Are the remnants of old-growth mountain forests always relevant to inspire close-to-nature forest management and efficient biodiversity conservation?

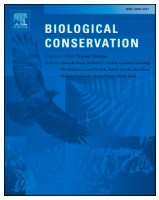
Laurent Larrieu, Sylvain Burri, Gilles Corriol, Nicolas Gouix, Sylvie Ladet, Fabien Laroche, Sophie Maillé, Vanessa Py-Saragaglia, Jean-Marie Savoie, Antoine Brin

Biological Conservation 279 (2023) 109954

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon



Are the remnants of old-growth mountain forests always relevant to inspire close-to-nature forest management and efficient biodiversity conservation?

Laurent Larrieu [a,b,*], Sylvain Burri [c], Gilles Corriol [d], Nicolas Gouix [e], Sylvie Ladet [a], Fabien Laroche [a], Sophie Maillé [f], Vanessa Py-Saragaglia [g], Jean-Marie Savoie [h], Antoine Brin [h]

[a] Université de Toulouse, INRAE, UMR DYNAFOR, Castanet-Tolosan, France
[b] CNPF-CRPF Occitanie, France
[c] TRACES, UMR 5608 CNRS Université Toulouse Jean Jaurès, 5, Allées A. Machado, 31058 Toulouse Cedex 1, France
[d] Conservatoire botanique national des Pyrénées et de Midi-Pyrénées, Vallon de Salut, BP 70315, 65203 Bagnères de Bigorre cedex, France
[e] Conservatoire d'espaces naturels d'Occitanie, Mercuès, France
[f] Nature En Occitanie, Observatoire des forêts des Pyrénées centrales, Bagnères de Bigorre, France
[g] GEODE, UMR 5602 CNRS-Université Toulouse Jean Jaurès, 5, Allées A. Machado, 31058 Toulouse Cedex 9, France
[h] Université de Toulouse, Ecole d'Ingénieurs de PURPAN, UMR INRAE-INPT DYNAFOR, Toulouse, France

ARTICLE INFO

Keywords:
Reference ecosystems
GIS metrics
Old-growth forests
Biodiversity-friendly forest management
Forest matrix

ABSTRACT

Primary and old-growth forests have been identified as a high priority for biodiversity conservation and for identifying benchmarks for biodiversity-friendly forestry. However, they remain rare and not randomly distributed across Europe, concentrated mainly in the boreal zone or in mountainous areas such as the Pyrenees where both ancient (i.e. with a high degree of continuity) and mature (i.e. with old-growth attributes) forests (hereafter AMFs) have been identified and accurately delimited on the French side of the border. Can these AMF remnants provide suitable benchmarks and insure biodiversity conservation? This study aimed to (i) identify factors that explain the current location of AMFs; (ii) assess the potential of these AMFs as reference ecosystems; and (iii) discuss the relevance of the current AMF network for biodiversity conservation. We used a set of 10,344 1 ha-plots, described by 10 metrics for both abiotic conditions and the socio-economic context, to compare AMFs with both forests that are ancient but not mature, and recent forests. AMFs significantly differed from other forests for most of the variables tested, but effect sizes were rather weak, with the exceptions of the occurrence of late frost, exposition and ownership type. Our study provides important insights for biodiversity conservation beyond the case of the northern slope of the Pyrenees. Indeed, our results clearly show that broad-scale patterns require complementary investigations at a regional scale to better understand the influence of past-human activity on the spatial distribution of reference ecosystems. We also illustrate the added value of including geological features and plant communities in the analysis of ecological representativeness of networks dedicated to biodiversity conservation.

1. Introduction

The key role of primary and old-growth forests for biodiversity conservation is recognised world-wide (Watson et al., 2018; Di Marco et al., 2019) such that the European Biodiversity Strategy 2030 (European Commission, 2020) highlights the necessity of mapping, monitoring and strictly protecting all of the EU's remaining primary and old-growth forests. Despite imperfect knowledge about their distribution, we know that these forests represent a small part of the total forest area across Europe (Sabatini et al., 2018) and are under threat of forestry exploitation because they are poorly protected (Sabatini et al., 2021).

Old-growth forests provide unique opportunities to understand forest dynamics under a natural disturbance regime and could be useful for defining benchmarks for forest managers who wish to promote biodiversity-friendly forestry in managed areas (Nagel et al., 2013). However, as observed by Sabatini et al. (2018), at the European-scale,

* Corresponding author at: Université de Toulouse, INRAE, UMR DYNAFOR, Castanet-Tolosan, France.
E-mail addresses: laurent.larrieu@inrae.fr (L. Larrieu), sylvain.burri@univ-tlse2.fr (S. Burri), gilles.corriol@cbnpmp.fr (G. Corriol), nicolas.gouix@cen-occitanie.org (N. Gouix), sylvie.ladet@inrae.fr (S. Ladet), fabien.laroche@inrae.fr (F. Laroche), vanessa.py@univ-tlse2.fr (V. Py-Saragaglia), jm.savoie@purpan.fr (J.-M. Savoie), antoine.brin@purpan.fr (A. Brin).

https://doi.org/10.1016/j.biocon.2023.109954
Received 29 July 2022; Received in revised form 27 January 2023; Accepted 6 February 2023
Available online 15 February 2023

the remnants of primary or old-growth forests are not randomly distributed. They tend to be located more frequently where forestry operations have low profitability, i.e. in rugged and rocky landscapes that are found in remote areas, far from centres of economic activity. Therefore, they might represent a relevant model system for developing close-to-nature management strategies for the full spectrum of ecological conditions encountered in managed forests (Brang, 2005). This situation may also reduce the effectiveness of old-growth forests for conserving biodiversity. Since the terms primeval and old-growth forests have different meanings (see e.g. Buchwald, 2005; FAO, 2015; Kirchmeir and Kovarovics, 2016), we hereafter use the terms "mature", "ancient" and "recent" to characterize forest patches. "Mature" indicates that stands have not been harvested for a long time and therefore have specific attributes, such as very large trees, large amounts of deadwood and a high density of habitat-trees (old-growth forest attributes sensu Bauhus et al., 2009) which are essential for thousands of forest-dwelling taxa (Stokland et al., 2012). "Ancient" defines forests present on maps of the mid-19th century. Since the minimum forest cover extent in France occurred around the mid-19th century, forests that feature on such maps likely have a high degree of continuity (Dupouey et al., 2007), which is an ecologically relevant feature (McMullin and Wiersma, 2019). In contrast, "Recent" (sensu Peterken and Game, 1984) indicates that the forest does not feature on these maps. Ancient and recent forests may or may not have been harvested. Since Sabatini et al. (2018, 2021) follow the FAO definition that defines primary forests as "naturally regenerated forest of native tree species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed", only those forest patches which are both ancient and mature (AMF) match with their specifications.

This study uses the northern slope of the Pyrenees as a case study, since it is one of the mountainous areas highlighted by Sabatini et al. (2021) that has experienced a long history of human use and high intensity of management. We used the digitalisation of historical maps (Grel et al., 2012) to locate ancient forests, and extensive mapping efforts of mature stand patches that were identified and accurately delimited through specific field work carried out over the last two decades (Savoie et al., 2011, 2015; Gouix et al., 2019). In addition, for this area, there is also relatively good knowledge of past humans activities spanning several millennia (Bal et al., 2010; Galop et al., 2013). The forest types we observe today in these long-unharvested areas, such as silver fir-dominated forest (*Abies alba* Mill.) with European beech (*Fagus sylvatica* L.) and yew (*Taxus baccata* L.), or mixed silver fir-beech forest, are the legacy of the additive effects of climate change and anthropogenic drivers since at least the Bronze Age (Saulnier et al., 2020).

During the last two millennia, economic pressures have driven various local and regional forest trajectories, generating shifts in forest structure and composition, i.e. promoting one tree species at the expense of others (e.g. fir for timber or beech for charcoal or in wooded pasture areas) (Bonhôte, 1998; Davasse, 2000; Fouédjeu et al., 2022). The increasing human population and associated needs for arable land, pastures and fuelwood during the 18th century and the first half of the 19th century resulted in reducing forest cover, which was lowest in the mid-19th century (Chevalier, 1956; Desplat, 1973). Due to the rural exodus, which began in the second half of the 19th century, forest cover has since doubled over the last 150 years in many valleys (Rousseau, 1990; Grel et al., 2012). Nowadays, remnants of ancient forests cover about 144,000 ha in the montane and subalpine zones on the northern slopes of the Pyrenees (Grel et al., 2012). About 10,500 ha of these ancient forests are mature (Savoie et al., 2015; Gouix et al., 2019), which indicates natural development over many decades, with minimal anthropogenic influence. The location of those forests which are both ancient and mature (AMF) undoubtedly depends on many factors, including forestry constraints and transportation facilities (e.g. proximity of tracks, trade routes and navigable rivers), past practices, legislation and regulations, as well as changes in ownership and economic policies. As not all of these factors were investigated by Sabatini et al. (2018), this study aims to (i) identify factors that explain the current location of AMFs across the northern slopes of the Pyrenees, particularly compared to forests that are ancient but not mature; (ii) to assess the potential of these AMFs as a reference for ecosystem functioning by evaluating their representativeness of environmental conditions in the surrounding managed forest matrix; and (iii) to discuss the relevance of the current AMF network for the conservation of forest-dwelling taxa, in relation to the array of geological substrates and plant communities, as well as the size and spatial connectivity of AMF patches.

2. Material and methods

2.1. Study area and sampling design

This study focused on forests located on the northern slope of the Pyrenees. Ancient forests, i.e. present on maps from the 19th century (Dupouey et al., 2002b) were mapped when located above 500 m asl (Grel et al., 2012). Of these, mature forest patches, i.e. with old-growth attributes (sensu Bauhus et al., 2009) were mapped, monitored and evaluated in the field over a period of 20 years using 1-ha plots following a standardized protocol (Savoie et al., 2011, 2015; Gouix et al., 2019; Sabatini et al., 2021) (Fig. 1 SM; Table 1 SM). From this database, we selected AMF patches that met the following conditions: (i) located above 1000 m asl (lower limit of the montane belt); (ii) covering at least 1 ha; (iii) belonging to the following forest types: montane fir and beech-fir forests, subalpine fir forests, montane and subalpine pine forests; (iv) forests with no traces of recent agro-pastoral use or harvesting such as stumps at decay stage 1–3 (see referential for decay stages in Appendix; Table 2 SM), no previously pruned trees or grazing areas; (v) containing the entire assemblage of shade-tolerant and long-lived tree-species expected under local environmental conditions (i.e. soil and climate); (vi) harboring >15 very large trees (diameter at breast height (dbh) > 67.5 cm, or 37.5 cm for tree species which never reach 67.5 cm irrespective of the environmental conditions, e.g. rowan, *Sorbus aucuparia*) and 30 large (diameter > 37.5 cm) deadwood items (both standing and downed) per ha. These features were assessed by field measurements; the thresholds used to select the most mature forest patches were the result of a preliminary study (Savoie et al., 2011). The sample of AMFs was composed of 371 patches, ranging from 1 to 286.5 ha, for a total surface area of 9883 ha. In the same geographical area (i.e. same county, above 1000 m asl), ancient but non-mature (hereafter "ancient") and recent (hereafter "recent") forests were identified and covered 144,081 ha and 94,117 ha, respectively. Overall, the studied area covered about 248,081 ha.

2.2. Data analysis

We established a set of 1 ha-plots by generating random points with a GIS, but controlling for the altitude range observed in AMF patches and their geographical extent. The number of plots used to characterize a given AMF patch was defined according to its surface area, from 1 per patch in the smallest ones to 19 plots in the largest. The number of plots that were randomly located in the other forest cover categories was determined according to plot density in AMF patches. Overall, 441, 5990 and 3913 plots (total = 10,344) were used to characterize AMFs, ancient but non-mature forest, and recent forest, respectively. We ensured that no plots overlapped. We characterized each plot with a set of eight environmental (altitude, slope, exposition, temperature, occurrence of late frost, water availability, geology, plant community) and three sociological (type of property, geographical location and population density) metrics that were available using GIS analysis at a large spatial scale (Table 3 SM).

In addition, for each AMF plot, we used field records to define the potential forest plant communities identified at the *association* level. Then we compared the list of plant associations present in AMF patches

with the comprehensive list of the 12 plant associations present in the study area (Corriol et al., 2021), after taking the selection of forest types into account.

We tested the relationship between quantitative variables and forest types using a Kruskal-Wallis test (Kruskal and Wallis, 1952), as most variables were not normally distributed, even after transformation (taking the log or the root-square of response variables). We then used the post-hoc multiple comparison test of Dunn (1961) to pinpoint which comparisons were statistically different. For qualitative variables (exposition types, occurrence of late frost, ownership type and geological substrate), we used a chi-square test of independence with the type of forest. In all cases, the p-value threshold was set at 0.05.

The influence of each independent variable (Table 3 SM) on the probability of AMF occurrence was modeled using a generalized linear model (GLM) with the logit function.

3. Results

3.1. Abiotic conditions

The median area of AMF patches was about 15 ha. Four percent (representing 0.2 % of the total AMF surface area) and 38 % (7 % in surface area) of the AMF patches cover <2 and 10 ha, respectively. AMFs tended to be located at higher elevations (median = 1568 m) compared to ancient (median = 1400 m) and recent (median = 1269 m) forests, but the highest values for both altitude and slope were not observed on AMF plots (Fig. 1A). AMFs tended to be located on steeper areas (median = 66 %) compared to ancient (median = 57 %) and recent (median = 53 %) forests, but not necessarily on the steepest ones (113 %, 170 % and 192 % for AMFs, recent and ancient forests respectively). There was no difference in terms of ruggedness between AMFs and the two other types of forest, but recent forests occurred in slightly less rugged contexts (Fig. 1C). The type of forest was statistically related with the type of exposition (chi-square = 65.62, $p < 0.001$; Fig. 1D) and the occurrence of late frosts (chi-square = 189.73, $p < 0.001$; Fig. 1E). It should be noted that exposition and occurrence of late frosts were not correlated (chi-square = 3.7506, p-value = 0.2897). AMFs were more frequently encountered on north-facing slopes and less frequently on south and east-facing slopes (Table 4 SM).

Water availability (P-ETR) was higher (20 to 27 %) in AMFs compared with the two other forest types (Fig. 1F), but the length of the period of vegetation growth was lower (Fig. 1G) by, on average, seven fewer days than ancient forests and 20 fewer days than recent ones. Among the 19 broad geological substrates present in the studied area, two substrates were significantly underrepresented within the AMF network, namely hard limestone and acidic metamorphic rock. Nine substrates were represented in fewer than 10 AMF patches, while limestone shales were totally absent (Table 5 SM).

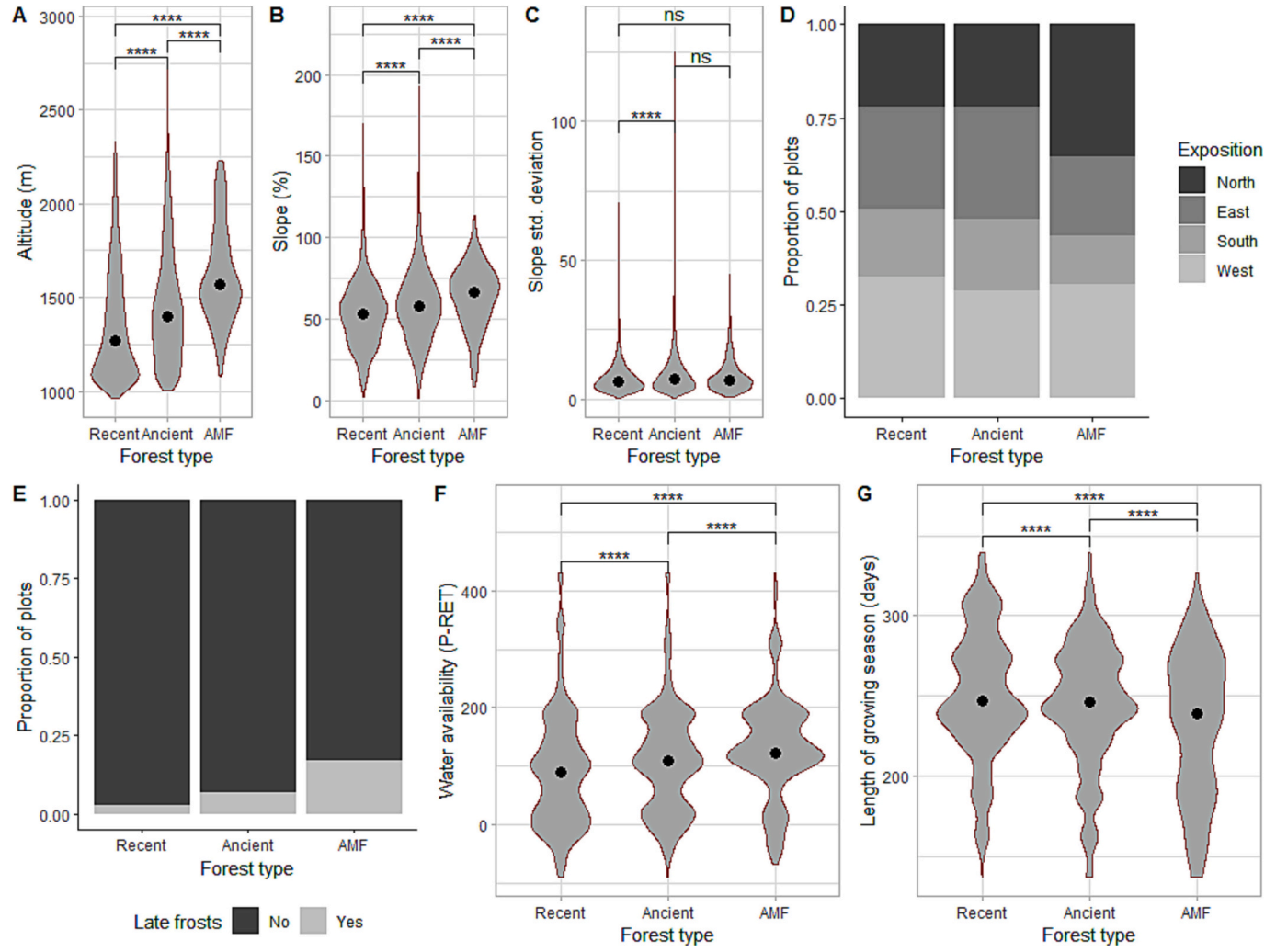


Fig. 1. Distribution of abiotic descriptors for each type of forest (AMF: ancient and mature forest). Results of pairwise Dunn tests are provided using asterisks (****: p-value < 0.00001).

3.2. Anthropic context

AMFs were located farther away from the nearest dirt track, asphalt road or church than the two other forest types (Fig. 2A, B, D). However, they were slightly closer to permanent streams (Fig. 2C). By way of contrast, recent forests tended to be closer to tracks, roads and churches compared with ancient forests (Fig. 2A, B, D).

The type of property had a statistically significant relationship with the distribution of forest types (Fig. 2F and Table 7 SM). AMFs tended to be more common in forests owned by local communities, whereas the opposite was true for private forests. There was no such relationship between state forests and AMFs, but ancient forests were more frequent in state forests than expected by chance, whereas the opposite was true for recent forests.

3.3. Prediction of AMF occurrence

All variables included in the model for predicting the occurrence of AMFs had a significant effect, except human population density (Fig. 3). However, the effect size for most of them was small. The three most influential variables were, in decreasing order, the ownership type, the occurrence of late frost and exposition.

3.4. Plant communities

Eight plant associations (66 %) were well represented in AMF patches, particularly *Scillo lilio-hyacinthi – Fagetum sylvaticae* (190 patches), *Goodyero repentis – Abietetum albae* (79 patches) and *Rhododendro ferruginei – Abietetum albae* (66 patches) (Table 6 SM). With 300 AMF patches, the montane belt was more present than subalpine (n = 141). However, *Ilici aquifolii – Fagetum sylvaticae* was not found on any patch in the montane belt, while *Polygalo calcareae – Pinetum sylvestris* and *Luzulo niveae – Fagetum sylvaticae* were both only present on two patches. For the subalpine stage, *Veronico officinalis – Pinetum sylvestris* and *Pulsatillo alpinae – Pinetum uncinatae* were only present on eight and two patches, respectively.

4. Discussion

4.1. Covariates selected to explain the occurrence of AMFs

Sabatini et al. (2018) used a large set of covariates to explain the occurrence of primeval forest across Europe. Population density, water availability, estimates of wood demand in 1828 according to McGrath et al., 2015, forest cover and terrain ruggedness each explained >7 % of the variance in primeval forest occurrence. However, since Sabatini et al. (2018) did not compare primary forests with surrounding managed forests and studied them at the European scale, most of these covariates are of too coarse a spatial resolution (often 30 arc s) to be used in this study. Due to the strong spatial juxtaposition of AMFs with the other forest types (Fig. 1 SM), we selected covariates that could be calculated at the plot level to maximize our explanatory power. Only meteorological data were considered at a lower resolution (i.e. 8 × 8 km scale) due to data availability constraints (Fig. 2 SM).

4.2. Spatial distribution and representativeness of AMFs for the whole set of environmental conditions

Our results were mostly in line with those of Sabatini et al. (2018), since AMFs occurred in higher, more remote and steeper areas than ancient and recent forests. Late frosts are a limiting factor for agricultural production, especially when they occur in combination with steep, north-facing slopes, which may explain why AMF patches were more frequent in areas with late frost. However, we did not find a link between ruggedness and the occurrence of AMFs.

The major dissonance with Sabatini et al. (2018)'s results concerns

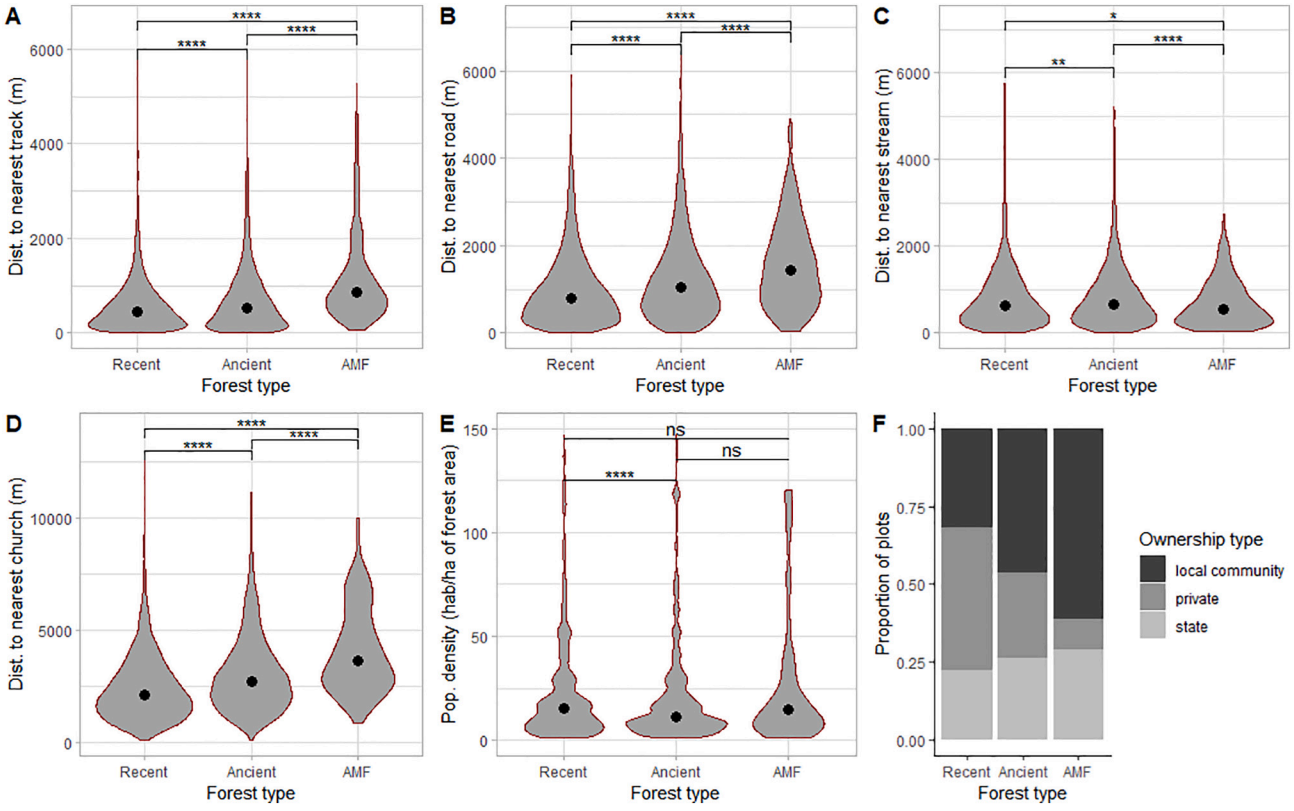


Fig. 2. Distribution of anthropic variables for each type of forest (AMF: ancient and mature forests). Results of pairwise Dunn tests are provided using asterisks (****: p-value < 0.00001; **: p-value < 0.01; *: p-value < 0.05).

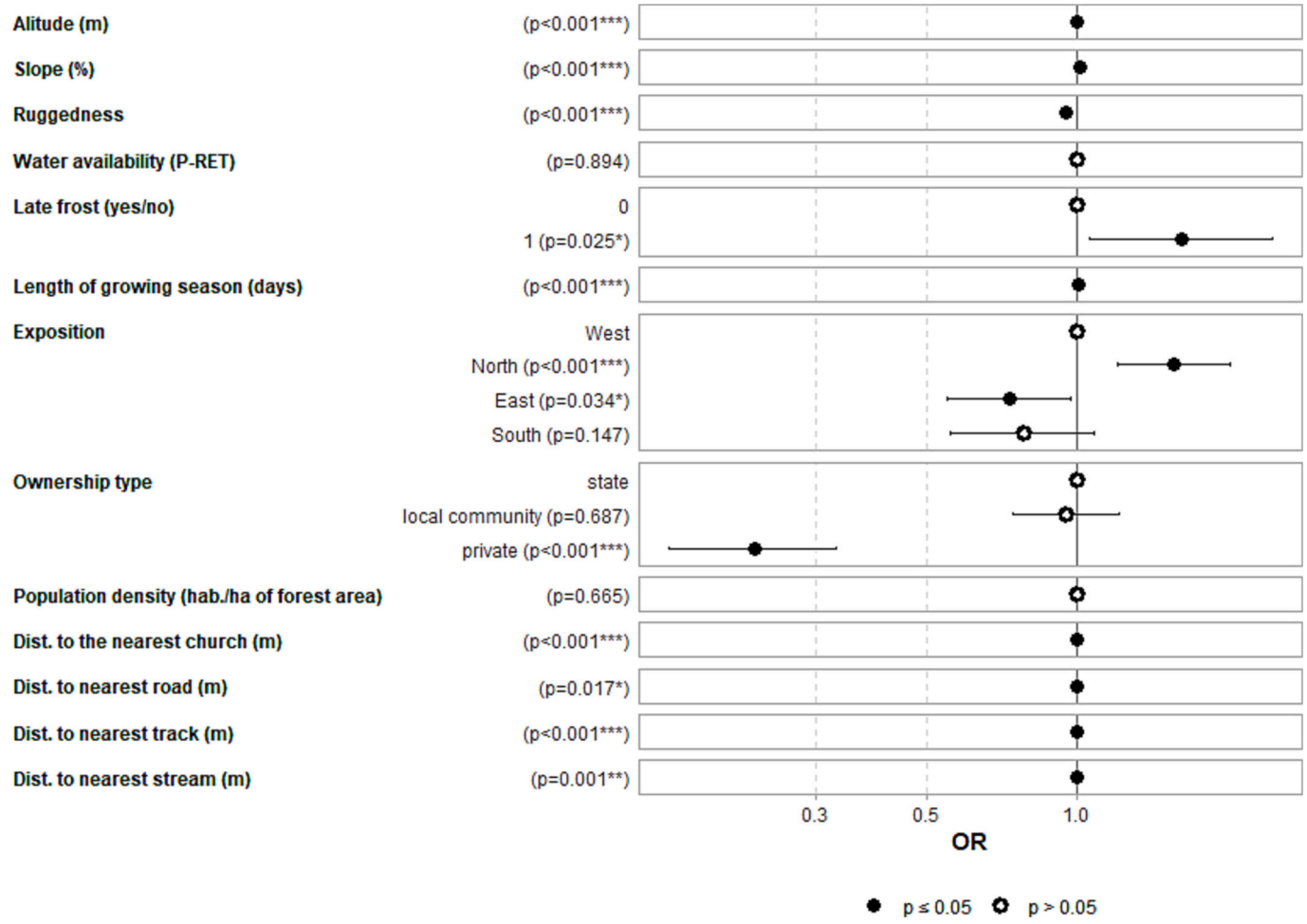


Fig. 3. Results of a logistic regression modelling the relationships between the probability of occurrence for an ancient and mature forest (AMF) and several anthropic and abiotic variables. Symbols represent the estimated odds ratio (OR) and horizontal lines represent the OR confidence intervals at 95 %. The OR value represents the amplitude of change in the probability of occurrence for an AMF for i) a one-unit increase in the continuous variable or ii) in comparison with a reference category for the categorical variables. The reference category is always the first one in the list (i.e. "0" for late frost, "West" for exposition and "state" for ownership type).

human population density (n/km^2) as one of the major drivers of AMF distribution. Based on current population density (Landscan dataset), Sabatini et al. (2018) showed that primary forests are more likely to occur farther away from major towns and in areas where population density is lower. In our case study, there was no significant correlation between current population density and the distribution of AMF patches. One reason could be the differences in spatial resolution between our and Sabatini et al.'s (2018) studies. Another could be that the effect of population density in Sabatini et al. (2018) may be accentuated by the use of other metrics such as the estimated 1850 Forest cover (Kaplan et al., 2009) and 1828 wood demand (McGrath et al., 2015), whose modelling was mainly based on population density. Overall, we think that current population density is not a satisfactory metric to explain current AMF distribution. As stated by Mather et al. (1999), the French "forest transition" started in the early 19th c. and, at that time, the human population was no longer a main driver in the decrease of European forest cover. Indirect evidence of the effects of earlier human settlements and population density is suggested by the fact that current AMFs were located farther away from the nearest church than the other two forest types. To investigate the role of the effect of population density on forest cover and maturity would require the use of early 19th c. population density, but such data, based on archival documentation, is not currently available for the entire northern Pyrenees range and model-based reconstructed population density is not available at the spatial scale used in our study. Not only must population density be considered, but mountain economy must be too. Once again, the modelling-based method proposed by McGrath et al. (2015) is not relevant at our microscale, because it is based on a pan-European generalization of wood consumption rates for domestic and industrial purposes and does not consider local technical particularities. To consider economic drivers in the evaluation of anthropogenic pressure on forests and their evolution, a historical and archaeological-based reconstruction of the intensity of craft and industrial activities, but also of agropastoral activities, is required. Such data should be annotated with detailed, high resolution, historical and palaeoecological studies to reconstruct local forest cover and composition in the past. What Kaplan et al. (2009) proposed for 1850 is not relevant for our study, and more broadly for mountain areas, because they considered mountain areas as unsuitable for agriculture and pasture, and so excluded these areas from their forest cover reconstruction.

We assume that AMF distribution may also be the legacy of previous human population density, forest management and harvesting practices, and, more broadly, of mountain land-use strategies implemented by local communities, as well as local and central authorities. All these variables must be considered according to their own dynamics. Such complexity and dynamics cannot be considered at a local scale through modelling, which glosses over the "wide range of locally appropriate and species-specific strategies" (McGrath et al., 2015). Understanding the

legacies from the past in AMF distribution requires an in-depth investigation of the complex history of mountain areas and resource management, and of the economy at a local scale over time. From a political perspective, the northern slope of the Pyrenees was divided into a mosaic of principalities before their integration into the Kingdom of France, mostly during the modern era (for details, please refer to the suppl. File). This heterogeneity was reflected in various natural resource management systems, which mostly depended on the power balance between local communities and their lords, and its evolution over time (Py-Saragaglia et al., 2019). The same variability applies to the economic trajectories of these territories, which depend on natural resource availability, transportation facilities (routes and the navigability of rivers), the proximity of rural and urban markets, changes in demand and supply, etc. Such economic choices drove important changes in forest structure and composition (Bonhôte, 1998; Davasse, 2000; Fouédjeu et al., 2022), whose legacies are still visible in current woodland (Fouédjeu et al., 2021). While in some parts of the mountain range, the first signs of over-exploitation (i.e. deterioration in the availability of wood resources, forest depletion and poor regeneration) can be detected in the late medieval period (Py-Saragaglia et al., 2019), they occur later in areas where forests were still abundant, especially in remote areas (17th–19th centuries). Integration under the French crown resulted in an attempt to standardize and rationalize forest management and forest product trade under the aegis of the centralized French Forest and Water Office, notably through more strict regulations, and sometimes by reducing the common rights of local communities. The increasing mountain population and related increase in the need for arable land, pastures, timber, and fire wood during the 18th century played an important role in forest cover decrease, which reached a peak in the mid-19th century (Chevalier, 1956; Desplat, 1973), even in the most remote and steepest valleys (Abadie, 1856).

Our results call into question several historical assumptions. For example, the higher rate of AMFs in community forests compared to state and private ones contradicts the supposed unsustainable management of forest resources by local communities, blamed by the centralized Forest and Water administration from at least the Modern Era (Poublanc, 2019). This result is in line, however, with recent studies that have highlighted communities' sustainable management of forest resources (Poublanc, 2020; Fouédjeu et al., 2021, 2022). One should also keep in mind that property rights and regimes may have changed over time, e.g. what today is a community forest may have been a state or private forest before, and vice versa. Likewise, a wide range of private and state forests existed as well (i.e. with or without common rights).

Our results contradict another common assumption: that forests located close to a permanent river are more exploited than more remote ones (Buridant, 2006; Jacob-Rousseau and Gob, 2020). Indeed, AMFs were even slightly closer to permanent rivers and streams than ancient and recent forests. This result seems, at first, to be in contradiction with historical data showing the importance of timber and log rafting, especially on the main Pyrenean rivers, for meeting urban demand and shipbuilding activities from the late medieval period onward (Higounet, 1949; Minovez, 1999). However, this may be explained, at least in part, by the metric chosen to characterize river navigability. Here, every stream and river with permanent water flow was classified as being navigable, but historical data shows that navigability also depended on many other parameters, e.g. waterfalls, congestion by rocks, riverbank development and dams. Headwaters close to montane forests were often only suitable for free log driving, while the lower parts could be used for timber rafts. Correcting the navigability factor would require a detailed historical study on each river. Moreover, as timber production-oriented forests were managed as high stand conifer forest (Agnoletti, 2020), they may have conserved better maturity attributes than charcoal-oriented broadleaf coppices. This assumption needs further comparative investigations.

In the 20th century, road networks, combined with aerial logging using long-distance cableways, were developed (Venet, 1963). This allowed the exploitation of forests which had been heretofore inaccessible. To improve our analysis, several additional factors should be considered, such as prior population dynamics and the industrial and production fabric network, to evaluate anthropogenic pressure on forest resources and its evolution, the balance between forest and pastoral economies, etc. It is through such microscale investigation on some test areas that we could better understand the distribution of AMFs.

4.3. Representativeness of AMFs for non-anthropised ecosystems

Post-glacial forest recovery (starting c. 12,000 cal yr BP) is documented by pollen and plant macrorest records. At the subcontinental scale, and considering the Holocene as a whole, the evolution of vegetation and forest composition is very strongly associated with climate variability, which has driven complex environmental changes since 12,000 cal yr BP (Marquer et al., 2017). At the pan-European scale, the maximum extent of forest cover occurred between c. 8000–6000 cal yr BP (Zanon et al., 2018). On the north side of the Pyrenees, the post-glacial period was characterized by the decline of *Pinus* and *Betula* and the spread of *Corylus* and *Quercus* due to a warmer and wetter climate. *Abies* started to spread from the Mediterranean Pyrenees c. 9000–8000 years ago and reached its optimum in the central Pyrenees c. 5000 years. *Fagus* spread later, from c. 5000–4000 years, probably through complex interactions between human activities, climate variability and forest ecosystem responses. Indeed, spatial distribution models using top-oclimatic factors have highlighted that the current extent of fir in the Pyrenees, as is the case at the broader level of southeastern Europe (Tinner et al., 2013), is more limited than expected, occupying 30 % of the optimal potential area and a narrower altitudinal interval (Alba-Sánchez et al., 2009). Thus, the main primary state of forests before the development of pastoralism and intensive logging activities was fir-dominated old-growth forest (with yew likely abundant under optimal site conditions, Saulnier et al., 2020) in the montane zone, and pine or mixed-pine dominated forest above. But the composition of tree cover varied according to soil conditions, topography, slope exposure and various disturbance factors, creating gaps hosting specific species and driving shifts in forest ecosystems with long-term legacies. Consequently, current AMFs probably do not offer a perfect picture of what primary forests would have looked like because they did not develop with their full array of wildlife, free from human pressures.

Despite this, we think AMF remnants are relevant for inspiring forest management in the ancient forests, since the main differences are in terms of structure due to the presence of more attributes of maturity in AMFs. The case of recent forests is quite different, since past use led to agricultural legacies that have massively disturbed the ecosystem over long periods, such as tilling, soil amendment and fertilization. Thus, significant changes in chemical and structural soil properties can be detected several centuries later (Koerner et al., 1997), or even several millennia after forests come back (Dupouey et al., 2002a), which likely impacts forest dynamics. Moreover, Koerner et al. (1997) suggest taking the agricultural past into account in the management of recent forests. While in the context of lowlands, some forests that were considered to be primeval (according to FAO, 2015) show evidence of very early human agricultural activities (e.g. Białowieża forest, Stereńczak et al., 2020), it is very unlikely that Pyrenean AMFs were cultivated due to their topographical features. However, recent archaeological results obtained in Białowieża question the long-term impact of very ancient agricultural use on soil ecosystems (Stereńczak et al., 2020). This highlights that is necessary to take into account the long-term history of human land use and management strategies to accurately characterize their legacy for current forest ecosystems.

4.4. Relevance of an AMF network for the conservation of forest-dwelling taxa

4.4.1. Range of geological substrates and plant communities

The AMF network includes a wide range of geological substrates, but not the whole set of substrates present in the study area. Furthermore, the AMF network includes only a few patches located on "hard limestone" and "acidic metamorphic rock", whereas these broad categories encompass a wide variety of substrates. An additional ten broad categories are only present in a few patches or are even totally absent from the AMF network. As both substrates and deadwood strongly influence soil characteristics (Harmon et al., 1986), the current AMF network likely does not currently play a conservation role for a part of forest biodiversity, particularly for taxa that are sensitive to soil features, such as plants (Rameau et al., 1993) or saprotrophic and mycorrhizal fungi (Adamo et al., 2021).

The entire set of plant communities present in the studied part of the northern slope of the Pyrenees is not represented in the AMF patch network. Particularly, *Ilici aquifolii – Fagetum sylvaticae* only occur in the managed matrix. This habitat naturally covers a large part of the lower belt of the montane zone where soils are acidic and nutrient poor. The lower belt is the most impacted by management since it is the closest to villages and roads. *Polygalo calcareae – Pinetum sylvestris* and *Pulsatillo alpinae – Pinetum uncinatae* are linked to limestone substrates which are poorly represented in the areas where pine naturally thrives, on the northern side of the Pyrenees. *Luzulo niveae – Fagetum sylvaticae* are strictly located in the eastern part of the Pyrenees. It is crucial to set aside stands that belong to those habitats not yet represented or underrepresented (<10 patches in the AMF network) in order to both ensure the conservation of associated biodiversity and to ensure enough plots for the long term to replicate scientific observations. This is all the more crucial given the small size of AMF patches on average.

Furthermore, it should be noted that the plant community best represented here, classically described as *Scillo lilio-hyacinthi - Fagetum*, has an internal variability linked to local environmental conditions (in particular, gradients of acidity, soil thickness, water balance, Atlantic climate influences) that led to the description of numerous variants, sometimes assigned the rank of sub-associations. We have chosen a synthetic syntaxonomic approach, because the heterogeneity of these descriptions and classifications, which is strongly author-dependent, does not currently provide a consistent description at the scale of the Pyrenees. However, this broad conception makes sense in terms of a dynamic series, since it covers all the non-acidophilic, nutrient-rich, ombrophilous beech-fir forests of the Pyrenean montane zone under the influence of the Atlantic climate.

4.4.2. Spatial connectivity of AMF patches

With a low total surface area (about 4 % of the forest cover of the study area) composed of many patches (N = 371), the AMF network is highly fragmented. However, some species such as the saproxylic beetle *Calytis scabra* are exclusively found in France in the Pyrenean AMFs. At the landscape scale, the viability of a species depends on a minimum amount of resources and their ability to use them, according to the distances between these resources and the dispersal abilities of the species (Johnson et al., 2002). Ranius et al. (2019) highlight the importance of the spatial configuration of habitats for deadwood dwelling species. For example, saproxylic beetle diversity and abundance at the plot scale in lowland forests is greatly enhanced by an increase beyond 20 % in the total area of permanent set-aside patches within a radius of 2500 m (Bouget and Parmain, 2016).

Fahrig (1998), and Flather and Bevers (2002), have shown in theoretical studies that fragmentation can affect the viability of species when the amount of favorable habitat is <20–30 % of the landscape. Indeed, several empirical studies focusing on species with different ecologies converge on a threshold of about 20–30 % (summary in Nilsson et al., 2001). Therefore, relying on the current archipelago of AMFs to conserve species associated with late-succession stages is risky. We urgently need to increase the quality of forest stands in between AMF patches, as this matrix can play a vital role for many species (Driscoll et al., 2013), by increasing the amount of habitat and by improving landscape connectivity.

Retaining deadwood, especially made of large diameter standing or lying pieces, and habitat-trees should be favoured everywhere, as advocated by Komonen and Müller (2018). However, as stated by Ranius et al. (2019), efforts should be prioritised in stands located nearby AMFs. Public policy may help forest managers in orienting stands in this new direction when conflicts arise between retention forestry and wood production.

4.4.3. Size of AMF patches

Jakoby et al. (2010) modeled the dynamics of deadwood in beech forests and showed that, below 2 ha, a patch could not guarantee varied dead wood resources over the long term. Bouget et al. (2013) highlighted that the diversity of deadwood forms was a key factor for the diversity of saproxylic beetles (>2600 species in mainland France; Bouget et al., 2019). Larrieu et al. (2014) showed that a patch smaller than 10 ha of long-term unharvested beech-fir forest could not guarantee a diversity of TreMs, whereas each TreM type constitutes the living environment for distinct communities, sometimes strictly associated with a single TreM type (Larrieu et al., 2018). Moreover, several authors recommend (e.g. Lindenmayer and Franklin, 2002) setting a minimum size for forest patches dedicated to biodiversity conservation that takes into account the most frequent natural disturbance regime in the region concerned. This should at the very least promote a naturally shifting mosaic of development phases. Natural disturbances vary considerably in size in the European mountain forest ecosystems, from several thousand square meters for gap dynamics (Wissel, 1992) to several thousand ha for large windthrow and insect outbreaks (Kulakowski et al., 2017). Therefore, very few current AMF remnants provide an area large enough to allow the whole array of natural disturbances to occur, while conserving the biological legacies of disturbance within the forest.

However, small patches should not be neglected for biodiversity conservation (Wintle et al., 2019), and the exploitation of all AMFs should be avoided, even if they harbor only a fraction of biodiversity. Some of these patches are the last known refuges of rare species such as the beetle *Peltis grossa* (Savoie et al., 2011).

5. Conclusion

As expected, high elevation, steep and north-facing slopes are significant environmental features that explain the occurrence of AMFs in mountain areas. However, ownership type is the most influential feature and a large part of variance in AMF occurrence seems to be explained by historical issues. We argue that forest managers should conduct historical ecology studies in AMFs to better understand the legacies of past practices and integrate this knowledge into conservation strategies.

Although the AMF network is composed of several hundred patches, is distributed along the whole mountain range, and represents about 4 % of the total forest area, it is too patchy, covers too little surface area and is not representative enough of the range of abiotic conditions and plant communities to ensure alone the conservation of biodiversity associated with mountain forest ecosystems in the Pyrenees. Since the Pyrenees is an extensive mountain range, and is very diverse in terms of environmental conditions and past-use by humans, we believe these insights are sufficiently generalizable to be relevant to other temperate mountain areas in Europe.

6. Practical recommendations

6.1. Protect and enhance the current network of both ancient and mature remnants

The current AMF network should be strictly preserved and used as a foundation to set-up a larger network encompassing (i) other forest patches set aside and dedicated to biodiversity conservation, large enough to play this role fully, according to both the provision of key features and the expression of natural processes; these new patches should also help improve its representativeness for at least geological and plant community features; (ii) forests managed following an integrative approach (Kraus and Krumm, 2013). Since it is unlikely that the 20 % threshold of permanent set-aside area at the landscape scale will be reached soon, the spatial design of the complementary AMF patches should be considered to ensure connectivity for most taxa.

6.2. Using patches of both ancient and mature forest as a showcase of the forest ecosystem

Most forest managers have never had the opportunity to see the nature of forests with high naturalness. However, the high values reached by some AMF features such as deadwood volume, basal area, dbh of the largest trees and density of habitat trees, cannot be observed in managed stands, since silviculture controls the range of these values (e.g. Paillet et al., 2015). Therefore, it would be relevant and informative for forest managers to visit some AMFs where accurate data is available, in order to evaluate the gap between the range of values they observe in managed forests and the average values assessed in AMFs. Such visits organized for Swiss forest managers in several Ukrainian AMFs led to fruitful discussions in the field, and changes in practices (Bütler, pers. comm.). Further, marteloscopes (i.e. plots set-up for forest management training where all the trees are located, tagged and described accurately) following the template of the international Integrate Network (https://intégratenetwork.org) should be set up in some AMF patches, and training sessions could be organized. Obviously, sites and periods for visits and training should be chosen with the aim of reducing disturbance for forest-dwelling taxa. Another option would be to use virtual tours such as those provided by the e-platform *Habitat.sylvotheque.ch* (Bütler et al., 2021); using 360° photospheres, this platform enables visits to two parts of the UNESCO beech forest of Uholka (Ukraine).

CRediT authorship contribution statement

JMS, LL, NG, and SM handled the fieldwork. LL, NG, FL and AB designed the general structure of the manuscript. SL did all the geomatic analysis. FL and AB run statistical analysis. All authors contributed to discussion of the results and the writing of the final document.

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

The authors do not have permission to share data.

Acknowledgements

We thank Y. Wiersma and two anonymous reviewers for their help in improving the manuscript. Evan Fisher and then Mark Hewison checked the English language of successive versions.

Funding

This study was funded through the “CONECTFOR” project (Characterization and preservation of forested areas of high ecological value and their ecological connectivity), which benefits from the financial support of the European Regional Development Fund POCTEFA V-A France-Spain-Andorra (POCTEFA 2014–2020); the French State (DREAL Occitanie and ANCT), the Regional Council of Occitanie; and of the partners of the project. It also benefited from the “BENDYS” project (The last European old-growth fir-beech forests: a long-term and global study for their better understanding, conservation and management) which benefits from the financial support of ANR (ANR-19-CE03-0010).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.109954.

References

Abadie, J.-B., 1856. L’indicateur des Hautes-Pyrénées. Paris.
Adamo, I., Castano, C., Bonet, J.A., Colinas, C., de Aragon, J.M., Alday, J.G., 2021. Soil physico-chemical properties have a greater effect on soil fungi than host species in Mediterranean pure and mixed pine forests. Soil Biol. Biochem. 160.
Agnoletti, M., 2020. Storia del bosco. Il paesaggio forestale italiano. Edizioni Laterza, Bari-Roma.
Alba-Sánchez, F., López Sáez, J.A., Benito de Pardo, B., López Merino, L., 2009. Historia paleoecológica y Modelo de idoneidad de abies Alba mill. En la cordillera pirenaica. Pirineos 164, 93–116.
Bal, M.-C., Rendu, C., Ruas, M.-P., Campmajo, P., 2010. Paleosol charcoal: reconstructing vegetation history in relation to agropastoral activities since the neolithic. A case study in the eastern french Pyrenees. J. Archaeol. Sci. 37, 1785–1797.
Bauhus, J.R., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. For. Ecol. Manag. 258, 525–537.
Bonhôte, J., 1998. Forges et forêts dans les Pyrénées ariégeoises : pour une histoire de l’environnement. PyréGraph, Toulouse.
Bouget, C., Parmain, G., 2016. Effects of landscape design of forest reserves on saproxylic beetle diversity. Conserv. Biol. 30, 92–102.
Bouget, C., Larrieu, L., Nusillard, B., Parmain, G., 2013. In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. Biodivers. Conserv. 22, 2111–2130.
Bouget, C., Brustel, H., Noblecourt, T., Zagatti, P., 2019. Les Coléoptères saproxyliques de France : Catalogue écologique illustré, 79. Muséum national d’Histoire naturelle. Patrimoines naturels, Paris.
Brang, P., 2005. Virgin forests as a knowledge source for central European silviculture: reality or myth? For. Snow Landsc. Res. 79 (1/2), 19–32.
Buchwald, E., 2005. A hierarchical terminology for more or less natural forests in relation to sustainable management and biodiversity conservation. In: Third Expert Meeting on Harmonizing Forest-related Definitions for Use by Various Stakeholders. Proceedings. Food and Agriculture Organization of the United Nations, Rome, pp. 17–19.
Buridant, J., 2006. Flottage des bois et gestion forestière: l’exemple du bassin parisien, du XVIe au XIXe siècle. Revue forestière française 54–8, 389–398.
Bütler, R., Rosset, C., Larrieu, L., 2021. Reconnaître les arbres-habitats grâce à l’application habitat.Sylvotheque.Ch. Schweiz. Z. Forstwes. 172 (4), 242–245.
Chevalier, M., 1956. La vie humaine dans les Pyrénées ariégeoises, 2. Editions M.-Th. Génin, Toulouse.
Corriol, et al., 2021. Catalogue of the Elementary Vegetation Types of the Pyrenees and Midi-Pyrenees. Working Document. Conservatoire botanique national des Pyrénées et de Midi-Pyrénées.
Davasse, B., 2000. Forêts, charbonniers et paysans dans les Pyrénées de l’est du Moyen Âge à nos jours : une approche géographique de l’histoire de l’environnement. GEODE, Toulouse.
Desplat, C., 1973. La forêt béarnaise au XVIIIe siècle. Annales du Midi 85 (112), 147–171.
Di Marco, M., Ferrier, S., Harwood, T.D., Hoskins, A.J., Watson, J.E., 2019. Wilderness areas halve the extinction risk of terrestrial biodiversity. Nature 1–4.
Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B., Smith, A.L., 2013. Conceptual domain of the matrix in fragmented landscapes. Trends Ecol. Evol. 28, 605–613.
Dunn, O.J., 1961. Multiple comparisons among means. JASA 56, 54–64.
Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C., 2002b. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83, 2978–2984.
Dupouey, J.L., Sciama, D., Koerner, W., Dambrine, E., Rameau, J.C., 2002. La végétation des forêts anciennes. In: Rev. For. Fr. LIV - 6-2002, pp. 521–532.
Dupouey, J.-L., Bachacou, J., Cosserat, R., Aberdam, S., Vallauri, D., Chappart, G., Corvisier-de Villèle, M.-A., 2007. Vers la réalisation d’une carte géoréférencée des forêts anciennes de France. Le Monde des Cartes 191, 85–98.
European Commission, 2020. Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the

Committee of the regions. EU Biodiversity Strategy for 2030. Bringing nature back into our lives. Brussels, 23 p. https://eur-lex.europa.eu/resource.html?uri=cellar:a3c806a6-9ab3-11ea-9d2d-01aa75ed71a1.0001.02/DOC_1&format=PDF.
Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? Ecol. Model. 105, 273–292.
FAO, 2015. Global Forest Resources Assessment 2015. Terms and Definitions. Rome.
Flather, C.H., Bevers, M., 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. Am. Nat. 159, 40–56.
Fouédjeu, L., Paradis-Grenouillet, S., Larrieu, L., Saulnier, M., Burri, S., Py-Saragaglia, V., 2021. The socio-ecological legacies of centuries-old charcoal making practices in a mountain forest of the northern Pyrenees. For. Ecol. Manag. 502, 119717.
Fouédjeu, L., Burri, S., Saulnier, M., Larrieu, L., Paradis-Grenouillet, S., Py-Saragaglia, V., 2022. Did the charcoal-based iron industry really drive the decline in forest cover in the northern pyrenees? Anthropocene 38, 100333.
Galop, D., Rius, D., Cugny, C., Mazier, F., 2013. Chapter 3. A history of long-term human-environment interactions in the French Pyrenees inferred from the pollen data. In: Lozny, L.R. (Ed.), Continuity and Change in Cultural Adaptation to Mountain Environments. From Prehistory to Contemporary Threats, Studies in Human Ecology and Adaptation, 7. Springer, pp. 19–30.
Gouix, N., Bouteloup, R., Corriol, G., Cuypers, T., Hannoire, C., , et al.Savoie, J.M., 2019. Inventaire et caractérisation des noyaux de « vieilles forêts de plaine » Pour une continuité de la trame forestière entre Pyrénées et Massif-Central. In: Rapport final. Conservatoire d'espaces naturels Midi-Pyrénées / Ecole d'ingénieurs de Purpan.
Grel, A., Heintz, W., Larrieu, L., 2012. Digitalisation et géoréférencement des cartes minutes de l'Etat-major du Parc National des Pyrénées pour une analyse des forêts anciennes. In: Rapport INRA Dynafor/Region MP Feder.
Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Lattin, J.D., Cline, S.P., Aumen, N.G., Sedell, J.R., Cromack, K., Cummins, K.W., Gregory, S.V., Anderson, N. H., Lienkaemper, G.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 133–302.
Higounet, C., 1949. In: Privat, E. (Ed.), Le comté de Comminges. De ses origines à son annexion à la couronne.
Jacob-Rousseau, N., Gob, F., 2020. Le flottage du bois et ses conséquences écologiques, de l'Antiquité à l'époque contemporaine. In: Baud, A., Charpentier, G. (Eds.), Chantiers et matériaux de construction de l'Antiquité à la révolution industrielle en Orient et en Occident, Archéologies, 3. MOM Ed., Lyon, pp. 175–192.
Jakoby, O., Rademacher, C., Grimm, V., 2010. Modelling dead wood islands in european beech forests: how much and how reliably would they provide deadwood? Eur. J. Forest 129, 659–668.
Johnson, D.D.P., Kays, R., Blackwell, P.G., Macdonald, D.W., 2002. Does the resource dispersion hypothesis explain group living? Trends Ecol. Evol. 17 (12), 563–570.
Kaplan, J.O., Krumhardt, K.M., Zimmermann, N., 2009. The prehistoric and preindustrial deforestation of Europe. Quaternary Sci. Rev. 28 (3016–3034), 2009. https://doi.org/10.1016/j.quascirev.2009.09.028.
Kirchmeir, H., Kovarovics, A., 2016. Nomination on Dossier Primeval Beech Forests of the Carpathians and Other Regions of Europe" as Extension to the Existing Natural World Heritage Site Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany. Klagenfurt, 409 p.
Koerner, W., Dupouey, J.L., Dambrine, E., Benoit, M., 1997. Influence of past land use on the vegetation and soils of present-day forest in the Vosges mountains, France. J. Ecol. 85, 351–358.
Komonen, A., Müller, J., 2018. Dispersal ecology of deadwood organisms and connectivity conservation. Conserv. Biol. 32, 535–545.
Kraus, D., Krumm, F. (Eds.), 2013. Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity. European Forest Institute, Freiburg.
Kruskal, W.H., Wallis, W.A., 1952. Use of ranks in one-criterion variance analysis. J. Am. Stat. Assoc. 47, 583–621.
Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T.A., Panayotov, M., et al., 2017. A walk on the wild side: disturbance dynamics and the conservation and management of european mountain forest ecosystems. For. Ecol. Manag. 388, 120–131.
Larrieu, L., Cabanettes, A., Brin, A., Bouget, C., Deconchat, M., 2014. Tree microhabitats at the stand scale in montane beech–fir forests: practical information for taxa conservation in forestry. Eur. J. For. Res. 133, 355–367.
Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., et al., 2018. Tree related microhabitats in temperate and Mediterranean european forests: a hierarchical typology for inventory standardization. Ecol. Indic. 84, 194–207.
Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Washington. The USA.
Marquer, L., Gaillard, M.-J., Sugita, S., Poska, A., Trondman, A.-K., Mazier, F., et al., 2017. Quantifying the effects of land use and climate on holocene vegetation in Europe. Quat. Sci. Rev. 171, 20–37.
Mather, A.S., Fairbairn, J., Needle, C.L., 1999. The course and drivers of the forest transition: the case of France. J. Rural. Stud. 15 (1), 65–90.
McGrath, M., Luyssaert, S., Meyfroidt, P., Kaplan, J., Bürgi, M., Chen, Y., Naudts, K., 2015. Reconstructing european forest management from 1600 to 2010. Biogeosciences 12, 4291–4316. https://doi.org/10.5194/bg-12-4291-2015.
McMullin, R.T., Wiersma, Y.F., 2019. Out with OLDgrowth, in with ecological continNEWity: new perspectives on forest conservation. Front. Ecol. Environ. 17, 176–181.
Minovez, J.-M., 1999. Grandeur et décadence de la navigation fluviale : l'exemple du basin supérieur de la Garonne du milieu du XVIIe au milieu du XIXe siècle. Histoire, économie et société 18e année (3), 569–592.
Nagel, T.A., Zenner, E.K., Brang, P., 2013. Research in old-growth forests and forest reserves: implications for integrated forest management. In: Kraus, D., Krumm, F. (Eds.), Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity. European Forest Institute, Freiburg, pp. 44–50.
Nilsson, S.G., Hedin, J., Niklasson, M., 2001. Biodiversity and its assessment in boreal and nemoral forests. Scand. J. For. Res. 10–26.
Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., 2015. Quantifying the recovery of old-growth attributes in forest reserves: a first reference for France. For. Ecol. Manag. 346, 51–64.
Peterken, G.F., Game, M., 1984. Historical factors affecting the number and distribution of vascular plants in the woodland of Central Lincolnshire. J. Ecol. 72 (1), 155–182.
Poublanc, S., 2019. Les forêts du Midi décrites comme dévastées au XVIIe siècle sont-elles une construction culturelle? Histoire et sociétés rurales 52 (2), 39–66.
Poublanc, S., 2020. Chapter 9. Managing Southern French Forests under—and before—Colbert: between law and custom, ca. 1500–1700. In: Dowling, A., Keyser, R. (Eds.), Conservation's Roots. Managing for Sustainability in Preindustrial Europe. New York, Oxford, Berghahn, pp. 1100–1800.
Py-Saragaglia, V., Burri, S., Fouédjeu, L., 2019. Les forêts montagnardes du versant Nord des Pyrénées. In: Bépoix, S., Richard, H. (Eds.), La forêt Au Moyen Âge. Les Belles Lettres, Paris.
Rameau, J.C., Mansion, D., Dumé, G., 1993. Flore Forestière Française. IDF, Paris.
Ranius, T., Snall, T., Norden, J., 2019. Importance of spatial configuration of deadwood habitats in species conservation. Conserv. Biol. 33, 1205–1207.
Rousseau, P., 1990. L'évolution des forêts françaises métropolitaines d'après les statistiques forestières. In: Rev. For. Fr. XLII - 1-1990, pp. 56–68.
Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., et al., 2018. Where are Europe's last primary forests ? Diversity and Distribution 24, 1426–1439.
Sabatini, F.M., Bluhm, H., Kun, Z., Aksenov, D., Atauri, J.A., et al., 2021. European Primary Forest Database v2.0. SCIENTIFIC DATA.
Saulnier, M., Cunill Artigas, R., Fouédjeu, L., Buscaino, S., Métailié, J.-P., Galop, D., Py-Saragaglia, V., 2020. A study of late holocene local vegetation dynamics and responses to land use changes in an ancient charcoal making woodland in the Central Pyrenees (Ariège, France), using pedoanthracology. Veg. Hist. Archaeobotany 29, 241–258.
Savoie, J.M., Bartoli, M., Brin, A., Brustel, H., Celle, J., Corriol, G., et al., 2011. Forêts pyrénéennes anciennes de Midi-Pyrénées. Rapport d'Etude de projet FEDER 2008-2011. Ecole d'Ingénieurs de PURPAN/DREAL Midi-Pyrénées.
Savoie, J.M., Bartoli, M., Blanc, F., Brin, A., Brustel, H., Cateauet, et al., 2015. Vieilles forêts pyrénéennes de Midi-Pyrénées. Deuxième phase. Evaluation et cartographie des sites. In: Recommandations. Rapport FInal. Ecole d'Ingénieurs de PURPAN/DREAL Midi-Pyrénées.
Stereńczak, K., Zapłata, R., Wójcik, J., Kraszewski, B., Mielcarek, M., Mitelsztedt, K., et al., 2020. ALS-based detection of past human activities in the Białowieża forest—new evidence of unknown remains of past agricultural systems. Remote Sens. 12, 2657.
Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in Dead Wood. Cambridge University Press, Cambridge, UK.
Tinner, W., Colombaroli, D., Heiri, O., Henne, P.D., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J.R.M., Carraro, G., Conedera, M., Joos, F., Lotter, A.F., Luterbacher, J., Samartin, S., Valsecchi, V., 2013. The past ecology of Abies alba provides new perspectives on future responses of silver fir forests to global warming. Ecol. Monogr. 83, 419–439.
Venet, J., 1963. In: Utilisation combinée de la route et des câbles. RFF août-septembre 1963, pp. 682–697.
Watson, J.E.M., Venter, O., Lee, J., Jones, K.R., Robinson, J.G., Possingham, H.P., Allan, J.R., 2018. Protect the last of the wild. Nature 563, 27–30. https://doi.org/10.1038/d41586-018-07183-6.
Wintle, B.A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Moilanen, A., Gordon, A., Lentini, P.E., Cadenhead, N.C.R., Bekessy, S.A., 2019. Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. PNAS 116, 909–914.
Wissel, C., 1992. Modeling the mosaic cycle of a middle European beech Forest. Ecol. Model. 63, 29–43.
Zanon, M., Davis, B.A.S., Marquer, L., Brewer, S., Kaplan, O.J., 2018. European Forest cover during the past 12,000 years : a palynological reconstruction based on modern analogs and remote sensing. Front. Plant Sci. 9 (2018) https://doi.org/10.3389/fpls.2018.00253.