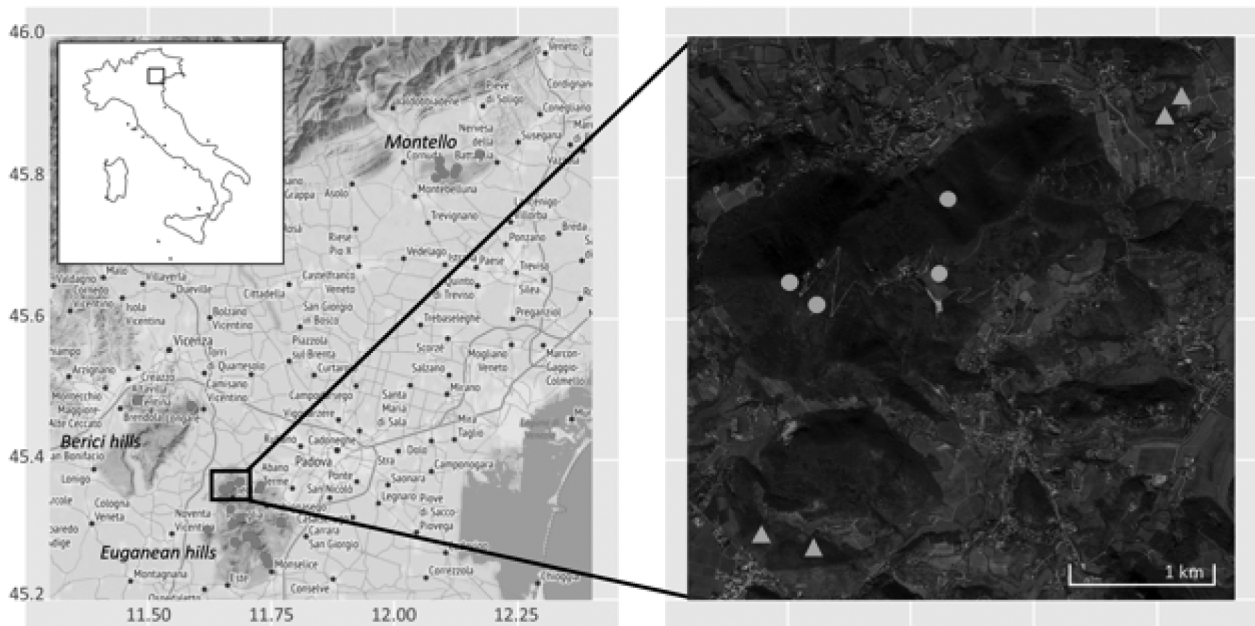


Fig. 1. Distribution of the 25 paired stands (50 plots) within the hilly areas of Veneto in north-eastern Italy (left; background map: map tiles by Stamen Design, under CC BY 3.0.; data by OpenStreetMap, under ODbL). Example of paired plots in the Euganean hills: sweet chestnut dominated plots in orange, black locust dominated plots in green, coppice plots are in triangles and over-aged plots in circles (right; background map: Google maps; Map data ©2015 Google). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Scientific, Carlsbad, CA) using the Qubit™ DNA HS Assay Kit (Thermo Fisher Scientific).

Quantitative Real Time PCR (qPCR) was performed to quantify the ammonia-oxidising archaea gene (*amoA*) from the DNA extracted by soil samples. According to Zanardo et al. (2016), the gene is a reliable marker to detect AOA involved in nitrification. RealTime qPCR was performed in triplicate technical replicates using a QuantStudio 5 system (Life Technologies, Carlsbad, CA, USA). The qPCR reaction volume was equal to 5 µL, 1 µL of purified DNA solution and 4 µL of reaction mix, composed of 1.2 µL PCR-grade water, 0.15 µL each of F and R primers and 2.5 µL Power SYBR Green PCR Master Mix with Taq polymerase (Applied Biosystems, Foster City, CA, USA). The qPCR thermal conditions were set to a pre-denaturing stage at 95 °C for 10 min, followed by 40 cycles with a denaturation step at 95 °C for 15 sec, an annealing step at 57 °C for 60 sec and an extension at 72 °C for 60 sec. A negative control of sterile MilliQ water was run. The Ct threshold cycles were transformed into gene copies using an equation obtained from a calibration procedure as follows. A standard curve was obtained using known amounts of the target gene cloned in a plasmid of known length. Data from PCR amplification were used to calculate the gene copies number of the target based on the Ct value (Zanardo et al., 2016). Briefly, as template for the standard curve, we used the purified recombinant plasmid in which we had cloned the amplicon of the target gene into vector pGem-T (Promega Corp., Madison, WI, USA), inserted into *Escherichia coli* strain JM101 by electroporation and subsequently purified. Knowing the size of the vector (3015 bp) and that of the insert (635 bp) from its literature reference (Francis et al., 2005), upon measuring the plasmid DNA concentration spectrophotometrically (by 260 nm wavelength absorbance), we calculated the number of copies per ng of DNA and the corresponding amounts to be used for each of the quantitative PCR calibration curves that were performed with serially diluted amounts of the purified plasmid-cloned archaeal *amoA* gene. The following interpolative fitting equation $y = 1E + 35x - 21.52$ meant to convert PCR cycle threshold values into number of actual gene copies, was obtained in Microsoft Excel and judged satisfactory for the target quantification, on the basis of its high R^2 value (0.9783). The primers used both for that amplification and for those done in the present report

from DNA extracted from soil were Arch-amoA-F 5'-STA ATG GTC TGG CTT AGA CG-3' and Arch-amoA-R 5'-GCG GCC ATC CAT CTG TAT GT-3' (Francis et al. 2005). The qPCR methodology details, including the forward and reverse primer sequences, are reported by Zanardo et al. (2016).

We also measured soil physical characteristics. We recorded in each plot shear strength as the mean value of 8 measurements on the top 1–2 cm of soil with the scissometer T100 and the penetration resistance as the mean value of 8 measurements on the top 3–5 cm of soil with the penetrometer P100. Soil moisture content was measured with the TDR (Time Domain Reflectance) FieldScout 300 at a 12.8 cm soil depth.

2.3. Data analysis

To analyse vascular plant species diversity, we collated data from the different layers. This allowed us to analyse overall species composition and to compute the total number of species. Cover values were transformed according to Tüxen and Ellenberg (1937). We also used data for AOA and gene abundance by collating data at the plot level. To analyse forest structure we calculated common parameters: living volume, basal area, mean diameter, mean height, number of stems and deadwood volume. Volume of both living trees, standing dead trees and broken-top snags, as done in other works (e.g. Goodburn and Lorimer, 1998; Brunet and Isacson, 2009), was calculated by applying the allometric equations available in Tabacchi et al. (2011). We applied the specific equation of the tree species; where this was not possible, we used the general equation for other hardwoods. Volume of ground logs was calculated using the truncated cone formula. The value for one pair of plots was excluded as in one sweet chestnut forest the overall value was strongly influenced by the presence of two large stumps, making it an important outlier.

All analyses were performed in R statistical software (R Core Team, 2022). Plant species composition was analysed and represented using non-metric multidimensional scaling (NMDS; 'metaMDS' function of the 'vegan' R package) by grouping per origin (sweet chestnut or black locust forests) and management (coppice or over-aged). NMDS was set with Bray-Curtis dissimilarity index and four dimensions. Differences

between forest types, management regimes and their interaction were tested through a non-parametric multivariate analysis of variance with the 'adonis2' function of the 'vegan' R package.

We investigated the species that could be used as indicators of sweet chestnut and black locust forests and of the different management regimes by considering all surveyed plants. We used the Indicator Value that considers species specificity and fidelity (Dufrêne and Legendre, 1997). The analysis was performed using the multipatt function with the 'IndVal.g' association function of the 'indicspecies' package (De Cáceres and Legendre, 2009) that enables indicator species to be associated to specific groups. We grouped composition based on forest type (sweet chestnut or black locust forests) and management regime (coppice or over-aged). We considered indicator species also for the combinations of these groupings. Generalised linear mixed-effect models (GLMMs) and linear mixed-effect models (LMMs) were used to test the effects of forest type and management regime as well as their interaction on biodiversity, stand structure and soil variables. Models included the pair as a random factor to account for spatial dependence in the sampling design. Effects on species richness, shear strength, and penetration resistance were tested through an LMMs applying the 'lmer' function of the 'lme4' package (Bates et al., 2015). To investigate the effects on abundance of AOA (ammonia-oxidising archaea), as data distribution was influenced by the abundance of zero values, we used the 'glmmTMB' function of the 'glmmTMB' package (Magnusson et al., 2021) with a negative binomial distribution. To test differences in stand structural variables (i.e., stand living volume, basal area, mean diameter, mean height, number of stems and deadwood volume), we ran GLMMs using gamma distribution applying the 'glmer' function of the 'lme4' package (Bates et al., 2015). The Anova function (test = χ^2) for LMMs and the Wald t-statistic for GLMMs were used for model comparison. The best-fit model was obtained based on Akaike's information criterion (AIC).

3. Results

3.1. Vascular plant composition and richness

A total of 170 plant species were recorded (overall number of species: sweet chestnut = 120, coppice = 73, over-aged = 92; black locust = 120, coppice = 79, over-aged = 83). The distribution of plots based on species composition is represented in the NMDS ordination (stress: 0.13; Fig. 2) and species composition differed between sweet chestnut and black locust forests ($R^2 = 0.46$, $F = 40.012$, $p < 0.001$). No effect of management regime ($R^2 = 0.01$, $F = 0.911$, $p = 0.43$) or of its interaction

with forest type ($R^2 = 0.01$, $F = 0.903$, $p = 0.402$) was observed. No difference was observed between the composition of coppiced or abandoned coppice of sweet chestnut and black locust forests. Some species of conservation value were observed, such as the orchid *Epipactis helleborine* (L.) Crantz in an over-aged sweet chestnut stand. Interestingly, sweet chestnut, in the tree layer, was found within two black locust forests (mean basal area contribution = 8%); whereas, black locust (mean basal area contribution = 4%) was recorded in six sweet chestnut forests.

Twenty one species were significantly overrepresented for the combination of forest types and management regimes (Table 1). Two species were indicators of sweet chestnut forests and three of black locust forests. Interestingly, four species were overrepresented in over-aged sweet chestnut stands but none in the coppice ones. Instead, five species were overrepresented in over-aged black locust stands and four in the coppice ones. One species was also overrepresented in black locust and over-aged sweet chestnut stands and one in black locust and coppice sweet chestnut stands.

Even if fixed effects in the GLMM showed no significant differences, a tendency towards higher vascular plant species richness in black locust stands was observed (mean sweet chestnut = 14.4, SE = 1.29; mean black locust = 15.6, SE = 1.22; Fig. 3a). The tendency towards an influence of the interaction between forest type and management regime on species richness seemed to be more relevant in sweet chestnut forests,

Table 1

The Indicator Species Analysis, carried out with all species, identified 21 indicator species and were divided by forest types (sweet chestnut or black locust), their management (coppice or over-aged) and their combinations.

Group	Species	IndVal.g	p-value
Sweet chestnut forests	<i>Castanea sativa</i> - sweet chestnut	0.994	0.001
	<i>Quercus petraea</i> (Matt.) Liebl. - sessile oak	0.685	0.067
Black locust forests	<i>Robinia pseudoacacia</i> - black locust	0.993	0.001
	<i>Sambucus nigra</i> L. - elder	0.928	0.001
	<i>Lamium orvala</i> L. - balm-leaved archangel	0.558	0.091
	NONE		
Sweet chestnut coppice forests			
Sweet chestnut over-aged forests	<i>Sorbus torminalis</i> (L.) Crantz - wild service tree	0.500	0.020
	<i>Pteridium aquilinum</i> (L.) Kuhn - eagle fern	0.499	0.092
	<i>Arbutus unedo</i> L. - strawberry tree	0.408	0.092
	<i>Prenanthes purpurea</i> L. - purple lettuce	0.408	0.098
	<i>Galeopsis pubescens</i> Besser - downy hemp-nettle	0.564	0.021
Black locust coppice forests	<i>Potentilla indica</i> (Andrews) Th. Wolf - mock strawberry	0.522	0.012
	<i>Carex pilosa</i> Scop. - hairy sedge	0.521	0.020
	<i>Symphytum tuberosum</i> L. subsp. <i>angustifolium</i> (A.Kern.) Nyman - tuberous comfrey	0.426	0.045
	<i>Ulmus minor</i> Mill. subsp. <i>minor</i> - field elm	0.655	0.003
	<i>Rubus ulmifolius</i> Schott - elmleaf blackberry	0.535	0.015
Black locust over-aged forests	<i>Parietaria officinalis</i> L. - lichwort	0.533	0.022
	<i>Alliaria petiolata</i> (M. Bieb.) Cavara and Grande - garlic mustard	0.530	0.066
	<i>Geum urbanum</i> L. - wood avens	0.523	0.046
	<i>Polygonatum multiflorum</i> (L.) All. - Solomon's seal	0.65	0.097
	<i>Crataegus monogyna</i> Jacq. - common hawthorn	0.614	0.091
Coppice forests			
All black locust forests and sweet chestnut over-aged forests	<i>Hedera helix</i> L. subsp. <i>helix</i> - English ivy	0.818	0.082
All black locust forests and sweet chestnut coppice forests			

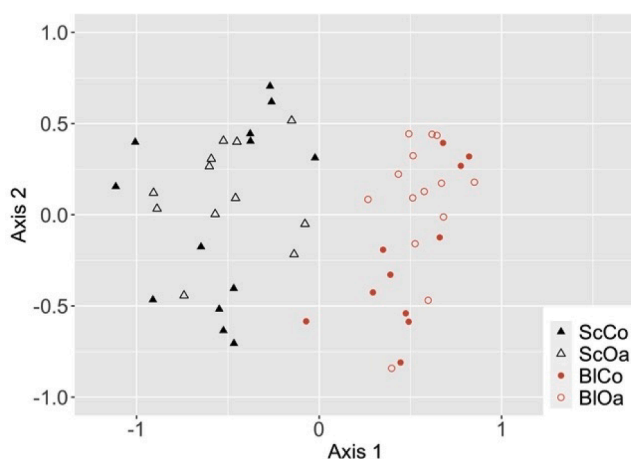


Fig. 2. NMDS plot based on the total species cover. The different symbols indicate forest types (sweet chestnut, Sc = black triangle; black locust, Bl = red circle). Full and empty symbols are used to indicate coppice (Co) or over-aged (Oa) forests, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

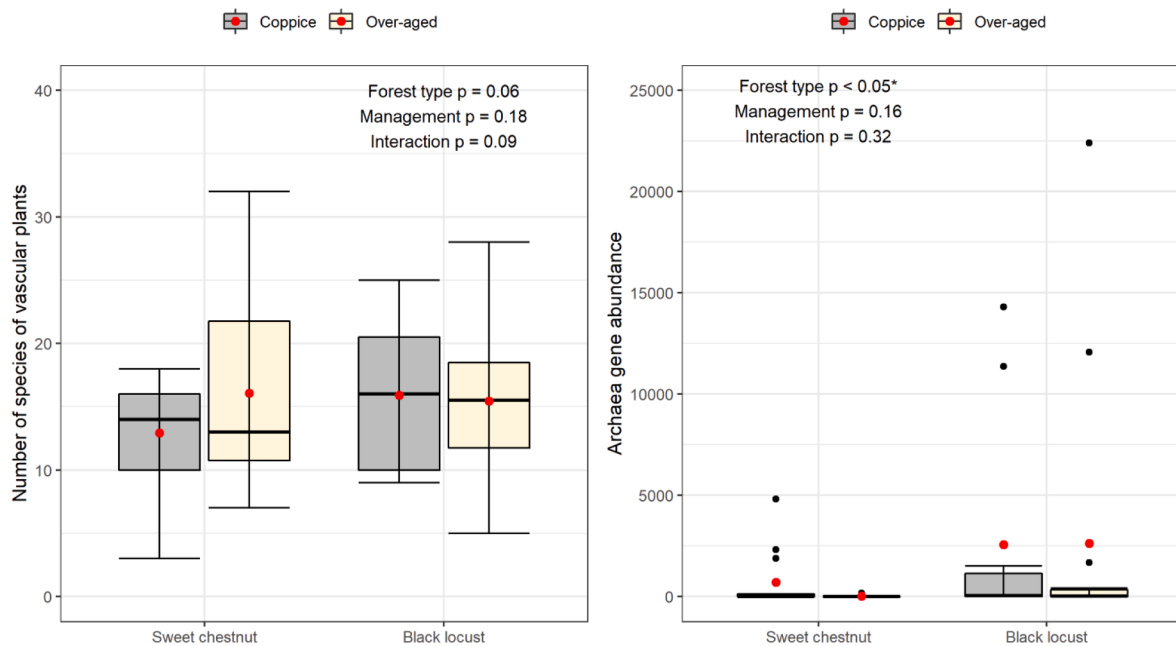


Fig. 3. The effect of forest type, management regime and their interaction on total vascular plant species richness (a). The effect of forest type, management regime and their interaction on AOA gene abundance (b). Yellow and grey symbols refer to over-aged and coppice forests, respectively. Dots indicate the mean values. Lines of the bars represent minimum, first quartile, median (thicker line), third quartile and maximum values, black dots are outliers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

although not significant.

3.2. Ammonia-oxidising archaea abundance

We observed a significant lower abundance of AOA in sweet chestnut compared to black locust stands ($\chi^2(1) = 5$, $p < 0.05$; Fig. 3b). However, management regime and interaction between forest type and management regime did not influence the abundance of AOA.

3.3. Soil characteristics

No significant difference was observed between forest types and the interaction of forest types with management regimes for soil moisture, shear strength and penetration resistance (Fig. 4). The management

regime did not influence shear strength and penetration resistance, but played an important role for soil moisture: over-aged forests had lower soil moisture than coppice forests ($\chi^2(1) = 4.49$, $p < 0.05$; Fig. 4).

3.4. Stand structure

Sweet chestnut and black locust forests had a similar stand structure (Fig. 5). The management regime played a role in determining mean diameter, number of stems and deadwood volume. Lower mean diameter ($\chi^2(1) = 6.88$, $p < 0.01$) and deadwood volume ($\chi^2(1) = 4.86$, $p < 0.05$) were observed in coppice stands; whereas, a higher number of stems was found in coppice compared to over-aged stands ($\chi^2(1) = 13.09$, $p < 0.001$). Interaction between forest type and management regime was statistically significant for number of stems ($\chi^2(1) = 11.08$,

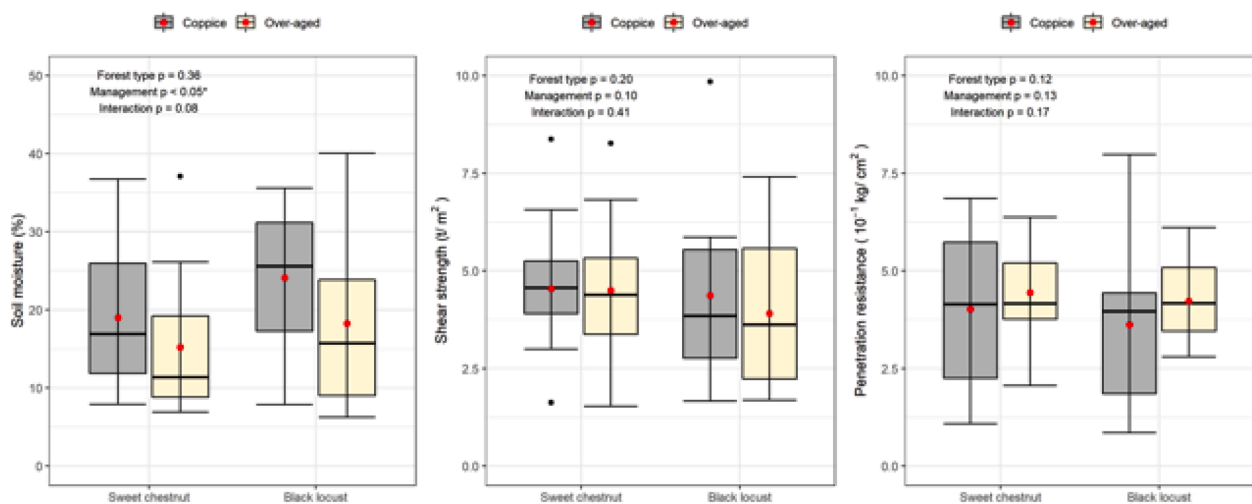


Fig. 4. Soil moisture (left), shear strength (centre) and penetration resistance (right) compared between forest types, management regimes and their interaction. Red dots indicate the mean values. Lines of the bars represent minimum, first quartile, median (thicker line), third quartile and maximum values, black dots are outliers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

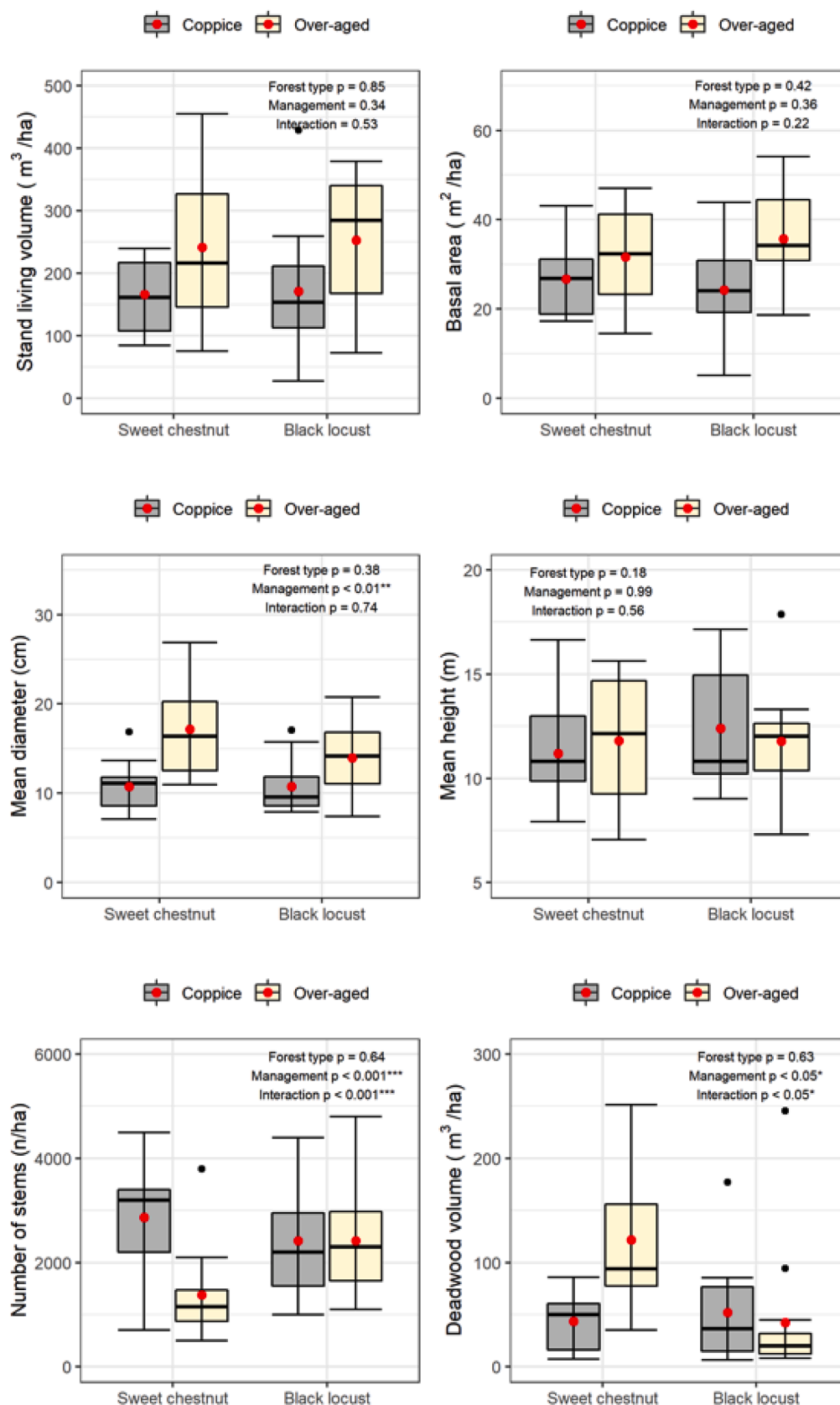


Fig. 5. Living volume, basal area, mean diameter, mean height, number of stems and deadwood volume compared between sweet chestnut and black locust stands, coppice and over-aged management regimes and their interaction. Red dots indicate the mean values. Lines of the bars represent minimum, first quartile, median (thicker line), third quartile and maximum values, black dots are outliers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$p < 0.001$) and deadwood volume ($\chi^2(1) = 4.13$, $p < 0.05$). A strong difference was observed in sweet chestnut forests where the number of stems was higher in coppice forests; whereas, deadwood volume was lower in coppice forests.

4. Discussion

This study deepens the knowledge on sweet chestnut forests' biodiversity in Europe and it compares results with those for black locust forests, providing indications on the likely effects of the spread of this non-native tree species. The study takes into account the possible effects of the major forest management regimes for these two forest types. We are not aware of studies focusing on sweet chestnut stands' biodiversity and the effects brought by black locust, as well as the management on both vascular and AOA diversity.

4.1. Vascular plant richness and composition

As suggested by some previous research non-native tree species may not have a strong impact on plant species diversity (Sitzia et al., 2012). In fact, a relatively low difference in the number of plant species was recorded between sweet chestnut and black locust stands; with the non-native tree dominated forests hosting a higher number. Although not expected, black locust has already been reported to host a higher diversity than native forest habitats (Wohlgemuth et al., 2022). The management regime did not bring differences in plant richness. However, over-aged sweet chestnut forests hosted a higher overall number of species than coppice, although not significantly. It was confirmed that the plant composition of sweet chestnut forests is relatively heterogeneous (Gutián et al., 2012; Konstantinidis et al., 2008) and it is different from that of black locust forests. The abandonment of coppicing does not seem to strongly influence composition of sweet chestnut or black locust forests. However, there are a number of species that show a level of specificity and fidelity to sweet chestnut forests, black locust forests and their different management regimes. The presence of different indicator species for the considered forest groups confirmed that the array of silvicultural activities ensure the maintenance of a relatively high plant species diversity (Gondard et al., 2006).

Indeed, our results are not totally in line with previous research suggesting that within coppice stands management variations, including over-aging, can result in differences in floral species richness (Mattioli et al., 2016). Additionally, our study contrasts with others indicating that abandonment of sweet chestnut stands leads to homogenous and reduced plant diversity (Gondard et al., 2006). Interestingly, studies dealing with other forest types indicate that coppice age and its conversion to high forest influences both richness and composition (Della Longa et al., 2020). However, landscape factors and geographic conditions may play an important role in determining plant composition of sweet chestnut forests (Gutián et al., 2012; Konstantinidis et al., 2008). This is also evinced by the overrepresented species reported for over-aged sweet chestnut stands, such as *Arbutus unedo* L., a species linked to Mediterranean climate conditions and relatively common on the Euganean hills.

Nevertheless, it has been already highlighted that abandoned sweet chestnut coppices are colonised by other tree species, including non-natives (Pezzi et al., 2011; Zlatanov et al., 2013). This is certainly related to being light-demanding and with low competitiveness compared to late-successional species (Conedera et al., 2021) and as, in many cases, we would expect different potential vegetation. However, the literature highlights that coppices can have favourable understory conditions for forest specialist plant species (Cervellini et al., 2017). Some indicator species reported for sweet chestnut forest groups (i.e. *Castanea sativa*, *Quercus petraea* (Matt.) Liebl., *Pteridium aquilinum* (L.) Kuhn, *Sorbus torminalis* (L.) Crantz) were also reported among those representing the habitat type of community interest dominated by sweet chestnut (habitat code 9260) according to the national interpretation

manual (Biondi et al., 2009). However, also some of the indicator species for the black locust forest groups are reported in that list (e.g., *Sambucus nigra* L., *Lamium orvala* L.). Furthermore, other studies (e.g., Campagnaro et al., 2018c) have linked some of the same species to black locust stands and their different characteristics (e.g., *Sambucus nigra* L., *Ulmus minor* Mill., *Parietaria officinalis* L., *Potentilla indica* (Andrews) Th. Wolf, *Geum urbanum* L.). It seems that most of the indicators of black locust forests need a certain degree of light or do not tolerate strong cover.

4.2. Soil conditions

Both shear strength and penetration resistance are used to estimate soil damage severity by harvesting interventions (Picchio et al., 2020). However, a study in sweet chestnut forests indicated that both shear strength and penetration resistance are affected by harvesting operations, even if differences in physical, chemical and biological values between undisturbed soils and those characterising mature coppice stands tend to disappear (Venanzi et al., 2016). In our study, physical soil features did not differ between forest types and management regimes, thus confirming that mature coppices have similar soil values to unharvested areas, if measurements are taken years after the last coppicing. The same study (Venanzi et al., 2016) reported no impact on soil moisture content; however, this is in contrast to the differences between management regimes observed in our study. Furthermore, as the effects of heavy machinery can be observed even decades after the intervention (Mohieddinne et al., 2019), it seems reasonable that operations in the analysed forests were probably carried out with small machinery and caused relatively little soil damage. This is consistent with the findings of Venanzi et al. (2020), who pointed out that soil recovery after light silvicultural operations is relatively fast. Nevertheless, soil moisture in our study may be influenced by the different cover found in coppice and over-aged forests, with coppice stands being more dense, especially in sweet chestnut dominated forests.

4.3. Ammonia-oxidising archaea abundance

Gene abundance of AOA was lower in sweet chestnut than black locust forests. AOA are considered indicators of changes in soil nitrogen cycle as they mediate the first phases of nitrification (Stopnišek et al., 2010; Zhang et al., 2012; Stevanato et al., 2016). A higher abundance in black locust stands, i.e. soils invaded by a woody legume, was expected due to its nitrogen fixation associated with symbiotic rhizobia in black locust root nodules (Cierjacks et al., 2013). Soils hosting legumes experience a burst of mineral nitrogen availability upon the decay and turnover of legume plant residues that liberate nitrogen (N) in the form of ammonium ion, which is the direct substrate for the first AOA nitrification reaction. While the higher levels of AOA recorded are not necessarily only related to nitrogen availability in soils because of the wide range of soil conditions surveyed and the paired sampling approach, a direct catabolic link and a corresponding qPCR response exist between reduced N and AOA abundance (Zanardo et al., 2016). Therefore, based on our results, a lower nitrification is expected under sweet chestnut trees. And, interestingly, the American chestnut was reported to have a reduced number of N-cycling functional genes in the nitrification pathway (Kelly et al., 2021).

Land use management was reported to be an important factor determining the abundance of AOA in soil (Zhalnina et al., 2012). Furthermore, AOA abundance was found to be positively related to disturbance in forest soils (Osburn and Barrett, 2020). However, no differences were observed between coppice and over-aged stands. Indeed, we must bear in mind that many local factors (e.g. nitrogen content, moisture content) could also have played a role in shaping the abundance of AOA (Bates et al., 2011; Zhalnina et al., 2012).

4.4. Stand structure

The structure of sweet chestnut and black locust forests in this study is very similar. This may be explained by the wide range of soil and climatic conditions considered, and therefore of fertility and growing conditions, and the balanced distribution of plots compared to the different management regimes. Deadwood is an indicator of the conservation status of forest habitat types (Cantarello and Newton, 2008) and plays a key role in nutrient availability and soil fertility and for many plant and animal organisms (Winter and Möller, 2008). Nevertheless, its presence increases fire risk, in particular in neglected coppices (Manetti et al., 2017). Mean values of deadwood volume in Italian sweet chestnut forests range between 9 and 19 m³/ha and are among the highest compared to other forest types (Pignatti et al., 2009). Indeed, our values are higher because of the management regimes as well as the local conditions and some stands exceed the threshold (>40 m³/ha) currently proposed as a biodiversity conservation objective. Therefore, pointing out these forests for their role in biodiversity conservation. Managers should also take into account that sweet chestnut over-aged coppices have high deadwood with consequent increased fire vulnerability; therefore, this suggests cleaning and thinning interventions to reduce fire damage risk and spread (Garfi et al., 2022). Furthermore, although not considered in this study, the impact of well-known sweet chestnut diseases or insect attacks (recorded in the study area; e.g., Marcolin et al., 2021) may have played a role in increasing mortality (Manetti et al., 2020) and, subsequently, deadwood amount.

Reported values seem to confirm the variability already reported in the literature referring to Italian sweet chestnut forests. For example, the range reported for number of stems, mean height and basal area in coppice with standards are in line with those reported in Manetti et al. (2022). Hence, the variation, and range of values, number of stems, mean diameter and deadwood volume may be used as indicators of over-aged conditions and neglected or abandoned coppices when information on their age or last intervention is not available. Furthermore, the comparison of trends for mean diameter and number of trees is in line with the correlations found between these parameters in sweet chestnut forests (Alterio et al., 2021).

Interestingly, not all the same stand structure features seemed to differ between coppice and over-aged black locust stands. Indeed, the influence of management regimes seems less important for structural features in black locust forests. Based on these results, deadwood volumes may generally be used as proxies for over-aging stands.

5. Conclusion

Sweet chestnut forests and their management are traditional elements of many Italian hilly landscapes including those investigated in this study. We have identified relevant changes in certain key components of plant biodiversity, soil conditions and forest structure related to the substitution and spread of black locust forests as well as the management changes increasingly observed in the last decades (i.e. over-aging). Sweet chestnut hosts a peculiar plant biodiversity and its forest structure features have the potential to be important for many different species; while black locust is modifying plant diversity and composition as well as soil processes, as evinced by results on AOA abundance. This work can contribute at setting conservation objectives within Natura 2000 sites. The analysed forest attributes and their values can be used to quantify and compare forest structure and functions; furthermore, most of these can be derived from forest planning instruments (Trentanovi et al., 2018; Alterio et al., 2023).

Indeed, management regime showed to be an important factor shaping forest characteristics and, more specifically, those of sweet chestnut compared to black locust forests. Based on our results, to achieve a variety of forest structures and plant composition a heterogeneous array of management practices should be maintained within hilly landscapes, as also proposed for other parts of Europe (Gondard

et al., 2006), with the opportunity of controlling the spread of the non-native black locust tree. Furthermore, in general, the abandonment of coppicing in the analysed areas could result in landscape simplification (Della Longa et al., 2020). Control of the expansion of black locust forest is a crucial management action within Natura 2000 sites that would benefit the conservation of sweet chestnut forests (Campagnaro et al., 2018c; 2022).

CRediT authorship contribution statement

Thomas Campagnaro: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Giovanni Trentanovi:** Conceptualization, Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Simone Iacopino:** Data curation, Investigation, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Andrea Squartini:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – review & editing. **Flora Giulia Simonelli:** Data curation, Investigation, Writing – review & editing. **Edoardo Alterio:** Formal analysis, Investigation, Visualization, Writing – review & editing. **Giovanni Bertoldo:** Investigation, Writing – review & editing. **Giuseppe Concheri:** Methodology, Writing – review & editing. **Stefano Grigolato:** Conceptualization, Writing – review & editing. **Alessia Portaccio:** Investigation, Writing – review & editing. **Andrea Rizzi:** Data curation, Investigation, Writing – review & editing. **Roberto Rizzieri Masin:** Investigation, Writing – review & editing. **Piergiorgio Stevanato:** Methodology, Writing – review & editing. **Stefano Tassinazzo:** Investigation, Writing – review & editing. **Tommaso Sitzia:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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