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Diversity of secondary woody species in relation to species richness and cover of dominant trees in thermophilous deciduous forests

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ABSTRACT

One of the prominent compositional features of thermophilous deciduous forests of southern Europe is their richness in secondary woody species (AWS). To date, no studies have focused on the diversity and contribution to the ecosystem functions and socio-economic benefits provided by these species. Here, we first characterized species richness and diversity for three main functional groups of AWS, sporadic trees, shrubs and vines, in 53 representative stands of central Italy. Secondly, we explored variations in AWS diversity and composition along a four-level gradient of species richness of dominant trees under comparable site conditions. The 40 AWS taxa recorded showed a remarkable taxonomic singularity at both the genus and the family rank. Dominant tree species richness had no significant effect on AWS species richness and composition, while Shannon diversity of AWS, especially shrubs, was associated with cover of the dominant trees. Each AWS possessed, on average, ca. five ability traits over a total of 13 considered that contributed to important ecosystem functions or expected socio-economic benefits such as wood and food production, conservation of genetic resources (wild crop relatives) and ornamentals. This highlights the key role of AWS, and in particular of sporadic trees, for enhancing multifunctionality of thermophilous deciduous forests.

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Introduction

According to the European Environment Agency classification (EEA), thermophilous deciduous forests represent one of the main forest types on the continent, covering large areas especially in Italy (40% of the ICP Level I plots; Barbati et al. 2007). Numerous communities have been recognized within this forest type based on the phytosociological system (Pignatti 1998; Blasi 2010). Different species of *Quercus* are usually dominant in late successional stages, as a result of their competitive ability under a broad range of ecological conditions and key functional traits such as large size and longevity. Next to monospecific stands, *Quercus* spp. may also form various mixtures with two or more co-dominant tree species such as *Castanea sativa* Miller and *Ostrya carpinifolia* (L.) Scop., depending on local environmental factors, management and successional stage. *Quercus* spp., *C. sativa* and *O. carpinifolia* are usually the focus of silvicultural management, which is traditionally based on coppice-with-standards cycles of 14–18 years for the production of firewood.

Most of the diversity in native woody species in thermophilous forests, however, is not found in the dominant tree component but in the associated woody species (AWS) occurring in the lower tree and shrub layers. Three functional groups of AWS can be distinguished, that is, sporadic or secondary trees, shrubs and woody vines. Sporadic trees are mostly or exclusively found in forests but always subordinate to dominant trees in terms of stature and biomass. They have a relatively

low abundance and frequency (solitary plants or in small groups) due to their low competitive capacity, the often non-optimal ecological conditions or because past silvicultural management have not favored them with respect to dominant trees, as shown for *Sorbus torminalis* (L.) Crantz in central Europe (Rasmussen 2007). Shrubs and vines are major structural and compositional components of thermophilous deciduous forests, thanks to their species richness and abundance in most associations dominated by *Quercus* spp. (Pignatti 1998).

Overall, AWS affect the functional and structural diversity of this ecosystem and the interactions between its components. Negative effects by competition can occur on the abundance and diversity of the understory herbaceous plants (Barbier et al. 2009), while they may contribute to the processes of niche differentiation and facilitation (*complementarity effect*) which are known to increase the performance of the community (Loreau and Hector 2001). In addition, AWS enhance forest multifunctionality as they often provide different ecosystem services, such as production of valuable timber (Savill et al. 2009), gene reservoirs for cultivated varieties, ornamentals, products for folk medicine and, in the case of shrubs, useful material for environmental restoration practices (Clauser & Foggi 2005). Favoring natural tree mixtures with uneven structure is one of the strategies that may help to achieve multifunctionality at different spatial scales, an increasingly important goal of the European silviculture

(Bauhus et al. 2013; Forest Europe 2011). Multifunctionality is especially important in Mediterranean forests, where the valuation of non-market goods and services is still scarcely developed, and where, instead, ecosystem services are fundamental for the livelihood of society (Nocentini & Coll 2013). For these reasons, encouraging an increase in the proportion of valuable non-dominant broadleaved species is important to improve resilience to drivers of change and reduce ecological risks in European forests (Spiecker 2009).

To date, however, both the functional linkages and diversity relationships between canopy trees and AWS in the lower layers of thermophilous temperate forests are still unknown. Dominant trees are “ecosystem engineers” determining many physical and biotic characteristics of their habitat and consequently influencing several aspects of plant life in the lower forest layers (Barbier et al. 2008). As shown for the understory vegetation in temperate ecosystems, dominant trees can have differential effects on the amount and spatial distribution of key resources such as light and nutrients (Gilliam 2007; Mölder et al. 2008; Vockenhuber et al. 2011; Axmanová et al. 2012), therefore possibly affecting also AWS through the same mechanisms. On the other hand, the cover of the dominant trees may also affect the diversity and abundance of the AWS as a result of competition for primary resources, especially light.

Accordingly, this study aims at: (1) providing a qualitative and quantitative characterization of AWS in representative thermophilous deciduous forest stands of central Italy; (2) understanding the effects of dominant tree species richness and cover on the species richness, diversity and composition of this component; (3) summarizing key traits of AWS that contribute to ecosystem functions or the provisioning of expected socio-economic benefits as defined in the Millennium Ecosystem Assessment (2003). This also allowed a first quantitative estimation of the contribution of AWS to the multifunctionality of thermophilous deciduous forests, and to explore variations of AWS richness per function along a species richness gradient of dominant trees.

Materials and methods

Study area and field sampling

Sampling sites were located in the Italian study region of the FunDivEUROPE project (<http://www.fundiveurope.eu/>), more precisely on the hills of central Tuscany (Appendices 1 and 2). In this region, thermophilous deciduous forests cover between 45% and 55% of the total forest area (Hofmann et al. 1998; Mori & Torreggiani 2010).

A total of 53 plots of 30 × 30 m were established in multiple-layered and uneven-aged stands originating from the abandonment of the traditional coppice management since at least 50 years, mainly included in nature reserves and/or in Rete Natura 2000 sites (Appendix 2; Bussotti et al. 2012). Plots were selected to cover a species richness gradient of dominant trees (Baeten et al. 2013): monocultures (13 plots), 2-species mixtures (17 plots), 3-species mixtures (13 plots) and >3 (4–5)-species mixtures (10 plots). Mixtures were composed of different combinations of the following five species

of dominant trees (hereafter indicated as “trees”): *Quercus cerris* L., *Q. ilex* L., *Q. petraea* (Matt.) Liebl., *Castanea sativa* and *Ostrya carpinifolia*. To avoid complete dilution of a single species on AWS diversity, that would prevent to separate diversity from identity effects (Nadrowski et al. 2010), almost all possible tree combinations were included. All five species had comparable frequencies in the combinations, and were mixed in given proportions of basal area in order to respect a minimum evenness. A most important aspect during the plot selection procedure was to ensure that the effect of tree species richness was not confounded with major site-, soil- and stand-related factors. Therefore, spatial clustering of plots of particular species richness levels was strictly avoided because this would have increased the probability of covariation (Baeten et al. 2013). All plots were first characterized for site-, soil- and stand-descriptors such as altitude, slope aspect and inclination, bedrock type, soil texture and depth, stand age, vertical structure, management type and others; the full list of these descriptors is given in Baeten et al. (2013, Appendix 2). After assessing the percentage of overstorey canopy cover, AWS composition was analyzed recording the sporadic trees listed in the Regional Forest Law of Tuscany 39/2000 (article 12, DPGR 48/R/20039) and Mori et al. (2007), and then the shrubs and woody vines; Pignatti (1982) and Clauser and Foggi (2005) were used to check identification of AWS. The abundance of AWS was estimated using a modified Braun–Blanquet cover-abundance scale. For plants smaller than 0.5 m, shorter intervals were used (0–5%, 6–10%, 11–15%, 16–20%); higher intervals were not used since cover of single species in this layer was never >20%. A conventional value of 0.1% was given to AWS plants occurring with only a few juvenile individuals (seedlings).

Data analysis

First, substantial lack of covariation between main environmental factors and tree species richness levels was assessed based on the site descriptors mentioned above. NMDS analysis using Gower dissimilarities with extension to ordinal variables and PERMANOVA (Baeten et al. 2013) showed that soil and stand conditions did not differ between the levels of tree species richness (p and F values in Appendix 3); minor differences in site variables were due to a factor that is a priori irrelevant for this study (plot accessibility). Next, lists of sporadic trees, shrubs and woody vines found in the plots were prepared, and taxonomic singularity (TS) was measured as the inverse of the average species number per genus and genera number per family, respectively (Selvi & Valleri 2012).

Statistical analyses were performed with R 3.0.1 (R core team 2013). Compositional dissimilarities between the plots were calculated based on the Bray–Curtis distance, using cover data. NMDS was then used to visualize the results, using PerManova with 999 permutations to test the effect of tree species richness as numeric covariate.

AWS species richness, Shannon–Wiener index (H') and evenness index (J) were calculated for the three functional groups. The effects of the tree species richness, cover (numeric continuous variable) and their interaction on AWS

richness and diversity were then analyzed using a mixed model structure, which took into account the random effect due to the differences in tree combinations (Combination) [R-syntax: $y \sim \text{tree species richness} * \text{Cover} + (1 | \text{Combination})$; *nmle* package, Pinheiro et al. 2013]. We also examined the effect of canopy tree cover on AWS cover using linear regression analyses.

The potential contribution of AWS to forest multifunctionality was estimated considering eight major functions related to stability, resilience and interactions with other biotic components of the ecosystem; in addition, we selected five major provisioning services among those reported in the Millennium Ecosystem Assessment (2003) and in the survey of World Economic Plants (Wiersema & León 2013; Table 3). Each species was scored with binary variables (1: possessing ability traits contributing to a given function/service; 0: without ability traits related to that function/service). Information on single species was retrieved from literature sources, some of which including information about the forms of utilization of the various species in our region, mainly Pignatti (1982), Clauser and Foggi (2005), Mori et al. (2007), Paula and Pausas (2009) and Agerer (1987–2012) for ectomycorrhizae, and Wiersema and León (2013) for species with economic value. After calculating the number of species for each of the 13 ability traits in every plot, a Kruskal–Wallis non-parametric analysis was performed to test the differences in the number of AWS species for each trait between the four tree richness levels. A biplot scattergram from principal component analysis performed with PAST (Hammer et al. 2001) was finally applied to summarize the dissimilarities between the plots of the four tree levels based on the number of AWS for each expected ecosystem functions/services.

Results

In total, 40 taxa of AWS were recorded in 53 plots, belonging to 34 genera and 22 families (Table 1). NMDS did not support separation of the plots (Figure 1), and PerManova revealed a non-significant effect of tree species richness level on AWS composition (p -value = 0.072).

Sporadic trees

Among the 11 taxa recorded, *Taxus baccata* L. was the only gymnosperm. With four genera and five species, the Rosaceae were largely prevalent, but genus *Acer* was also well represented. *Sorbus torminalis* and *S. domestica* L. occurred in 79% and 40% of the plots, respectively, while five species were observed in only one plot. Both *Sorbus* species were more frequent in the pooled mixtures than in monocultures, and *Malus sylvestris* was only found in mixed plots. However, frequencies of the sporadic trees did not differ significantly along the tree species richness gradient.

In both monocultures and mixtures, ground cover of the sporadic trees was variable depending on the plots but always <40%; the >3-tree mixtures were characterized by a significantly higher cover (10%; Kruskal–Wallis H test = 8.433; p -value < 0.05; Table 2).

Richness of sporadic trees did not differ significantly between the four tree species richness levels. Mixed plots included up to four species, while monocultures included a maximum of three species (Table 2). Sporadic trees were absent in a nearly double proportion of the monocultures (three plots, 23.1%) than that of the pooled mixed plots (five plots, 12.5%); the >3-tree mixtures always included at least one species unlike the other levels. Both Shannon H' and evenness J were higher in monocultures and two-tree mixtures, but no significant differences were found ($H = 0.446$, p -value > 0.05). TS was fairly high, 0.63 and 0.73 at the family and genus levels, respectively, especially in >3- and 2-tree mixtures. No trend of variation occurred along the gradient.

Shrubs

As many as 23 species were recorded in the stands, belonging to 20 genera and 13 families (Table 1); with 7 species and 5 genera, the Rosaceae was again the most represented family. Almost half of the taxa (10) were Mediterranean evergreens, supporting the thermophilous character of the stands examined.

Chi-square tests did not show significant differences of frequency between the four diversity levels, although contrasting trends of variation were observed. While widespread species such as *Phillyrea latifolia* L. and others were more commonly found in monocultures, a higher frequency in the >3-tree mixtures emerged for ecologically more specific taxa such as the two evergreens *Ilex aquifolium* L. and *Daphne laureola* L. and the deciduous *Cornus mas* L., all belonging to the ancient forest species group.

Ground cover was widely variable within all plot types, and differences along the tree richness gradient were not significant. The mean number of shrub species per plot ranged from 5 to 5.8, without differences between monocultures and mixed plots; the minimum number of species was higher in the >3-tree plots (three vs. two in the other levels). Mean Shannon diversity, evenness J and TS were comparable along the four tree richness levels. Unlike with sporadic trees, Shannon H' was always >0 due to the presence of at least two shrubs, and overall TS was higher, 0.72 and 0.86 at the family and genus levels, respectively (Table 2).

Woody vines

Three evergreen and three deciduous vine species were recorded, belonging to different families and genera and thus accounting for the highest possible TS (1.0 at both levels). *Hedera helix* L. was the most frequent vine, reaching 100% of presence in monocultures and 60% of the >3-tree mixtures. The rare wild grape *Vitis vinifera* ssp. *sylvestris* was instead found only in 3- and >3-tree plots.

Overall, ground cover was very low (mean 5%, max 15%) and nearly invariable along the tree richness gradient. Species richness, Shannon H' and J were also comparable, with the highest H' values in 2- and 3-tree mixed plots; TS at genus and family level was the same in the four levels and decreased progressively along the tree gradient.

Table 1. List of the sporadic trees, shrubs and woody vines recorded in the forest plots, with family and percentage of plots for each level of dominant tree species richness (1, 2, 3, >3, with number of plots, *n*) where the species have been recorded.

Species	Family	1 <i>n</i> = 13	2 <i>n</i> = 17	3 <i>n</i> = 13	>3 <i>n</i> = 10	TOT <i>n</i> = 53
Sporadic trees						
<i>Acer campestre</i> L.	Aceraceae	15.4	23.5	23.1	20.0	18.9
<i>Acer monspessulanum</i> L.	Aceraceae	15.4	11.8	15.4	10.0	11.3
<i>Acer pseudoplatanus</i> L.	Aceraceae	7.7	0.0	0.0	0.0	1.9
<i>Malus sylvestris</i> Mill.	Rosaceae	0.0	11.8	15.4	20.0	9.4
<i>Prunus avium</i> L.	Rosaceae	15.4	5.9	0.0	20.0	7.5
<i>Pyrus pyraister</i> Burgsd.	Rosaceae	7.7	0.0	0.0	0.0	1.9
<i>Sorbus domestica</i> L.	Rosaceae	30.8	41.2	46.2	40.0	39.6
<i>Sorbus torminalis</i> (L.) Crantz	Rosaceae	69.2	82.4	69.2	90.0	75.5
<i>Taxus baccata</i> L.	Taxaceae	0.0	5.9	0.0	0.0	1.9
<i>Tilia cordata</i> Mill.	Tiliaceae	0.0	0.0	0.0	10.0	1.9
<i>Ulmus minor</i> L.	Ulmaceae	0.0	5.9	0.0	0.0	1.9
Shrubs						
<i>Arbutus unedo</i> L.	Ericaceae	76.9	58.8	84.6	90.0	75.5
<i>Cornus mas</i> L.	Cornaceae	38.5	35.3	23.1	50.0	35.8
<i>Corylus avellana</i> L.	Betulaceae	0.0	0.0	7.7	0.0	30.2
<i>Crataegus laevigata</i> (Poir.) DC.	Rosaceae	7.7	5.9	7.7	10.0	1.9
<i>Crataegus monogyna</i> Jacq.	Rosaceae	15.4	11.8	0.0	50.0	7.5
<i>Cytisus scoparius</i> (L.) Link.	Leguminosae	30.8	23.5	15.4	20.0	17.0
<i>Daphne laureola</i> L.	Thymeleaceae	53.8	47.1	53.8	80.0	22.6
<i>Erica arborea</i> L.	Ericaceae	30.8	41.2	30.8	30.0	56.6
<i>Erica scoparia</i> L.	Ericaceae	23.1	11.8	15.4	0.0	34.0
<i>Euonymus europaeus</i> L.	Celastraceae	0.0	0.0	0.0	10.0	13.2
<i>Hippocrepis emerus</i> (L.) Lassen	Leguminosae	30.8	29.4	38.5	20.0	1.9
<i>Hypericum androsaemum</i> L.	Clusiaceae	0.0	5.9	7.7	0.0	3.8
<i>Juniperus communis</i> L.	Cupressaceae	53.8	64.7	84.6	100.0	73.6
<i>Ilex aquifolium</i> L.	Aquifoliaceae	15.4	11.8	0.0	10.0	9.4
<i>Laurus nobilis</i> L.	Lauraceae	0.0	0.0	7.7	0.0	1.9
<i>Ligustrum vulgare</i> L.	Oleaceae	7.7	11.8	15.4	0.0	9.4
<i>Mespilus germanica</i> L.	Rosaceae	0.0	5.9	7.7	0.0	3.8
<i>Phyllirea latifolia</i> L.	Oleaceae	38.5	29.4	23.1	20.0	28.3
<i>Prunus spinosa</i> L.	Rosaceae	0.0	5.9	0.0	0.0	1.9
<i>Pyracantha coccinea</i> M. Roem.	Rosaceae	0.0	5.9	0.0	0.0	1.9
<i>Rubus hirtus</i> W. et K.	Rosaceae	46.2	35.3	23.1	20.0	32.1
<i>Rubus ulmifolius</i> Schott	Rosaceae	38.5	35.3	38.5	50.0	39.6
<i>Viburnum tinus</i> L.	Caprifoliaceae	15.4	23.5	30.8	20.0	22.6
Woody vines						
<i>Clematis vitalba</i> L.	Ranunculaceae	7.7	11.8	7.7	0.0	7.5
<i>Hedera helix</i> L.	Araliaceae	100.0	94.1	92.3	60.0	88.7
<i>Lonicera etrusca</i> Santi	Caprifoliaceae	23.1	17.6	0.0	0.0	11.3
<i>Rosa sempervirens</i> L.	Rosaceae	0.0	17.6	30.8	30.0	18.9
<i>Smilax aspera</i> L.	Smilacaceae	15.4	29.4	23.1	10.0	20.8
<i>Vitis vinifera</i> L. <i>sylvestris</i> (Gmel.) Hegi	Vitaceae	0.0	0.0	7.7	10.0	3.8

Effect of tree species richness and cover on AWS diversity

No random effect of the combination of dominant tree species was found on the three AWS diversity parameters (SR, H' and J), and no relationship between tree richness and AWS diversity was observed. On the contrary, the linear model showed that variation of diversity H' of the whole set of AWS significantly increased with ground cover of dominant trees ($r = 0.32$; p -value = 0.0199; Figure 2(a)), and evenness J was also positively associated ($r = 0.34$; p -value = 0.0046; Figure 2(b)).

Finally, tree species richness did not affect the overall abundance of AWS (p -value = 0.674).

Functional abilities

The number of AWS for each of the 13 abilities was variable depending on the trait (Table 3). Entomophily and endozoochory were the most represented ecosystem abilities. Resprouting capacity was also common, as well as avoidance

of predation by wild ungulates by means of various strategies (toxicity, smell and spines). Ectomycorrhizae-forming and fire-resistant species were on average 2–3 per plot, while ability for nitrogen-fixation was present, on average, in less than one species per plot.

Concerning the expected benefits of socio-economic type, species with ornamental value were particularly numerous, and those with folk-medicinal use or producing valuable wood or edible fruits were also well represented. There was on average more than one wild crop relative per plot.

No significant differences were found in the mean number of species per function/benefit between the tree richness levels. Principal component analysis accounted for 79.3% of the total variation with the first two axes and produced a scattergram with plots of the four levels widely mixed in the ordination space (Figure 3). All traits examined were mainly associated with the positive part of the first component, without any clear association with specific plot types. Entomophily, endozoochory and ornamental value were strongly associated with the first axis ($r = 0.97$ and 0.96 , respectively). The second PCA axis produced a clear separation between

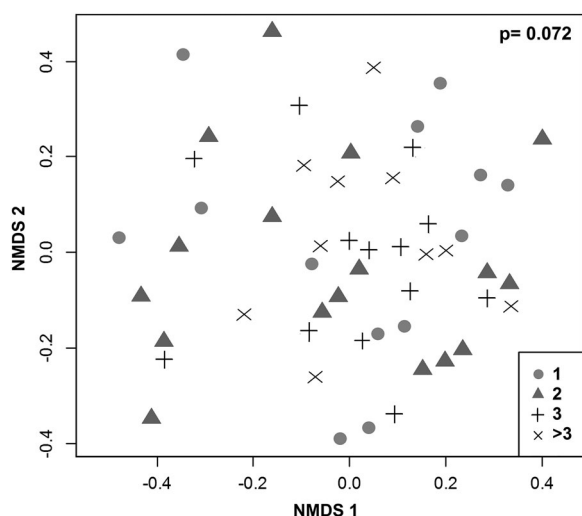


Figure 1. Scattergram from non-metric multidimensional scaling with the Bray Curtis distance based on cover values, summarizing the variation in AWS composition between plots in function of species richness of dominant trees (1, 2, 3, >3). *p*-values indicate the significance of the difference between the levels of tree species richness, based on PerManova with 999 permutations.

the traits associated with the expected benefits, with positive correlations, and most of those with mainly an ecosystem function on the negative part. Fire resistance and resprouting capacity were the more strongly correlated functions ($r = -0.60$ and -0.47 , respectively), while wood production was the more represented benefit.

Discussion

The present findings confirm that woody species are a key diversity component of the Mediterranean forest flora (Scarascia et al. 2000; Barbati et al. 2007). The overall mean ratio AWS/dominant tree species, similar to that used for assessing diversity proportions between understory and tree species in temperate forests (Gilliam 2007), was 5.51 ± 3.64 with a maximum of 15 for the monospecific stands. TS of the AWS at the family and genus level resulted ca. three times higher than in the vascular flora of the study region (Selvi 2010), suggesting a similarly high phylogenetic diversity in this forest component. Phylogenetic diversity is a key aspect for an increased

Table 2. Effect of species richness of dominant trees (1, 2, 3, >3) on species richness Shannon index, evenness, TS at genus and family levels, and ground cover of the secondary woody species (AWS), separately for the three functional groups (sporadic trees, shrubs and vines).

		1	2	3	>3	<i>p</i>
Sporadic trees	Species richness	1.6 (1.0–2.4)	1.9 (1.3–2.5)	1.7 (0.8–2.6)	2.1 (1.4–2.8)	0.859
	Shannon	0.37 (0.11–0.63)	0.42 (0.26–0.59)	0.27 (0.05–0.49)	0.32 (0.05–0.58)	0.931
	Evenness	0.72 (3.60–1.00)	0.83 (0.29–1.00)	0.43 (0.07–0.81)	0.49 (0.03–1.00)	0.682
	TS genus level	0.65 (0.41–0.90)	0.77 (0.62–0.93)	0.49 (0.26–0.73)	0.87 (0.71–1.02)	0.111
	TS family level	0.73 (0.47–0.1.00)	0.87 (0.73–1.01)	0.63 (0.35–0.91)	0.83 (0.67–0.99)	0.63
	Ground cover (%)	7 (0.3–13.3)	6 (2.3–9.9)	7 (2.0–12.3)	10 (1.8–18.0)	0.038*
Shrubs	Species richness	5.2 (3.9–6.6)	5.0 (4.1–5.9)	5.2 (4.2–6.1)	5.8 (4.0–7.6)	0.904
	Shannon	1.12 (0.87–1.37)	1.10 (0.88–1.83)	0.95 (0.69–1.22)	1.25 (0.88–1.62)	0.622
	Evenness	0.72 (0.24–1.00)	0.70 (0.24–1.00)	0.59 (0.26–0.82)	0.73 (0.53–0.98)	0.268
	TS genus level	0.98 (0.94–1.01)	0.99 (0.96–1.01)	1.00 (1.00–1.00)	0.98 (0.94–1.01)	0.845
	TS family level	0.87 (0.79–0.95)	0.89 (0.83–0.95)	0.89 (0.82–0.96)	0.89 (0.82–0.96)	0.974
	Ground cover (%)	29 (13.4–44.9)	30 (19.0–42.0)	36 (25.2–46.9)	28 (16.4–40.6)	0.624
Vines	Species richness	1.5 (1.1–1.9)	1.7 (1.2–2.2)	1.6 (1.0–2.2)	1.1 (0.6–1.6)	0.502
	Shannon	0.20 (0.00–0.41)	0.29 (–3.53–4.10)	0.31 (0.00–1.10)	0.16 (0.00–0.69)	0.731
	Evenness	0.62 (0.37–1.00)	0.65 (0.34–1.00)	0.71 (0.34–1.00)	0.78 (0.34–1.00)	0.817
	TS genus level	1.00 (1.00–1.00)	0.94 (0.82–1.07)	0.92 (0.76–1.09)	0.90 (0.67–1.13)	0.978
	TS family level	1.00 (1.00–1.00)	0.94 (0.82–1.07)	0.92 (0.76–1.09)	0.90 (0.67–1.13)	0.978
	Ground cover (%)	4 (1.4–6.7)	4 (2.6–6.2)	5 (2.3–8.0)	4 (1.5–6.4)	0.859

Note: Means with minimum and maximum values (in parentheses). *p*-values indicate the significance of the difference between levels of dominant tree species richness as resulting from the Kruskal–Wallis test (* $p < 0.05$).

Table 3. Number of secondary woody species (AWS) contributing to main ecosystem abilities and expected socio-economic benefits along a gradient of dominant tree species richness (1, 2, 3, >3) in thermophilous deciduous forests (mean \pm standard deviation); differences among tree richness levels are not significant ($p > 0.05$). Abbreviations used in figure 3 are indicated.

	1	2	3	>3	<i>p</i>
<i>Ecosystem function</i>					
Strong resprouting capacity after disturbance (cutting, etc.) (<i>resprout</i>)	4.6 \pm 1.3	4.6 \pm 1.7	4.8 \pm 1.4	4.3 \pm 1.33	0.922
Ability for vegetative propagation (rhizomes, stolons, etc.) (<i>veg prop</i>)	2.1 \pm 0.5	2.3 \pm 1.2	2.2 \pm 1.0	1.8 \pm 1.0	0.797
Ability to fix nitrogen through endosymbiont organisms (<i>N-fix</i>)	0.5 \pm 0.7	0.5 \pm 0.5	0.5 \pm 0.5	0.4 \pm 0.5	0.919
Ability to form ectomycorrhizae (<i>mycor</i>)	2.1 \pm 1.0	2.0 \pm 0.9	2.1 \pm 0.9	2.2 \pm 0.6	0.978
Ability for fire resistance (different strategies) (<i>fire resistance</i>)	2.6 \pm 1.5	2.8 \pm 1.6	2.9 \pm 1.7	2.7 \pm 1.7	0.997
Entomophily (nectar-producing flowers) (<i>entom</i>)	7.9 \pm 2.2	7.8 \pm 2.7	7.9 \pm 3.2	8.6 \pm 2.7	0.788
Endozoochory (fleshy fruits or endosperm-rich seeds) (<i>fleshy fruit</i>)	7.0 \pm 2.1	7.0 \pm 2.3	6.9 \pm 2.6	7.9 \pm 2.5	0.775
Ability to avoid ungulate predation (smell, poison, spines) (<i>ungulate reject</i>)	3.9 \pm 3.9	3.9 \pm 1.7	3.5 \pm 1.2	3.6 \pm 1	0.933
<i>Socio-economic benefit</i>					
Food production (including aromatic plants) (<i>food</i>)	2.9 \pm 1.7	2.8 \pm 1.2	2.8 \pm 1.4	3.5 \pm 1	0.382
Wood production (<i>wood</i>)	3.8 \pm 1.3	3.6 \pm 1.4	3.8 \pm 1.6	4.5 \pm 0.8	0.284
Wild relative of cultivated crops (<i>crop</i>)	1.3 \pm 0.5	1.2 \pm 0.6	1.3 \pm 0.6	1.1 \pm 0.6	0.801
Ornamental value (<i>ornamental</i>)	6.8 \pm 2.1	6.9 \pm 2.4	6.9 \pm 2.7	7.5 \pm 2.1	0.887
Folk medicine (<i>medicine</i>)	4.3 \pm 1.7	4.5 \pm 1.5	4.5 \pm 1.3	5.0 \pm 0.7	0.420

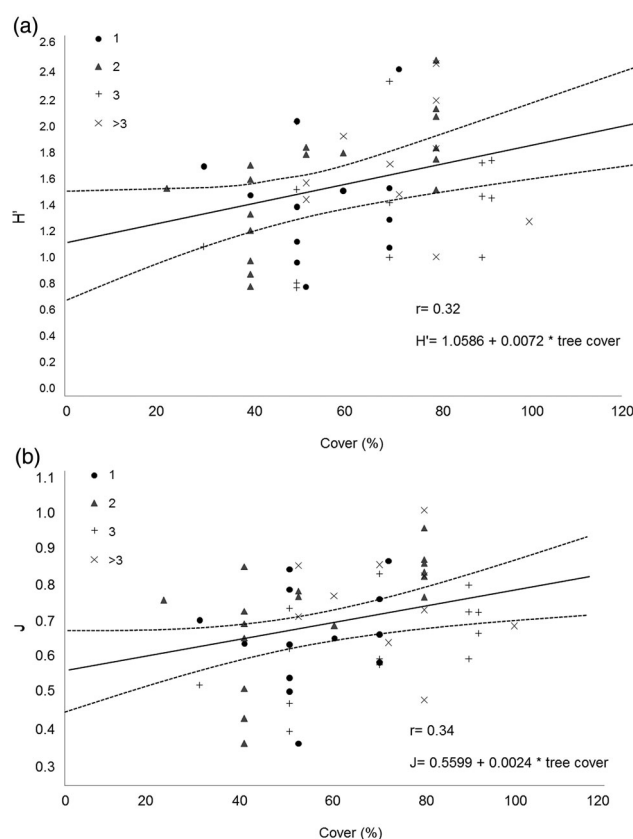


Figure 2. Effect of canopy cover % of dominant tree species (Cover) on: (a) Shannon–Wiener index (H') and (b) evenness (J) of AWS. Regression line and 95% confidence intervals are shown, together with tree species richness levels of the plots (1, 2, 3, >3).

productivity, stability and level of ecosystem functions in a community, since distantly related species are more likely than closely related species to exhibit different functional traits and occupy different niches (Cadotte et al. 2012; Srivastava et al. 2012).

Half of the total number of sporadic tree species found in the whole range of forest types of Tuscany was observed in our plots, among which some were relatively rare such as *Taxus baccata* and *Tilia cordata*. The Rosaceae was the most represented group, in line with the Tuscan Forest Inventory that reports ca. 42 millions of individual trees of this family (over a total of ca. 90 millions with $\text{dbh} \geq 8$ cm), half of which belonging to the genus *Sorbus* (Hofmann et al. 1998). In particular, *S. torminalis* resulted the most frequent species, showing its good conservation status in contrast to most of central Europe where it became increasingly rare due to unfavorable forest management (Rasmussen 2007). This suggests the potential utilization of *S. torminalis* in the local forestry considering both its valuable timber and ecological importance for other functions, such as nourishment of animals and birds (Paganová 2008).

Relationships between AWS and species richness of canopy trees could be explored here, thanks to an experimental design that allowed us to separate diversity from identity effects of dominant trees, while keeping variation of conditions among sites at minimum. Accounting for site variation is crucial when investigating the effects of tree species richness on the diversity of lower forest layers, as this is potentially

one of the most important confounding factors in natural habitats (Barbier et al. 2009). Working in French mountain forests, for example, Zilliox and Gosselin (2014) found that the effects of tree species abundance and richness on the diversity of the understory were different depending on aspect, soil acidity, region and altitude. Although slight variations in soil acidity and/or fertility between our study sites cannot be excluded due to the geomorphological complexity of our region, the lack of covariation between tree richness levels and major site-, soil- and stand-related factors made the sites largely comparable (Baeten et al. 2013).

No significant differences were observed in the frequency of the species along the tree richness gradient, though the present data suggest aspects that seem worth of further investigation. Locally widespread taxa such as *Rubus hirtus* and *Juniperus communis* showed a decreasing frequency with increasing tree richness, while an opposite, positive trend occurred for *Ilex aquifolium* and *Malus sylvestris*, two species that are ecologically more restricted and linked to ancient forests (*sensu* Hermy et al. 1999). The latter was never observed in monocultures, similarly to the rare wild grape which was exclusively found in the 3- and >3-tree stands. This might indicate a positive effect of canopy tree mixture for these three ancient forest species of shady habitats, suggesting further investigation to bring light on this point.

No clear effects of dominant tree richness on the diversity of sporadic trees emerged here, which would mean that monospecific and mixed stands are equally favorable habitats.

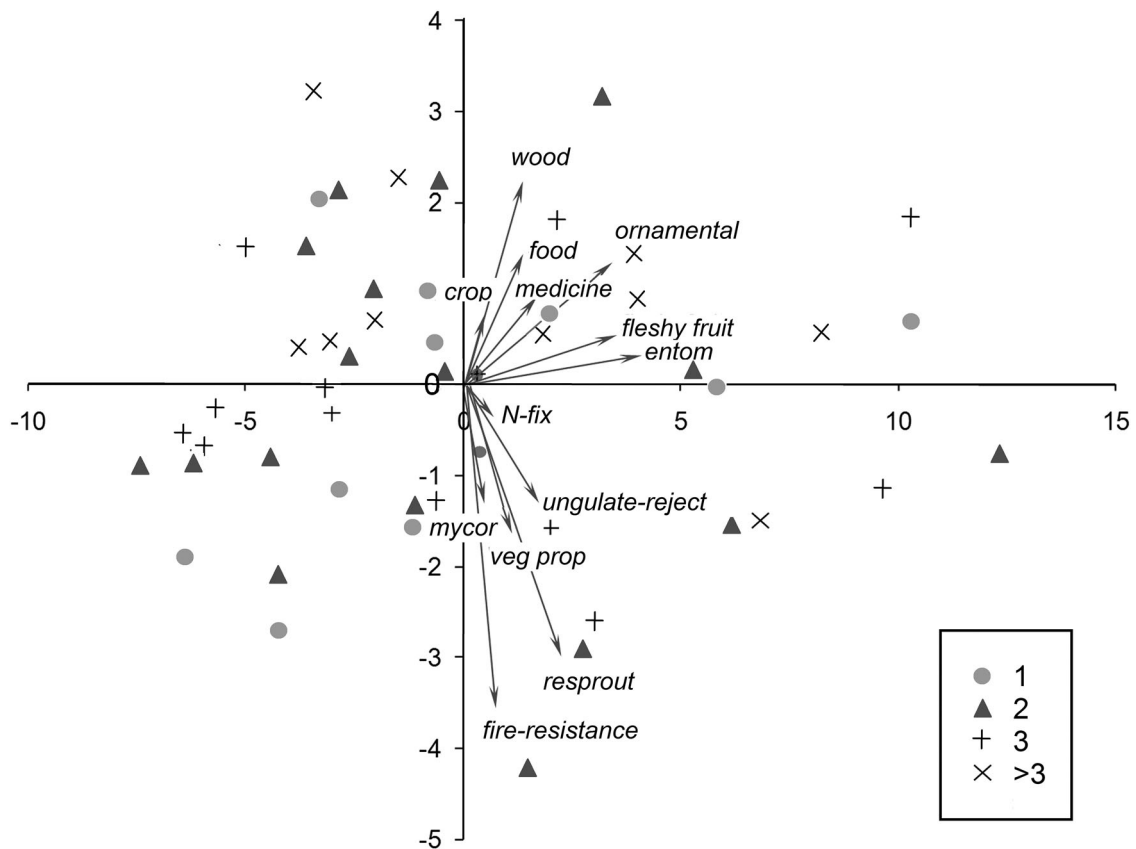


Figure 3. Biplot scattergram from principal component analysis showing relationships between plots in the four levels of species richness of dominant trees (1, 2, 3, >3) and ecosystem functions or expected socio-economic benefits provided by AWS (abbreviations explained in Table 3).

While several studies have examined the responses of the herb layer to tree diversity in European temperate forests (e.g. Mölder et al. 2008; Vockenhuber et al. 2011), no information exists on the linkage between dominant and subordinate tree species in the deciduous woodlands of the Mediterranean region. In our study, mixed plots included up to four sporadic trees and >3-tree mixtures always harbored at least one sporadic species, while in monocultures these were lacking in a number of plots and never more than three. One possible explanation for such a small difference may be that at the regional or local scale factors leading to a higher richness in dominant trees might also be responsible for a better development of sporadic trees.

The shrub component showed a large variation in cover across all plots, in line with findings in Catalanian forests (Vilà et al. 2005), where average cover was about twice than in our sites (63% vs. 30%). Also, the higher shrub cover in the richest tree mixtures observed here supports the significant increase with increasing tree richness found in these Spanish forests (Vilà et al. 2005). In the present study, however, diversity and evenness of shrubs was not affected by tree richness, but responded positively to increasing tree cover, regardless of the number of tree species. Despite the importance of light, some studies on the understory vegetation showed that this factor is not always crucial for the diversity of the herb layer (e.g. Mölder et al. 2008) and that increasing canopy cover can affect positively the proportion of understory species typical of closed stands, thanks to

their functional adaptation to shade (Wulf 2003; Vockenhuber et al. 2011). Since shade tolerance is a key trait of most shrubs of thermophilous forests, a similar positive effect can be supposed here although this cannot explain satisfactorily the increase in their overall diversity with increasing cover by canopy trees.

Although preliminary and limited to only some of the numerous ecosystem functions/services, our analysis is the first one showing the remarkable proportion of minor woody species with a potential ability for important functions or the provisioning of socio-economic benefits. Each species, on average, shows 5.2 of the 13 expected abilities considered, several of which are not possessed by the dominant trees of Fagaceae and Betulaceae. In terms of species number per functional ability, however, there was no trend of variation among the tree richness levels, suggesting comparable levels of benefits and ecosystem processes provided by AWS in mono-specific vs. mixed stands. On the other hand, PCA suggested a separation between the expected benefits and most of the ecosystem functions, which may indicate the need of more investigation separately for the two groups. Estimating the mean level of a given function may in fact require to consider other parameters besides species number, such as measures of species abundance.

In conclusion, AWS are a key diversity component of thermophilous deciduous forests and have the potential of providing a significant contribution to their multiple ecosystem functions and services as a result of their broadly different

abilities and functional traits. From the perspective of a sustainable forest management, conservation of these species should therefore be a priority in especially the southern European countries. Although specific silvicultural options may be adopted to favor single species for given purposes (e.g. timber production from some sporadic trees), our findings suggest that maintaining canopy closure is likely to positively affect overall AWS diversity. On the other hand, no clear effects of dominant tree species richness could be found, implying that monospecific and mixed stands may represent equally favorable habitats for these plants. The strategy of leaving the old coppice forests to their natural development towards uneven, multiple-layered mixed stands with elevated canopy cover appears therefore favorable or at least not detrimental for overall AWS diversity. In agreement with Wulf (2003), however, we stress that more attention and research should be devoted to these minor woody plants to gain a better knowledge of their ecological requirements and functional interactions with dominant canopy trees in temperate forests.

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Disclosure statement

No potential conflict of interest was reported by the authors.

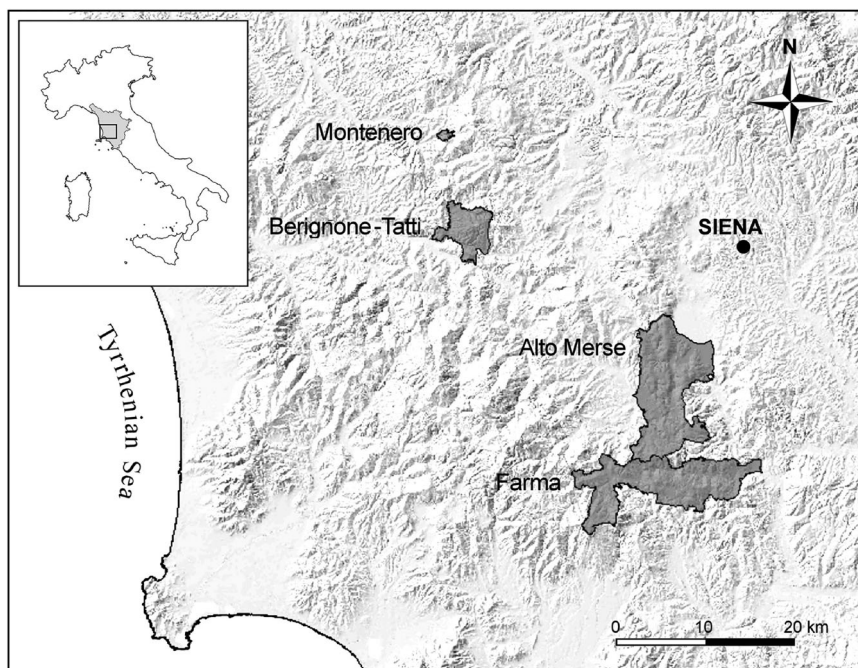
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Appendix 1

Study area (Tuscany, central Italy), with indication of the four Sites of Communitarian Interest of Rete Natura 2000 including the forest stands examined in this study.



Appendix 2

Species mixtures and geographical data of the 53 forest plots examined, with the name of the forest area and the Rete Natura 2000 code of the corresponding Site of Communitarian Interest (coordinates according to the reference system WGS84).

Appendix 2

Species mixture	Lat.	Long.	Altitude (m)	Area	Natura 2000 code
QI	43° 25.9'	10° 59.7'	393	Berignone-Tatti	IT5170006
QI	43° 04.4'	11° 13.0'	417	Farma	IT51A0003
QI	43° 21.4'	10° 58.0'	376	Berignone-Tatti	IT5170006
QC	43° 04.7'	11° 14.8'	551	Farma	IT51A0003
QC	43° 05.1'	11° 14.8'	246	Farma	IT51A0003
QP	43° 21.2'	10° 58.4'	397	Berignone-Tatti	IT5170006
QP	43° 10.2'	11° 12.2'	421	Alto Merse	IT5190006
OC	43° 26.0'	10° 55.0'	416	Montenero	IT5170005
OC	43° 13.6'	11° 11.3'	345	Alto Merse	IT5190006
CS	43° 10.5'	11° 12.1'	402	Alto Merse	IT5190006
CS	43° 04.8'	11° 11.7'	484	Alto Merse	IT5190006
CS	43° 04.9'	11° 11.7'	445	Farma	IT51A0003
CS	43° 04.9'	11° 11.0'	467	Farma	IT51A0003
QI;QP	43° 21.3'	10° 58.2'	395	Berignone-Tatti	IT5170006
QI;QP	43° 04.6'	11° 14.7'	434	Farma	IT51A0003
QI;OC	43° 21.2'	10° 57.0'	343	Berignone-Tatti	IT5170006
QI;OC	43° 18.3'	10° 56.3'	143	Berignone-Tatti	IT5170006
QI;CS	43° 04.8'	11° 14.2'	377	Farma	IT51A0003
QI;CS	43° 04.8'	11° 13.5'	464	Farma	IT51A0003
QI;CS	43° 04.5'	11° 16.8'	372	Farma	IT51A0003
QI;QC	43° 04.4'	11° 13.1'	412	Farma	IT51A0003
QI;QC	43° 04.8'	11° 14.2'	322	Farma	IT51A0003
QC;QP	43° 20.8'	10° 58.4'	443	Berignone-Tatti	IT5170006
QC;QP	43° 04.4'	11° 14.7'	543	Farma	IT51A0003
QC;QP	43° 21.3'	10° 58.2'	398	Berignone-Tatti	IT5170006
QC;OC	43° 18.3'	10° 56.2'	151	Berignone-Tatti	IT5170006

(Continued)

Appendix 2 Continued.

Species mixture	Lat.	Long.	Altitude (m)	Area	Natura 2000 code
QC;CS	43° 04.8'	11° 11.8'	479	Farma	IT51A0003
QC;CS	43° 09.5'	11° 12.6'	279	Alto Merse	IT5190006
CS;QP	43° 11.0'	11° 11.7'	435	Alto Merse	IT5190006
CS;QP	43° 10.5'	11° 12.3'	418	Alto Merse	IT5190006
QI;QP;OC	43° 21.2'	10° 58.3'	422	Berignone-Tatti	IT5170006
QC;QI;OC	43° 04.6'	11° 11.0'	429	Farma	IT51A0003
QC;QI;OC	43° 05.0'	11° 14.7'	288	Farma	IT51A0003
QI;CS;QP	43° 04.9'	11° 12.5'	438	Farma	IT51A0003
QI;CS;OC	43° 04.6'	11° 12.9'	450	Farma	IT51A0003
QI;CS;OC	43° 04.4'	11° 17.0'	355	Farma	IT51A0003
QC;QI;CS	43° 04.8'	11° 15.4'	278	Farma	IT51A0003
QC;QI;CS	43° 04.3'	11° 12.0'	444	Farma	IT51A0003
QC;QI;QP	43° 20.9'	10° 57.9'	533	Berignone-Tatti	IT5170006
QC;QI;QP	43° 20.7'	10° 57.5'	508	Berignone-Tatti	IT5170006
QC;QP;OC	43° 20.6'	10° 58.2'	454	Berignone-Tatti	IT5170006
QC;CS;QP	43° 04.4'	11° 14.8'	540	Farma	IT51A0003
QC;CS;QP	43° 10.2'	11° 12.1'	406	Alto Merse	IT5190006
QC;QI;QP;OC	43° 21.0'	10° 58.2'	470	Berignone-Tatti	IT5170006
QC;QI;QP;OC	43° 20.7'	10° 58.3'	467	Berignone-Tatti	IT5170006
QC;QI;QP;OC	43° 21.0'	10° 56.8'	328	Berignone-Tatti	IT5170006
QC;QI;QP;OC	43° 21.1'	10° 58.4'	425	Berignone-Tatti	IT5170006
QC;QI;CS;OC	43° 04.8'	11° 14.5'	382	Farma	IT51A0003
QC;QI;CS;OC	43° 05.1'	11° 13.6'	410	Farma	IT51A0003
QC;QI;CS;OC	43° 04.3'	11° 16.9'	429	Farma	IT51A0003
QC;QI;CS;QP	43° 04.5'	11° 14.7'	523	Farma	IT51A0003
QC;QI;CS;QP	43° 04.3'	11° 16.7'	519	Farma	IT51A0003
QC;QI;CS;QP;OC	43° 04.4'	11° 16.6'	480	Farma	IT51A0003

Note: QC, *Quercus cerris*; QI, *Quercus ilex*; CS, *Castanea sativa*; QP, *Quercus petraea*; OC, *Ostrya carpinifolia*.

Appendix 3

Results of comparison of site, soil or stand characteristics between the plots of the different tree species richness levels (using permutational analysis of variance, Gower index with extension to ordinal variables, as in Baeten et al. 2013). No significant differences occur in soil or stand characteristics. Univariate tests (linear model) of the individual 'site' variables showed that only the accessibility of the plots (distance from roads) differed between species richness levels: more diverse plots showed slightly lower accessibility (slope

109.2 m per tree richness level, p -value = 0.02). This has no effect on ecosystem properties and is irrelevant for the purposes of this study.

Variable group	F	p	R^2
Site (4 variables)	2.24	0.03	0.23
Soil (8 variables)	0.37	0.95	0.05
Stand (10 variables)	1.14	0.31	0.13

Notes: The number of different variables included in the analysis is indicated after each category. For a full description of these variables see Baeten et al. (2013), Appendix 2.