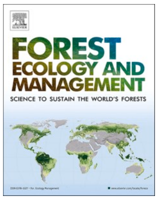
Forest Ecology and Management 614 (2026) 123827

Contents lists available at ScienceDirect

Forest Ecology and Management

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



Beyond management: Proforestation enriches tree-related microhabitat diversity, but forest types determine their composition across Mediterranean and Alpine forests

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ARTICLE INFO

Keywords:
Proforestation
Management abandonment
Forest structural complexity
Deadwood
TreMs

ABSTRACT

Proforestation, defined as the long-term protection of existing forests to allow the self-development of old-growth attributes, is increasingly promoted as a nature-based solution for biodiversity conservation. However, its effects on tree-related microhabitats (TreMs), key indicators of forest structural complexity, remain unevenly documented across forest types. Most existing studies have largely examined TreM richness and abundance, while effects on TreM composition across contrasting forest contexts have rarely been addressed.

We investigated how time since abandonment (TSA), as a proxy for proforestation duration, influences TreM richness, abundance, and composition across three different forest categories spanning Mediterranean to Alpine environments. Within each category, we compared actively managed forests with stands under proforestation for more than 20 and more than 60 years. TSA generally promoted TreM richness and abundance, albeit to a lesser extent in the Mediterranean forest site. In contrast, responses of individual TreM groups were strongly context-dependent, with some groups increasing and others decreasing along the proforestation gradient.

TreM composition differed significantly among abandonment stages in all forest categories, although the magnitude was generally modest, with long-term proforested stands supporting distinct assemblages primarily driven by turnover and associated with increasing deadwood availability. The pattern of these compositional shifts varied among forest categories, reflecting differences in environmental conditions and management history.

Our findings demonstrate that proforestation could not only enhance TreM availability but also influence TreM assemblages through long-term structural dynamics. Integrating long-term proforested stands into forest planning can represent an effective conservation strategy to promote biodiversity-related forest structures.

1. Introduction

Forest restoration is the process of assisting the recovery of a forest that has been degraded, damaged, or destroyed (Gann and Lamb, 2006) and is widely recognised as a central strategy for supporting carbon (C) sequestration, biodiversity, and ecosystem functioning (Aerts and Honnay, 2011; Lewis et al., 2019). Within this broad framework, rewilding has emerged as complementary approach, focusing on reinstating natural processes that would occur in the absence of human activity, primarily through the reduction or cessation of direct human management (Wentworth and Alison, 2016; Perino et al., 2019). Originally focused on the protection of extensive, well-connected areas to support large carnivores, the concept of rewilding has progressively broadened into a dynamic, process-based approach. Building on this concept, proforestation (i.e., the conservation practice of allowing existing forests to grow to their ecological potential through

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https://doi.org/10.1016/j.foreco.2026.123827
Received 13 February 2026; Received in revised form 10 April 2026; Accepted 19 April 2026

management abandonment (Moomaw et al., 2019)) has been recognised as an effective nature-based solution for climate change mitigation and biodiversity conservation (Buotte et al., 2020). Multiple studies have demonstrated that forest set-aside can strongly influence structural attributes, including stand complexity (Bouget et al., 2014; Paillet et al., 2015a) and deadwood accumulation (Vandekerkhove et al., 2009; Larrieu et al., 2012; Bouget et al., 2014; Paillet et al., 2015a; Motta et al., 2024). These structural changes have direct implications for biodiversity, as forest complexity is a key determinant of plant and animal diversity (Della Longa et al., 2020; Zeller et al., 2023) and provides measurable indicators of habitat quality and ecological integrity (Lindenmayer et al., 2000; McElhinny et al., 2005).

Forest structural complexity can be assessed using metrics that capture stand-level horizontal and vertical structure, as well as indirect indicators of fine-scale habitat features, such as lying and standing deadwood volume, which are widely used as structural proxies in European forest biodiversity monitoring protocols (Tomppo et al., 2010). Among the latter, tree-related microhabitats (hereafter TreMs) represent small, distinct structure on standing trees (e.g., cavities, cracks, conks, and dead branches), that are closely linked to the occurrence and diversity of a wide range of organisms, including plants, fungi, and animals (Larrieu et al., 2018). Positive relationships between TreM diversity or density and species richness or community composition have been reported across multiple taxonomic groups, highlighting their potential as indicators of forest biodiversity (Regnery et al., 2013a; Paillet et al., 2018; Basile et al., 2020).

In this context, several studies have also investigated how forest management practices influence TreMs (Winter et al., 2005; Martin et al., 2022). Silvicultural interventions can strongly affect the formation, persistence, and diversity of TreMs, primarily by modifying tree age structure, species composition, and the presence of large or senescent trees (Bouget et al., 2014; Paillet et al., 2015a; Dieler et al., 2017), all of which are key determinants of TreM occurrence and diversity (Asbeck et al., 2021). Comparative studies of managed and unmanaged or long-abandoned forests have documented variable effects of management on TreM richness, and abundance (Kozák et al., 2018; Martin et al., 2022). TreMs are often more abundant and diverse in unmanaged or long-abandoned forests compared to managed ones, both at tree-level (Marziliano et al., 2021; König et al., 2026) and at plot-level (Winter et al., 2005; Winter and Möller, 2008; Regnery et al., 2013b; Bouget et al., 2014; Lelli et al., 2019; Schall et al., 2021; Mamadashvili et al., 2023; König et al., 2026), although some studies have found no significant differences (tree-level: Vuidot et al., 2011; plot-level: Larrieu et al., 2012; Larrieu et al., 2014; Khanalizadeh et al., 2020), and others reported contrasting patterns depending on forest type or site conditions (plot-level: Lilja and Kuuluvainen, 2005; Winter et al., 2015; Paillet et al., 2017). Part of such a variability likely reflect methodological differences, including the use of distinct TreM classification systems, which can affect detection, interpretation and cross-study comparability (e.g., Winter and Möller, 2008; Vuidot et al., 2011; Kraus et al., 2016; Larrieu et al., 2018).

Overall, these findings indicate that the effects of proforestation on TreM diversity and abundance are context-dependent, varying with forest type, and biogeographical conditions. Despite this, research has largely focused on temperate and montane forests, whereas Mediterranean systems remain underrepresented (Santopuoli et al., 2022; Spina et al., 2024; Rota et al., 2025), particularly regarding the effects of proforestation on TreM abundance and richness (Regnery et al., 2013b; Marziliano et al., 2021). Additionally, comparative studies across contrasting ecological and biogeographical regions are still scarce (Vuidot et al., 2011; Bouget et al., 2014; Winter et al., 2015; Paillet et al., 2017, 2019; Mamadashvili et al., 2023; Larrieu et al., 2025), limiting our understanding of how management abandonment shapes TreM patterns at larger spatial scales. Furthermore, only few studies explicitly considered time since management abandonment (TSA) and compositional shifts over time remain largely unexplored (Winter et al., 2015; Paillet et al., 2017; Mamadashvili et al., 2023). This is particularly important as forest responses to proforestation are expected to follow non-linear trajectories over time, shaped by structural legacy effects and delayed ecological processes, making the explicit consideration of TSA essential for understanding long-term biodiversity outcomes. Moreover, as TreMs can be rapidly assessed in the field and are increasingly integrated into forest certification schemes and biodiversity-oriented management guidelines, understanding how proforestation affects their diversity and composition is highly relevant for both conservation planning and applied forest management.

The present study investigates the effects of proforestation on TreM richness, abundance, and composition across three forest sites spanning Mediterranean to Alpine environments in Southern Europe. These sites differ in forest category, climate and abandonment history, providing an opportunity to evaluate context-dependent responses along a broad ecological gradient (Paillet et al., 2017).

We specifically hypothesised that:

(i) TSA would have a positive effect on overall TreM metrics, with broadly consistent patterns across sites;
(ii) individual TreM groups would show heterogeneous, site-dependent responses, reflecting variation in forest category, species composition, and local conditions;
(iii) TreM assemblages would undergo compositional turnover across abandonment stages, with the patterns of change varying among sites.

By adopting a multi-site, comparative approach, this study aims to disentangle general and site-specific effects of proforestation on TreM, richness, abundance, and composition, providing key insights for biodiversity-oriented forest planning.

2. Materials and methods

2.1. Study sites

We conducted this study at three sites in north-eastern Italy and the Istrian Peninsula (Croatia), selected to capture a broad altitudinal and climatic gradient from Mediterranean to Alpine environments (Table 1).

The first study site is the Kontija Forest (45°14′ N, 13°68′ E), located in western Istria (Croatia) and characterised by a Mediterranean climate. The area is covered by mixed broadleaf forests classified as thermophilous deciduous forests, dominated by pubescent oak (*Quercus pubescens* Willd.), Oriental hornbeam (*Carpinus orientalis* Mill.), and manna ash (*Fraxinus ornus* L.), with occasional occurrences of field maple (*Acer campestre* L.), Turkey oak (*Quercus cerris* L.), field elm (*Ulmus minor* Mill.), Montpellier maple (*Acer monspessulanum* L.), and holm oak (*Quercus ilex* L.). Most forest compartments are actively managed under a shelterwood system through successive regeneration cuts. Two forest patches have been excluded from management and left to develop without silvicultural interventions. One patch has been unmanaged since the early 2000s, while another has been left unmanaged since 1964, when a strict forest reserve was established.

The second study site is the Eastern Cansiglio Regional Forest (46°07′ N, 12°44′ E), located in the outer Alpine zone along the border between the Friuli Venezia Giulia and Veneto. The selected stands are alpine coniferous forests, dominated by Norway spruce (*Picea abies* (L.) H. Karst.) and silver fir (*Abies alba* Mill.), with European beech (*Fagus sylvatica* L.) as a co-dominant species and scattered individuals of common ash (*Fraxinus excelsior* L.). Managed stands are even-aged high forests under a shelterwood system with thinnings. The two unmanaged stands consist of mature high forests that have developed without active management. For these stands, no management records are available since the 1990s and the 1960s, respectively, and they were designated as strict forest reserves in 2007 and 1972.

The third study site is the Val Alba Regional Forest (46°46′ N, 13°22′

Table 1
Main climatic and environmental characteristics of the three study sites. Climatic variables (mean annual temperature and mean annual precipitation) refer to the 1970–2000 period and were obtained from the WorldClim 2.0 dataset (Fick and Hijmans, 2017). Forest categories and types are classified according to the European Environment Agency technical report (European Environment Agency, 2006).

Site	Forest category	Forest type	Number of plots	Stand area range (ha)	Altitudinal range (m a.s.l.)	Mean annual temperature (°C)	Mean annual precipitation (mm)
Kontija	Thermophilous deciduous forest	Downy oak forest	27	8–15	90–100	13.9	837
Cansiglio	Alpine coniferous forest	Subalpine and mountainous spruce and mountainous mixed spruce-silver fir forest	27	14–15	1050–1120	7.2	1098
Val Alba	Mountainous beech forest	Central European mountainous beech forest	27	11–30	1100–1310	5.7	1554

E), located in the inner Alpine zone of Friuli Venezia Giulia. The selected stands are mountainous beech forests, dominated by European beech (*Fagus sylvatica* L.), with silver fir (*Abies alba* Mill.) as a co-dominant species and scattered individuals of Norway spruce (*Picea abies* (L.) H. Karst.) and European larch (*Larix decidua* Mill.). Managed stands are even-aged transitional high forests, currently subject to progressive thinning to complete conversion from former coppice management. In contrast, the two unmanaged stands are transitional high forests that have developed through natural dynamics following cessation of previous management, with last silvicultural interventions recorded in the 1980s and the 1960s, respectively.

At each site, three forest stands representing different stages of forest management abandonment were selected, for a total of nine stands (range: 8–30 ha) (Fig. 1). The three abandonment stages were: (i) recently or actively managed (M), (ii) abandoned for over 20 years (intermediate-abandonment, IA), and (iii) abandoned for more than 60 years (long-abandonment, LA). The selected forest compartments have similar environmental conditions and history before abandonment.

2.2. Dendrometric and TreM data

Within each stand, nine sampling plots were established, resulting in a total of 81 plots across all sites. Plots were randomly distributed following a triplet design, with three plots arranged around three central points (centroids) per stand. This design ensured spatial independence while maintaining a balanced sampling structure within each stand. Sampling design and dendrometric data collection followed the protocol of the Italian National Forest Inventory (Gasparini et al., 2022).

Briefly, all standing trees (both alive and dead) with a diameter at breast height (DBH) $\geq$ 9.5 cm were surveyed within a 13-meter radius plot (531 m^2). For each tree, we recorded species, DBH, vitality status (dead/alive), and the presence of TreMs. TreMs were visually assessed using the classification of Kraus et al. (2016), which distinguishes 64 distinct types and represents the most detailed catalogue currently available. This classification was chosen because TreM types can be aggregated into broader categories, facilitating comparison with studies using coarser schemes.

Surveys were consistently performed by the same pair of observers (G.M. and C.D.) across all plots and sites, a procedure that minimise observer bias (Paillet et al., 2015b) and aligns with recommendations by Larrieu et al. (2018), who emphasise that double-observer inventories tend to be completer and more systematic. All fieldwork was conducted during the winter 2024–2025 under leaf-off conditions to maximise visibility of microhabitats and structural features (Larrieu et al., 2018).

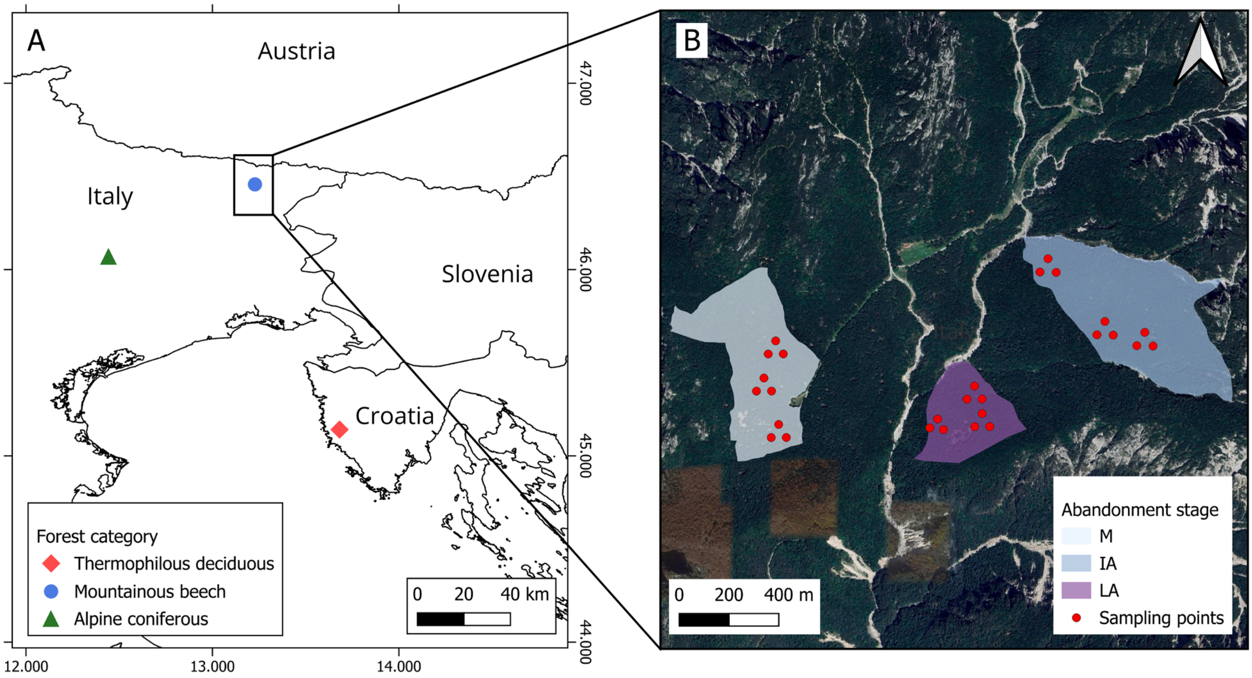

Fig. 1. Study sites and sampling design. A: Location of the three study sites. Coloured symbols indicate the centroid of each site (thermophilous deciduous forest, red square; alpine coniferous forest, green triangle; mountainous beech forest, blue dot). B: Sampling design using the mountainous beech forest as an example. Coloured stands represent the three abandonment stages (recently or actively managed – M, light blue; intermediate-abandonment – IA, blue; long-abandonment – LA, violet), each with nine sampling points. Coordinates are reported in EPSG:4326 (WGS84).

For each tree, the presence or absence of each distinct microhabitat type was recorded, regardless of how many times it occurred on the same individual (Paillet et al., 2017).

To investigate effects of TSA, we calculated four TreM-based indices at the plot level. First, TreM abundance, expressed as the total number of TreMs recorded in each plot (i.e., each TreM type observed on a tree counted as one occurrence) and standardised per hectare. Second, TreM richness, defined as the number of different TreM types per plot. Third, the density of TreM-rich trees, defined as trees bearing > 2 TreM types. This third metric was calculated in two ways: (i) as the total number of trees with > 2 TreM types per hectare, and (ii) as the proportion of such trees per plot, accounting for potential biases due to differences in overall tree density. The threshold of two TreMs per tree corresponded to the 75th percentile of microhabitat counts across all sampled trees, identifying individuals that substantially contribute to habitat availability (Supplementary Figure S1).

Finally, we assessed how the frequency per plot of specific TreM categories varied along TSA, following the 15-group classification of Larrieu et al. (2018), which aggregates the 64 types of Kraus et al. (2016) into broader functional groups (Supplementary Table S2). As in Vuidot et al. (2011), analysis focused on the most common groups (i.e., those occurring on > 20 trees per site) to ensure sufficient representation. For each group, we quantified the number of trees bearing at least one microhabitat of that group per plot both in absolute terms (i.e., number of TreM-bearing trees per hectare) and relative terms (i.e., proportion of TreM-bearing trees per plot), thereby controlling for differences in tree density among stands.

2.3. *Statistical analyses*

All statistical analyses were performed using RStudio (RStudio Team, 2024; R Core Team, 2024, version 4.4.2). Data processing and visualisation were performed using the *tidyverse* package (Wickham et al., 2019). The sampling design followed a nested structure, with three study sites, each containing three forest stands representing different abandonment stages. Within each stand, nine plots were sampled, resulting in a total of 81 plots. Following König et al. (2026), analyses were conducted at the plot level, treating plots as replicates within each abandonment stage. To assess potential spatial dependence among plots, we tested for spatial autocorrelation using Moran's I (Hartig, 2016), which indicated no spatial autocorrelation.

To assess the effects of TSA on TreM metrics, we fitted generalised linear models including the interaction between stage and forest category to test whether TSA effects varied across sites (Eq. 1):

$$\text{Trem metrics} \sim \text{abandonment stage} + \text{forest category} + \text{abandonment stage:forest category} \tag{1}$$

Following previous studies on TreMs (e.g., Regnery et al., 2013; Bouget et al., 2014), count data (TreM richness, TreM abundance, TreM-rich trees per hectare, and TreM-bearing trees per hectare) were modelled using Poisson or Conway-Maxwell-Poisson (COM-Poisson) error distributions, depending on the presence of over- or under-dispersion, using the *glmmTMB* package (Brooks et al., 2017). Proportion variables (proportion of TreM-rich trees and TreM-bearing trees per plot) were analysed using beta error distribution. Model fit and assumptions were evaluated using the *DHARMa* package (Hartig, 2016), through graphical diagnostics and tests for residual normality, homoscedasticity, and overdispersion. Pairwise comparisons were conducted with *emmeans* package (Lenth et al., 2018) with Sidak correction for multiple testing.

Differences in TreM composition among abandonment stages were evaluated using permutational multivariate analyses of variance (PERMANOVA) based on the Jaccard dissimilarity index with 999 permutations and applied to the plot-level matrix of TreM types (*adonis2* function, *vegan* package; Oksanen et al., 2007). PERMANOVA was performed separately for each forest category to test for stage-specific differences, and on the overall dataset to assess the effects of forest category, abandonment stage, and their interaction. Pairwise comparisons between stages were performed with Bonferroni correction to adjust for multiple testing. Additionally, PERMANOVA was repeated on the turnover and nestedness components of β-diversity to determine their contribution to overall compositional dissimilarity. We also conducted an analysis of multivariate homogeneity (PERMDISP) following PERMANOVA, using the *betadisper* function to test whether groups differed in dispersion (*vegan* package; Oksanen et al., 2007). Patterns in TreM composition were visualised using principal coordinate analysis (PCoA). Finally, an indicator value (IndVal) analysis was performed to identify TreM types significantly associated with specific abandonment stages, using the IndVal method implemented in the *indicspecies* package (De Cáceres and Legendre, 2009).

Statistical significance was considered at $p < 0.05$.

3. Results

Across the three study sites, a total of 2493 trees were inventoried, revealing significant differences in both the proportion of living and dead trees, as well as the distribution of trees across DBH classes (Supplementary Table S3, and Supplementary Figure S2, and S3). In addition, notable variations were observed in the overall frequency and the dominant types of TreMs (Supplementary Table S1).

In the thermophilous deciduous forest, 889 trees were measured. The most common TreM types were *epiphytic bryophytes*, which occurred on 21% of the trees, followed by *small insect galleries and bore holes* (15%), and *water sprouts* (12%).

In the alpine coniferous forest, 590 trees were recorded. *Epiphytic bryophytes* were again the most frequent TreM type, found on 58% of all trees. *Small buttress-root concavities* appeared on 41% of trees, while *large buttress-root concavities* were present on 30%.

In the mountainous beech forest, 1014 trees were inventoried. The most common TreM types were *small buttress-root concavities* (28%), followed by *small insect galleries and bore holes* (20%), and *large bark loss with early decay stage* (9%).

3.1. *Effects of TSA on TreM indices*

The influence of forest management cessation on TreM indices was generally consistent across study sites and metrics. However, pairwise comparisons revealed some site-specific differences (Fig. 2).

For TreM richness, significant increases were observed in long-abandonment stands compared to both managed (+33% and +58%) and intermediate-abandonment stands (+41% and +38%) in the alpine coniferous and mountainous beech forests, respectively, whereas no significant differences were found in the thermophilous deciduous one (Fig. 2A, and Supplementary Table S4).

For TreM abundance, a significant increase was found only in the mountainous beech forest, where the long-abandonment stand showed higher values than both managed and intermediate-abandonment ones (+93% and +50%, respectively; Fig. 2B, and Supplementary Table S4). In contrast, no significant variation was detected in the other forest categories.

The density of TreM-rich trees also increased with TSA across all sites (Fig. 2C, and Supplementary Table S4), although statistically significant differences were again found only in mountainous beech forest, where the long-abandonment stand exhibited substantially higher values compared to the other stages (+213% and +106%, respectively). Conversely, the proportion of TreM-rich trees per plot showed clearer responses across all forest categories. Intermediate- and long-abandonment stands had higher values than managed stands in the thermophilous deciduous (+133% and +156%, respectively) and alpine coniferous forests (+113% and +102%), whereas in the mountainous beech forest only the long-abandonment stand differed from the

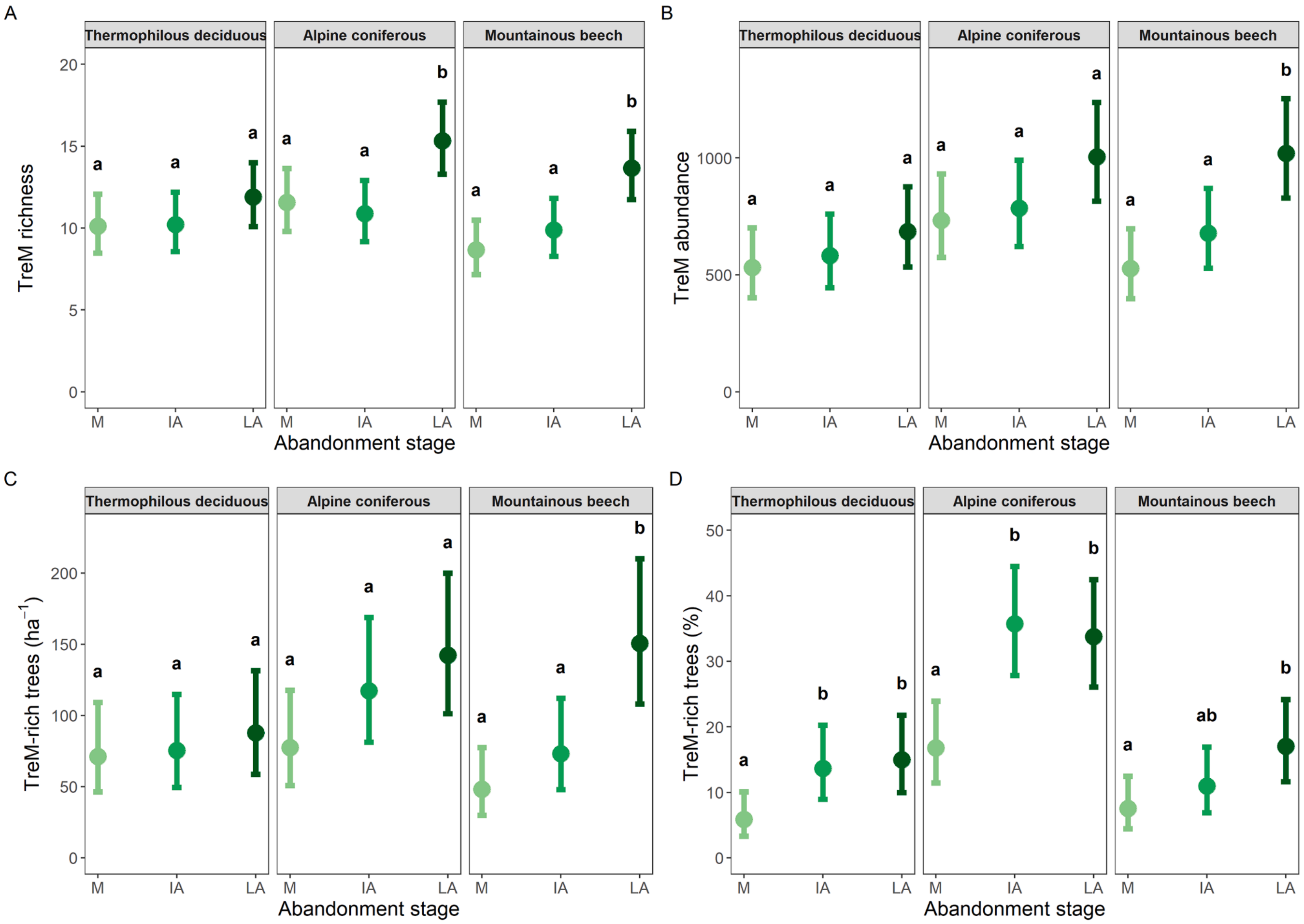

Fig. 2. Effects of TSA on TreM indices across the three forest categories. Estimate values from the generalised linear models are presented, along with 95% confidence intervals (vertical bars). Letters indicate significant differences between abandonment stages ($p < 0.05$). Abbreviations: M = recently or actively managed; IA = intermediate-abandonment; LA = long-abandonment.

managed one (+126%; Fig. 2D, and Supplementary Table S4).

3.2. Effects of TSA on TreM group densities

Analyses of the relationship between TSA and specific TreMs were limited to the most common groups, defined as those present on more than 20 trees per site (Supplementary Table S1, and S2). Accordingly, four groups were considered: *rot holes*, *insect galleries and bore holes*, *concavities*, and *exposed sapwood only*.

The response of TreM groups to proforestation revealed pronounced site-specific differences (Table 2). *Rot holes* showed significant differences only in the mountainous beech forest, with a significantly higher share of *rot hole*-bearing trees in the managed stand compared to the long-abandonment stand (+207%). *Insect galleries and bore holes* showed significant differences across forest categories, although patterns varied depending on the metric considered. In the thermophilous deciduous forest, the share of trees bearing *insect galleries and bore holes* was significantly higher in managed than in intermediate-abandonment stands (+119%). In the mountainous beech forest, the density of *insect galleries and bore holes*-bearing trees increased significantly along the abandonment gradient (+135% from managed to intermediate- and +126% from intermediate- to long-abandonment stand), while the proportion per plot peaked in the long-abandonment stand, showing values significantly higher than both managed and intermediate-abandonment stands (+507% and +182%, respectively).

Concavity-bearing trees exhibited significant patterns across all three forest categories, but with contrasting directions. In the mountainous beech forest, *concavities* followed a pattern similar to *rot holes*, with significantly higher relative values in the managed stand compared to the long-abandonment stand (+63%). In the alpine coniferous forest, *concavities* increased along the proforestation gradient, with significant differences between long-abandonment and managed stands in terms of number of trees per hectare (+51%), and between both intermediate- and long-abandonment stands compared to the managed stand in terms of the proportion of *concavity*-bearing trees per plot (+65% and +76%, respectively). In the thermophilous deciduous forest, the highest values were observed in the intermediate-abandonment stand, which had a significantly higher number of trees per hectare than both the managed and long-abandonment stands (+144% and +238%, respectively), while both managed and intermediate-abandonment stands showed significantly higher proportions of *concavity*-bearing trees than the long-abandonment stand (+188% and +363%, respectively).

Finally, *exposed sapwood only* followed a similar pattern to *insect galleries and bore holes*, increasing along the proforestation gradient in the mountainous beech forest for both metrics. The density of *exposed sapwood only*-bearing trees was significantly higher in the long-abandonment stand compared to both the managed and intermediate-abandonment stands (+174% and +128%, respectively), while for the proportion per plot, a significant difference was detected only between the long- and intermediate-abandonment stand (+174%). Similarly, in the thermophilous deciduous forest the share of *exposed sapwood only*-bearing trees was significantly higher in the long-abandonment compared to the intermediate-abandonment stand (+178%).

Table 2
Estimate values (± SE) of TreM-bearing trees per hectare and percentage for the four most common TreM groups across abandonment stages within each forest category. Values are derived from fitted generalised linear models. Different letters indicate significant differences between abandonment stages within the same forest category based on post-hoc tests ($p < 0.05$). Abbreviations: M = recently or actively managed; IA = intermediate-abandonment; LA = long-abandonment.

TreM group	Forest category	TreM-bearing trees	Abandonment stage		
			M	IA	LA
Rot holes	Thermophilous deciduous	ha^{-1}	20.9 (6.6)	12.6 (4.2)	12.6 (4.2)
		%	3.5 (1.2)	2.8 (1.0)	3.1 (1.1)
	Alpine coniferous	ha^{-1}	39.8 (11.8)	41.8 (12.4)	52.3 (15.0)
		%	7.8 (2.3)	10.8 (2.9)	10.8 (2.9)
	Mountainous beech	ha^{-1}	39.8 (11.8)	33.5 (10.2)	14.6 (4.8)
		%	8.3 (2.4) **a**	5.2 (1.7) **ab**	2.7 (0.9) **b**
Insect galleries and bore holes	Thermophilous deciduous	ha^{-1}	119.3 (26.0)	69.1 (17.3)	87.9 (20.8)
		%	19.7 (3.7) **a**	9.0 (2.3) **b**	15.7 3.3) **ab**
	Alpine coniferous	ha^{-1}	94.2 (21.9)	58.6 (15.2)	67.0 (16.9)
		%	21.2 (3.8)	20.8 (3.8)	16.6 (3.4)
	Mountainous beech	ha^{-1}	48.1 (12.9) **c**	113.0 (25.0) **b**	255.3 (42.9) **a**
		%	4.6 (1.4) **b**	9.9 (2.5) **b**	27.9 (4.3) **a**
Concavities	Thermophilous deciduous	ha^{-1}	52.3 (11.2) **b**	127.6 (19.9) **a**	37.7 (8.9) **b**
		%	11.5 (2.4) **a**	18.5 (3.0) **a**	4.0 (1.2) **b**
	Alpine coniferous	ha^{-1}	205.1 (26.0) **b**	230.2 (27.7) **ab**	309.7 (32.4) **a**
		%	41.7 (4.0) **b**	69.0 (3.7) **a**	73.2 (3.5) **a**
	Mountainous beech	ha^{-1}	265.7 (29.9)	307.6 (32.3)	322.2 (33.1)
		%	57.2 (4.0) **a**	46.5 (4.1) **ab**	35.0 (3.9) **b**
Exposed sapwood only	Thermophilous deciduous	ha^{-1}	37.7 (10.9)	16.7 (5.3)	33.5 (9.8)
		%	4.5 (1.5) **ab**	3.2 (1.1) **b**	8.9 (2.5) **a**
	Alpine coniferous	ha^{-1}	54.4 (14.9)	48.1 (13.4)	71.1 (18.5)
		%	14.9 (3.4)	7.8 (2.2)	12.0 (3.0)
	Mountainous beech	ha^{-1}	81.6 (20.6) **b**	98.3 (23.8) **b**	223.9 (42.8) **a**
		%	19.3 (4.0) **ab**	9.3 (2.5) **b**	25.5 (4.5) **a**

3.3. *Changes in TreM composition across abandonment stages and forest categories*

Overall, PERMANOVA results indicated significant effects of TSA in all forest categories, although the pattern and underlying mechanisms varied.

In the thermophilous deciduous forest, the PCoA showed slight clustering of plots from the long-abandonment stand, whereas managed and intermediate-abandonment stands largely overlapped (Fig. 3). This visual pattern was supported by PERMANOVA results (Table 3, $p = 0.01$), with pairwise comparisons revealing significant differences between the long-abandonment stand and both the managed and intermediate-abandonment stands, while no difference was observed between the latter two (Supplementary Table S7). However, the PERMDISP analysis indicated significant differences in compositional variability among stages ($p = 0.003$), suggesting that variation in dispersion may partly influence the observed PERMANOVA results. The observed dissimilarity was primarily driven by turnover, representing the replacement of TreM types among plots, indicating substantial differences in TreM composition across abandonment stages. Nestedness contributed little and was not significant (Table 3, $p = 0.006$ and $p = 0.785$, respectively). The indicator value analysis identified *large bark loss with advanced decay stage* (IN14; $p = 0.018$) as significantly associated with the long-abandonment stand.

In the alpine coniferous forest, PCoA ordination revealed a substantial overlap among all abandonment stages, indicating limited compositional differentiation (Fig. 4). Nonetheless, PERMANOVA detected a weak but significant effect of abandonment stage (Table 3, $p = 0.029$), primarily driven by differences between the managed and long-abandonment stands, as shown by pairwise comparisons (Supplementary Table S8). PERMDISP analysis indicated no significant differences among abandonment stages ($p = 0.40$), confirming that the observed compositional divergence is not confounded by differences in within-group variability. Neither turnover nor nestedness components were significant (Table 3, $p = 0.759$ and $p = 0.056$, respectively). Indicator value analysis identified *cancerous growth* (GR31; $p = 0.023$) as significantly associated with the long-abandonment stand.

The clearest pattern emerged in the mountainous beech forest, where plots from the three abandonment stages formed distinct clusters in the PCoA ordination space (Fig. 5). This pattern was strongly supported by PERMANOVA (Table 3, $p = 0.001$) and by significant pairwise differences among all stages (Supplementary Table S9). PERMDISP analysis indicated no significant differences among stages ($p = 0.56$). Turnover was the dominant process driving dissimilarity, whereas nestedness played a minor and non-significant role (Table 3, $p = 0.001$ and $p = 0.14$, respectively). Indicator value analysis identified several TreM types significantly associated with abandonment stages: *epiphytic bryophytes* (EP31; $p = 0.001$), *woodpecker foraging excavation* (CV14; $p = 0.034$), and *perennial polypore fungi* (EP12; $p = 0.012$) with the long-abandonment stand; *small branch rot-holes* (CV31; $p = 0.015$) with managed and intermediate-abandonment stands; *small bark loss with early decay stage* (IN11; $p = 0.018$) with managed and long-abandonment stands; and *annual polypores fungi* (EP11; $p = 0.002$) with intermediate- and long-abandonment stands.

When comparing TreM assemblages across the three forest categories, PCoA revealed some separation among categories, although differences between thermophilous deciduous and alpine coniferous forests were less pronounced and differentiation among abandonment stages was modest. Only long-abandonment plots showed partial segregation, whereas managed and intermediate-abandonment plots largely overlapped (Fig. 6). Stage-dependent differences in TreM composition were supported by the PERMANOVA results (Table 4), which indicated a highly significant effect of abandonment stage ($p = 0.001$). Pairwise comparisons revealed significant differences between long-abandonment and managed plots ($p = 0.006$) and between long- and intermediate-abandonment plots ($p = 0.027$), while no significant difference was observed between managed and intermediate-abandonment plots (Supplementary Table S10). PERMDISP analysis showed a significant difference among groups ($p = 0.024$), indicating some variation in within-group dispersion.

Site-dependent effects were also statistically supported, with PERMANOVA indicating a highly significant effect of forest category on TreM composition (Table 4, $p = 0.001$). The significant interaction

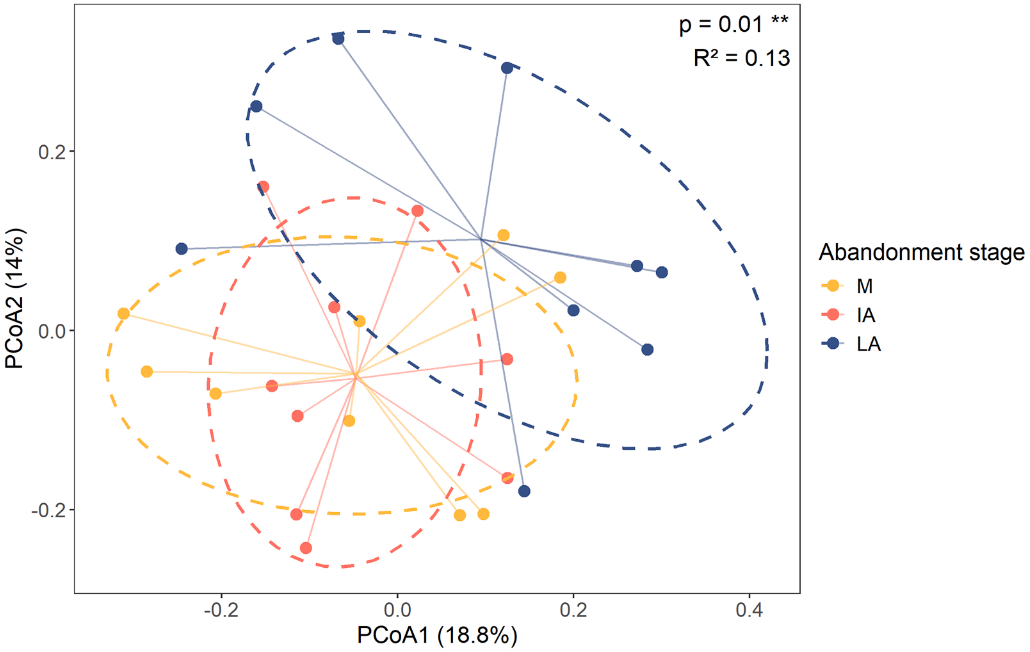

Fig. 3. PCoA results showing compositional differences in TreM assemblages across abandonment stages in the thermophilous deciduous forest. Data are based on a Jaccard distance matrix for plots from three abandonment stages: M = recently or actively managed (yellow points), IA = intermediate-abandonment (red points), and LA = long-abandonment (blue points).

Table 3

Results of PERMANOVA testing the effect of abandonment stage on TreM composition across forest categories. Total β-diversity was partitioned into turnover and nestedness components. For each component, the table reports the degrees of freedom (Df), sum of squares (SS), the model R^2, F-statistic, and associated p-value. Bold p-values indicate significant effects ($p < 0.05$).

Forest category	Component	Effect	Df	SS	R^2	F	*p*
Thermophilous deciduous	Overall β-diversity	Abandonment stage	2	0.5449	0.13362	1.8507	**0.01**
		Residual	24	3.5329	0.86638		
	Turnover	Abandonment stage	2	0.41872	0.20186	3.0349	**0.006**
		Residual	24	1.65564	0.79814		
	Nestedness	Abandonment stage	2	0.01151	0.01346	0.1637	0.785
		Residual	24	0.84319	0.98654		
Alpine coniferous	Overall β-diversity	Abandonment stage	2	0.5817	0.12285	1.6806	**0.029**
		Residual	24	4.1537	0.87715		
	Turnover	Abandonment stage	2	0.1730	0.05406	0.6858	0.759
		Residual	24	3.0271	0.94594		
	Nestedness	Abandonment stage	2	0.10925	0.2641	4.3066	0.056
		Residual	24	0.30443	0.7359		
Mountainous beech	Overall β-diversity	Abandonment stage	2	1.2939	0.28363	4.7512	**0.001**
		Residual	24	3.2681	0.71637		
	Turnover	Abandonment stage	2	0.85231	0.31587	5.5405	**0.001**
		Residual	24	1.84599	0.68413		
	Nestedness	Abandonment stage	2	0.10418	0.17848	2.6071	0.14
		Residual	24	0.47951	0.82152		

between forest category and abandonment stage (Table 4, $p = 0.001$) confirmed that compositional responses to TSA varied across sites. Partitioning β-diversity into its components revealed that these differences were largely driven by turnover, which was significant for forest category, stage, and their interaction (Table 4, $p = 0.001$, $p = 0.011$, and $p = 0.001$, respectively). In contrast, nestedness was not significant for any of the factors tested, suggesting that variation in TreM assemblages among plots primarily reflects the replacement of TreM rather than their loss or gain, with long-abandonment plots exhibiting a greater number of additional TreM types compared to those lost from managed plots. Consistent with this pattern, the indicator value analysis identified *bark pocket open at the bottom* (BA11; $p = 0.007$) as significantly associated with long-abandonment stands, while *woodpecker foraging excavation* (CV14; $p = 0.006$) and *large bark loss with advanced decay stage* (IN14; $p = 0.019$) were associated with both intermediate- and long-abandonment stands.

4. Discussion

4.1. Stronger TSA effects in the alpine coniferous and mountainous beech forests

This study examined how TSA affects TreM richness and abundance across three different forest categories, along with the impact on the density of individual TreM groups and the potential shifts in TreM assemblages. Our results showed a positive relationship between TSA and overall TreM metrics in the alpine coniferous and mountainous beech forests, while the effect in the thermophilous deciduous forest was weaker and limited to the proportion of TreM-rich trees per plot. Our findings for montane forest types are consistent with previous studies

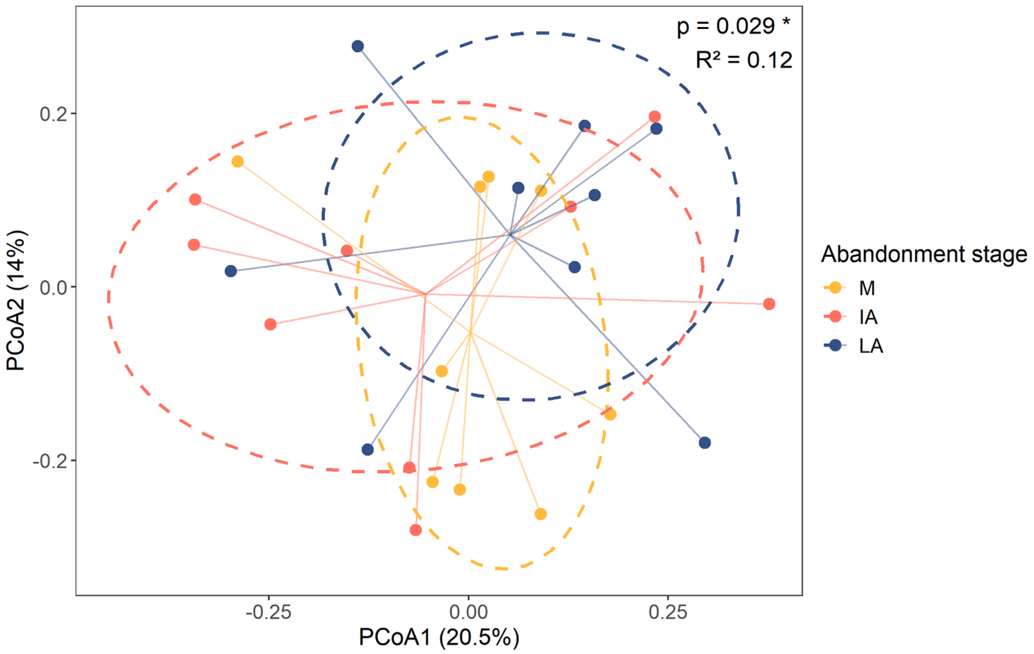

Fig. 4. PCoA results showing compositional differences in TreM assemblages across abandonment stages in the alpine coniferous forest. Data are based on a Jaccard distance matrix for plots from three abandonment stages: M = recently or actively managed (yellow points), IA = intermediate-abandonment (red points), and LA = long-abandonment (blue points).

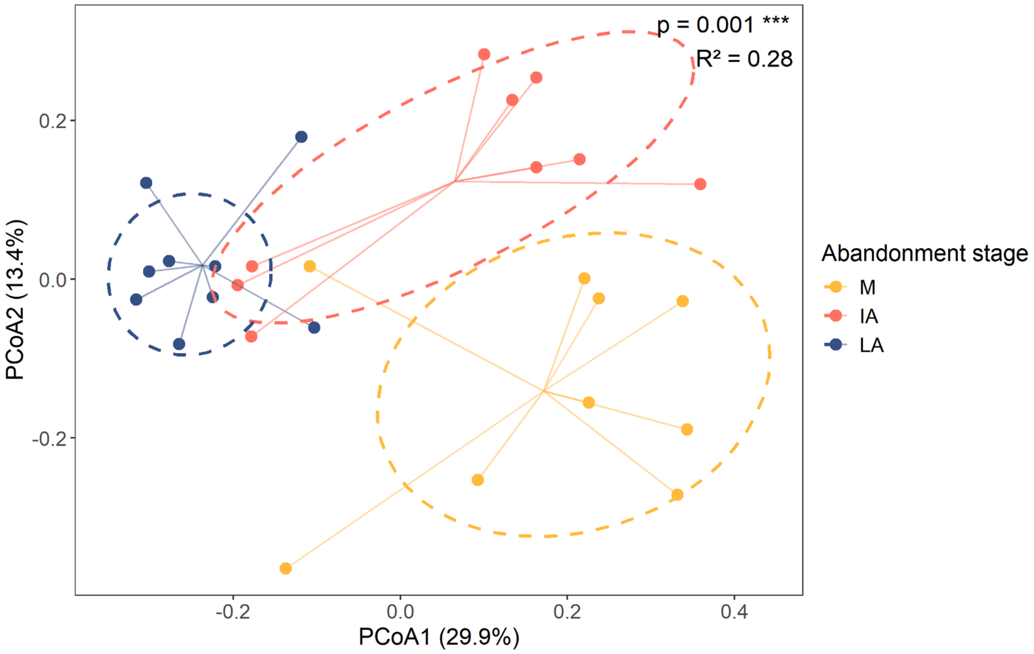

Fig. 5. PCoA results showing compositional differences in TreM assemblages across abandonment stages in the mountainous beech forest. Data are based on a Jaccard distance matrix for plots from three abandonment stages: M = recently or actively managed (yellow points), IA = intermediate-abandonment (red points), and LA = long-abandonment (blue points).

conducted in temperate forests, suggesting that proforestation, which typically leads to increased dead standing trees (Supplementary Table S3), can promote TreM abundance and richness. In particular, the formation of TreMs associated with wood decay and structural degradation was notably enhanced (Supplementary Table S1; Larrieu and Cabanettes, 2012; Paillet et al., 2017, 2019; Großmann et al., 2018).

The weakest response observed in the thermophilous deciduous forest is consistent with Paillet et al. (2017), who found that lowland oak-beech-hornbeam forests exhibited weaker responses to management abandonment compared to montane beech-spruce-fir forests and unmanaged stands. Several factors, such as climatic conditions, topography, and slower senescence dynamics of oak species, may delay the production of decay-related microhabitats, and likely explain this muted response in the thermophilous deciduous forest (Vandekerkhove et al., 2009; Larrieu et al., 2022). Regnery et al. (2013), who analysed a broader gradient of abandonment (0–30, 30–60, 60–90, and >90 years) in forests dominated by pubescent and holm oaks, reported a strong positive effect of TSA on the number of TreM-bearing trees per hectare,

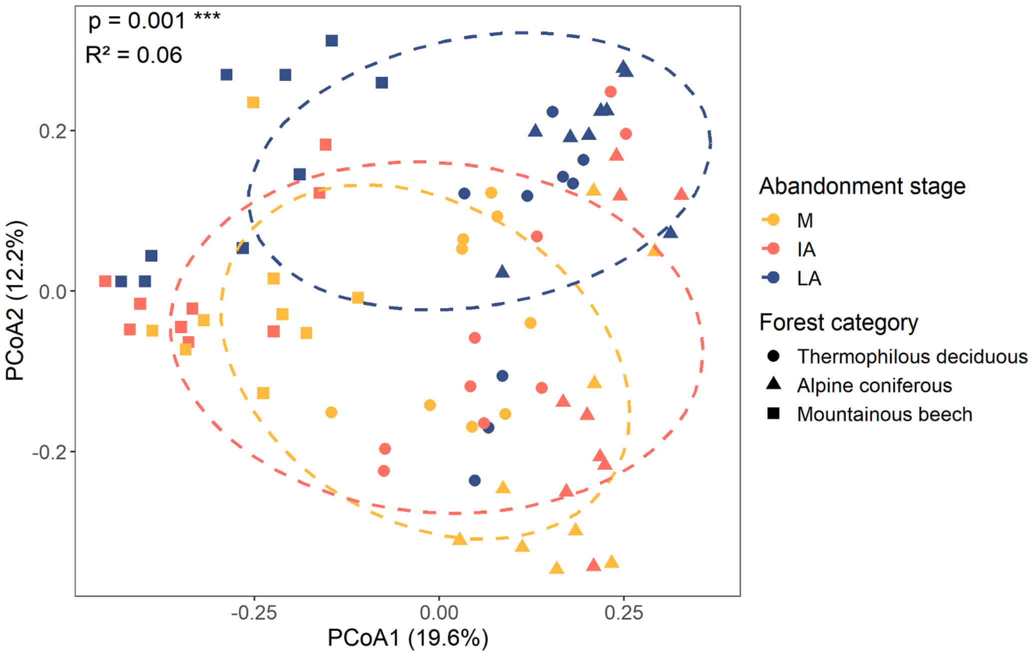

Fig. 6. PCoA results showing compositional differences in TreM assemblages across all forest categories. Data are based on a Jaccard distance matrix for plots from three abandonment stages: M = recently or actively managed (yellow points), IA = intermediate-abandonment (red points), and LA = long-abandonment (blue points). Symbols represent the three forest categories: thermophilous deciduous forest (squares), alpine coniferous forest (circles), and mountainous beech forest (triangles).

Table 4

Results of PERMANOVA testing the effects of abandonment stage, forest category, and their interaction on TreM composition across all plots. Total β-diversity was partitioned into turnover and nestedness components. For each component, the table reports the degrees of freedom (Df), sum of squares (SS), the model R^2, F-statistic, and associated p-value. Bold p-values indicate significant effects ($p < 0.05$).

Component	Effect	Df	SS	R²	F	*p*
Overall β-diversity	Abandonment stage	2	1.0914	0.06018	3.5865	**0.001**
	Forest category	2	4.7583	0.26240	15.6369	**0.001**
	Abandonment stage × Forest category	4	1.3292	0.07330	2.1840	**0.001**
	Residual	72	10.9547	0.60411		
Turnover	Abandonment stage	2	0.4504	0.03430	2.4833	**0.011**
	Forest category	2	5.1557	0.39271	28.4287	**0.001**
	Abandonment stage × Forest category	4	0.9937	0.07569	2.7396	**0.001**
	Residual	72	6.5287	0.49730		
Nestedness	Abandonment stage	2	0.13355	0.11742	2.9548	0.123
	Forest category	2	-0.71471	-0.62840	-15.8130	1.000
	Abandonment stage × Forest category	4	0.09138	0.08035	1.0109	0.484
	Residual	72	1.62712	1.43063		

with forests abandoned for more than 90 years exhibiting values 13 times higher than those abandoned for less than 30 years. In our study, TreM abundance in the thermophilous deciduous forest was approximately 30% higher in stands abandoned for more than 60 years than in managed forests (Fig. 2B, and Supplementary Table S4). Although the two studies rely on different TreM metrics and are therefore not directly comparable in magnitude, the contrast between them suggests that longer periods of abandonment (>90 years) are needed to generate more pronounced differences in oak-dominated forests, where structural ageing dynamics tend to be slower. In turn, this indicates that the > 60-year abandonment stage considered in this study may not fully capture advanced old-growth conditions in the thermophilous deciduous forest, potentially contributing to the weak response observed.

In alpine coniferous and mountainous beech forests, TSA effects were more pronounced, potentially due to harsher climatic conditions and topographical features that accelerated TreM formation (Paillet et al., 2017; Larrieu et al., 2022). This rapid response contrasts with findings from other studies in similar montane forests (Larrieu et al., 2012, 2014). The discrepancy can be attributed to differences in management history (e.g., more extensive harvesting prior to abandonment) and to the coarser TreM classifications used in those studies (5 and 7 categories, respectively) compared to the 64 types employed here. While low-resolution inventories are suitable for rapid assessments during forest management operations, they provide limited precision and may be less sensitive in detecting fine-scale structural differences associated with management abandonment (Larrieu et al., 2018).

4.2. Context-dependent responses of TreM group densities along the proforestation gradient

In accordance with our second hypothesis, we observed pronounced differences in how TreM groups responded to TSA, both among groups and across forest categories.

The most significant differences were found in the mountainous beech forest, where all TreM groups showed a marked response to abandonment. Specifically, *insect galleries and bore holes* and *exposed sapwood only* showed a positive response to TSA, increasing along the proforestation gradient. These differences may be related to the harsh climate and topographic conditions characterising this site, which may accelerate the accumulation of standing dead trees in this forest category (Supplementary Table S3). Such trees provide crucial substrates for the occurrence and diversity of saproxylic insects (Lassauce et al., 2011; Bouget et al., 2013), and the decay processes initiated after tree death play a major role in TreM formation, especially for TreMs linked to structural degradation, such as bark loss and sapwood exposure (Paillet et al., 2017). Similarly, the density of standing dead trees may explain the patterns observed in the thermophilous deciduous forest. In this forest category, *insect galleries and bore holes* and *exposed sapwood only* did not show a monotonic increase along the proforestation gradient; instead, they exhibited a non-linear response, with lower values in the intermediate-abandonment stage. Notably, this stage had the lowest density of standing dead trees (Supplementary Table S3), suggesting that the availability of deadwood may act as a primary driver for these TreM groups, more closely than TSA itself. This pattern indicates that, while TSA can promote the accumulation of deadwood over time, local stand conditions and recent management history may modulate this process, leading to transient stages where deadwood availability, and consequently TreM occurrence, is reduced.

On the other hand, in the mountainous beech forest, both *rot hole-* and *concavity*-bearing trees significantly decreased along the proforestation gradient. *Rot holes,* particularly *small branch rot-holes* (CV31; Supplementary Table S1), were more abundant in managed stands, likely due to mechanical damage occurring during harvesting operations (e.g., branch breakage caused by falling trees or machinery), which can promote their formation (Larrieu et al., 2022). Similarly, *concavities*, particularly *small dendrotelms at trunk base* (CV41; Supplementary Table S1), were more common in managed stands, where thinning operations expose tree surfaces to decay processes, promoting their development (Larrieu et al., 2012).

Notably, *concavities* also showed significant responses to TSA in the other two forest categories, albeit in different patterns. In the alpine coniferous forest, the response was driven by the formation of *small* and *large buttress-root concavities* (GR11 and GR12; Supplementary Table S1), which increased with TSA. This trend was likely influenced by stand-specific factors, such as high soil rockiness and shallow soils, which facilitate the formation of these features (Larrieu et al., 2022). In the thermophilous deciduous forest, *concavity*-bearing trees were more common in the intermediate-abandonment stand. Similarly to the pattern observed in the alpine coniferous forest, this was primarily driven by the high occurrence of *small* and *large buttress-root concavities* (GR11 and GR12). This response could be related to the different slopes characterising the stands: although generally low, the slope was higher in the intermediate-abandonment stand than in the other stands.

These results highlight the heterogeneous responses of different TreM groups to proforestation, with some TreMs linked to deadwood availability, while others more influenced by silvicultural interventions or topography (Larrieu et al., 2018). This variability reinforces our second hypothesis that the effects of TSA on TreMs depend on both the TreM group and forest context, rather than forest category alone.

4.3. TreM assemblages diverge across abandonment stages with different patterns among forest categories

Our compositional analysis confirmed that TSA significantly influenced TreM composition in all three forest categories. However, the magnitude of this effect was relatively modest ($R^2 = 0.13$, 0.12, and 0.28 for thermophilous deciduous, alpine coniferous, and mountainous beech forests, respectively), indicating that statistically significant differences did not translate into strong ecological differentiation.

In the thermophilous deciduous forest, TreM assemblages differed significantly between the long-abandonment stand and both the managed and intermediate-abandonment stands. However, the analysis of multivariate dispersion revealed significant differences among abandonment stages, suggesting that this pattern may partly reflect variation in dispersion rather than purely compositional turnover. This indicates that, although TreM assemblages diverge along the abandonment gradient, the effect should be interpreted with caution. In the alpine coniferous forest, significant differences were observed only between the managed and long-abandonment stands, whereas in the mountainous beech forest, clear separation of assemblages was evident across all three abandonment stages.

These patterns align with previous studies suggesting that TSA does not merely lead to an accumulation of TreMs but rather induces a reorganisation of assemblages driven by turnover (Larrieu et al., 2012; Paillet et al., 2017). The indicator value analysis suggests that shifts in TreM assemblages are primarily driven by the formation and persistence of specific TreM types in long-abandonment stands. Specifically, several TreM types directly (e.g., *large bark loss with advanced decay stage*, IN14) or indirectly (e.g., *woodpecker foraging excavation*, CV14) linked to deadwood formation and senescence processes were indicative of unmanaged or long-abandoned forests (Paillet et al., 2017). Other TreM types also characterise long-abandoned forests because they are generally disfavoured by forest management (e.g., *cancerous growth*, GR31; Larrieu et al., 2012; Cosyns et al., 2020; Courbaud et al., 2022). By contrast, TreM types associated with managed stands emerged only in the mountainous beech forest, where the separation among abandonment stages was most pronounced. At this site, *small branch rot-holes* (CV31) significantly characterised the managed stand, likely reflecting mechanical damage generated by silvicultural operations, as discussed above. Additionally, *small bark losses with early decay stage* (IN11) were associated with both the managed and the long-abandonment stands, potentially reflecting their dual origin: bark loss can be promoted by harvesting operations but may also develop naturally under unmanaged conditions (Courbaud et al., 2022). These findings partially contrast with the only other study explicitly addressing the effects of management abandonment on TreM assemblages (Mamadashvili et al., 2023), which found significant influences of tree dominant species (European and Oriental beech) and elevation, but no detectable effect of management abandonment (production vs. old-growth forests). This discrepancy highlights the need for further studies across different forest types and ecoregions to better understand how management abandonment shapes TreM assemblages.

While TSA consistently influenced TreM composition across forest categories, the strength of this effect varied, with the most pronounced divergence observed in the mountainous beech forest. This may be due to the conversion of the managed stand from coppice to high forest, resulting in a distinct TreM assemblage compared to both abandoned stands and managed stands in other forest categories. The frequent thinning operations in these transitional forests promoted the formation of management-related TreMs, while the accumulation of deadwood in unmanaged stands favoured TreMs associated with decomposition processes. These findings support the notion that silvicultural systems and management practices are key drivers of TreM composition (Asbeck et al., 2019; Santopuoli et al., 2022). The variability in these practices among our study sites likely contributed to the observed differences in TSA responses across forest categories, although additional site-specific factors such as climate conditions, topography and tree composition may also play an important role.

5. Conclusions

This study provides valuable new insights into the role of TSA, a major factor influencing TreM richness, abundance, and composition across a range of forest categories, from Mediterranean to Alpine environments. Our findings generally support our initial hypotheses.

Firstly, we hypothesised that TSA would have a positive effect on overall TreM metrics, with broadly consistent patterns across sites. Our results partially supported this hypothesis, showing that proforestation generally increased TreM abundance and richness, although effects were weaker in the thermophilous deciduous forest. These findings suggest that TSA plays an important role in shaping forest structural complexity, but also that a longer temporal framework than that considered in this study may be necessary to fully capture its effects on TreMs.

Secondly, we predicted that individual TreM groups would show heterogeneous, site-dependent responses, reflecting variation in forest category, species composition, and local conditions. This hypothesis was also supported, as we observed significant variability in TreM responses both among groups and across forest categories. For example, the density of TreM groups associated with deadwood (e.g., *insect galleries and bore holes*) showed a marked positive response in the mountainous beech forest, largely reflecting the higher density of standing dead trees, whereas other TreMs (e.g., *concavities*) exhibited contrasting patterns depending on the forest context. These varying responses highlight the complex interplay between silvicultural practices, local ecological conditions, and the specific processes driving TreM formation. This result underscores the heterogeneous nature of TreM dynamics and the importance of considering these factors when evaluating the effects of TSA on forest biodiversity.

Thirdly, we hypothesised that TreM assemblages would undergo compositional turnover across abandonment stages, with the extent of compositional differentiation varying among sites. Our analysis broadly supported this hypothesis, showing that TSA was significantly associated with compositional changes in TreM assemblages across all forest categories, although the magnitude of these changes remained moderate. Turnover, reflecting a shift from TreM types linked to silvicultural practices (e.g., rot-holes) to those associated with deadwood and senescence processes (e.g., bark loss), emerged as the dominant ecological mechanism. Long-term abandoned stands tended to converge towards a similar compositional configuration, primarily driven by an increase in standing dead trees. However, the extent of these compositional shifts varied among forest categories, particularly in the mountainous beech forest, where the transition from coppice to high forest played a significant role in shaping TreM assemblages. These findings highlight that while TSA leads to broad compositional shifts, the rate and extent of these changes are modulated by local factors such as forest category, silvicultural history, and site-specific conditions.

In conclusion, our study provides evidence that long-term management abandonment can enhance TreM richness and abundance across different ecological contexts, although the magnitude of this effect varied among sites. TSA not only promotes the development of TreM types that are rare or absent in managed stands but also drives broader shifts in TreM composition, primarily through turnover. Conversely, active silvicultural practices may favour the formation of specific TreM types that are uncommon in long-term abandoned forests, highlighting the role of management-driven processes in shaping TreM assemblages. Our results emphasise the need to integrate long-term set-aside areas into forest management strategies as a key tool for promoting forest biodiversity. In particular, in Mediterranean forests, where the positive effects of proforestation on TreM richness and abundance appear slower or delayed, such set-aside areas may be especially important to allow structural features to develop over longer time spans.

However, our comparative approach across different forest categories, combined with the absence of explicit structural covariates (e.g. deadwood availability, and effects of past management), constrains our ability to fully disentangle the relative contributions of TSA from those of underlying stand structure or broader drivers such as climate, topography, and tree species composition. Future studies incorporating detailed structural variables will be essential for a deeper understanding of the mechanisms driving TreM responses to proforestation. Additionally, investigating how shifts in TreM composition influence broader biodiversity would be valuable, as changes in microhabitat availability are likely to influence associated species communities.

Funding

This study was supported by the WILDCARD project funded by the European Climate, Infrastructure and Environment Executive Agency (CINEA) of the European Union under grant number 101081177. Author G.M. was also supported by the National Biodiversity Future Center – NBFC (project code CN_00000033) funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 – Call for tender no. 3138 of 16 December 2021, rectified by Decree n. 3175 of 18 December 2021 of the Italian Ministry of University and Research funded by the European Union – NextGenerationEU. Authors H.M and D.B. were supported by the project Dendro-Carbon (No. 400–01/23–01/6–2) funded under the National Recovery and Resilience Plan (NPOO), administered by the Croatian Ministry of Science, Education and Youth, funded by the European Union – NextGenerationEU. Views and opinions expressed are however those of the authors only and do not necessarily reflect those of the funders. Neither the European Union nor the granting authorities can be held responsible for them. Additionally, part of the activities at the Cansiglio and Val Alba sites were supported by a research agreement with the Forestry Service of Friuli Venezia Giulia (CUP G23C23000690002).

CRediT authorship contribution statement

Guido Marcoz: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Antonio Tomao:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Lorenzo Orzan:** Writing – review & editing, Visualization, Software, Investigation, Formal analysis, Data curation. **Natalie Piazza:** Writing – review & editing, Investigation, Data curation. **Giorgio Alberti:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Doroteja Bitunjac:** Writing – review & editing, Data curation. **Francesco Boscutti:** Writing – review & editing, Methodology. **Claire Duvaltier:** Writing – review & editing, Software, Investigation, Formal analysis, Data curation. **Hrvoje Marjanović:** Writing – review & editing.

Declaration of Competing Interest

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

Acknowledgements

We would like to thank the Forestry Office Poreč of the Croatian Forest LLC and Natura Histrica for granting permission to carry out our sampling campaign in Kontija Forest. We are also grateful to the Forestry Service of Friuli Venezia Giulia for facilitating access to the Val Alba and Cansiglio sites. Special thanks go to Masa Z. Ostrogović Sever for her invaluable support during field sampling in Kontija Forest, and to Alessandro Foscari for his assistance during field surveys in the Cansiglio and Val Alba forests.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123827.

Data availability

Data will be made available on request.

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