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Effects of forest management on mycorrhizal fungi dispersal by small mammals in Alpine forests

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ABSTRACT

Mycorrhizal associations are crucial for forest health, influencing nutrient cycling, plant growth, and forest resilience to disturbance. Many mycorrhizal fungi produce hypogeous sporocarps and rely on mycophagous animals, particularly small mammals, for spore dispersal. Despite the importance of these interactions, the effects of fine-scale forest management on mammal-mediated spore dispersal remains poorly understood. In this study, we (i) compared fungal spore communities dispersed by two widespread European small mammals, *Apodemus flavicollis* and *Clethrionomys glareolus*, and (ii) quantified which forest management–related habitat features most strongly influence both taxonomic richness and spore abundance in scat samples in subalpine forests of northern Italy. We collected scat samples from the yellow necked field mouse *Apodemus flavicollis* and the bank vole *Clethrionomys glareolus* across six sampling grids (replicated across three forest types subjected to different management regimes: a conifer reforestation, a logged beech forest, and an unmanaged mixed beech forest) over two consecutive years (2024–2025). *Clethrionomys glareolus* consistently dispersed more fungal taxa and spores than *Apodemus flavicollis*. We found a higher number of fungal taxa in unmanaged mixed beech forest compared to conifer reforestation and managed beech stands. We also found that stump volume, mean temperature during the 14 days preceding sample collection, and their interaction were the strongest predictors of both taxonomic richness and spore abundance. These findings suggest that retaining decaying wood and maintaining mixed-species stands can enhance animal-mediated fungal dispersal. Incorporating such features into forest management promote belowground biodiversity, thereby supporting key ecosystem functions such as nutrient cycling and regeneration.

1. Introduction

Small mammals play an important role in the dispersal of mycorrhizal fungi by consuming their fruiting bodies (i.e., sporocarps) and transporting spores across forest habitats (Fogel and Trappe, 1978; Maser et al., 1978, 2008). This dispersal process is essential for maintaining mycorrhizal associations, which affect forest productivity and resilience to disturbance, with important implications for ecosystem functioning and management (Luo et al., 2023, 2024; Che and Jin, 2025).

Mycorrhizal fungi form symbiotic networks with plant roots, mediating nutrient and water uptake while receiving photosynthates from their hosts (Parniske, 2008). This mutualism promotes seedling establishment and plant growth, ultimately influencing nutrient and carbon cycling and enhancing ecosystem stability (Simard et al., 1997; Smith and Read, 2002; Jonsson et al., 2001; Kiers et al., 2011). As a result, belowground biodiversity is increasingly recognized as a key driver of forest functioning and resilience, making its conservation an important target of forest management (Cameron et al., 2019; Redford, 2023), especially in Alpine forests, which are highly vulnerable to climate change and benefit from healthy mycorrhizal networks (Simard et al., 2010).

Mycorrhizal fungi often produce epigeous (i.e., mushrooms) or hypogeous sporocarps (i.e., truffles), which differ in their dispersal

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strategies: whereas epigeous fungi rely mainly on wind and water, hypogeus fungi have evolved endozoochorous dispersal mediated by animals that consume their sporocarps and disperse spores via faeces (Maser et al., 1978; Smith and Read, 2002; Piattoni et al., 2014; Borgmann-Winter et al., 2023). Animal gut passage may further enhance spore germination through physical scarification or nutrient enrichment in scat deposits (Frank et al., 2009).

The persistence and stability of this mutualism depend on both the diversity and biomass of hypogeous fungi, and the abundance and activity of their animal dispersers (Blažková et al., 2021; Stephens et al., 2021). Sporocarp formation and spore dispersal are ultimately influenced by habitat conditions shaped by tree species composition, stand structure, and dead wood availability, all of which are, in turn, affected by forest management (Gasperini et al., 2016; Tomao et al., 2020; Hollá et al., 2026).

At the forest stand scale, hypogeus fungi abundance and community composition are affected by tree species composition, due to host specificity and variation in carbon supply from host trees to belowground fungal symbionts (Colgan et al., 1999; Loeb et al., 2000). In addition, canopy structure and overall stand composition jointly regulate soil microclimatic conditions, influencing sporocarp production and fungal community structure (Tomao et al., 2020). Structural elements such as dead wood regulate fungal dynamics by buffering microclimatic variability and creating nutrient-rich microsites that promote sporocarp production and early root colonization (Rajala et al., 2011; Yang et al., 2021; Birch et al., 2023). They also contribute to seed–fungus coupling, as they provide foraging and caching sites for small mammals, which deposit seeds in inoculated patches, enhancing seedling establishment and growth (Brehm et al., 2019; Shemesh, 2025).

Forest management practices modify stand composition, structural complexity, and resource availability, with cascading effects on both small mammals and hypogeous fungi (Carey and Johnson, 1995; Fauteux et al., 2012; Gasperini et al., 2016). Simplified stands, such as clearcuts, reduce dead wood and habitat complexity, leading to lower small mammal abundance compared to structurally complex forests (Bowman et al., 2000; Sullivan et al., 2011). At the same time, management-driven changes in tree composition and microclimate directly influence sporocarp production, with species-specific responses ranging from increased sporocarp production in early- or mid-successional taxa (e.g., *Melanogaster* spp., *Rhizopogon* spp.) to restriction to mature or old-growth forests in others (e.g., *Elaphomyces* spp., *Leucogaster* spp.; Colgan et al., 1999; Castellano, 1999). These changes in habitat structure and biotic communities ultimately alter spore dispersal patterns, with reduced dispersal in intensively managed stands potentially limiting seedling colonization, while retention of structural elements such as dead wood can create localized dispersal hotspots that support the regeneration processes (Danks et al., 2013; Stephens et al., 2021). Understanding how management-driven modifications to microhabitat features affect the dispersal of mycorrhizal fungi is therefore essential for sustaining ecosystem processes.

Previous studies have mostly focused on patterns, comparing fungal communities across contrasting habitat types (e.g., meadows versus forests; Komur et al., 2021), across different disturbance levels (Gil-Fernández et al., 2025), and across geographic regions (Schickmann et al., 2012). While these studies have provided valuable insights, they operate at spatial scales that may not align with forest management practices. Management decisions are often implemented at finer scales, directly modifying key structural attributes such as dead wood availability and canopy cover. Despite the ecological importance of these features, their influence on animal-mediated fungal spore dispersal remains poorly understood. Stephens et al. (2021) showed that microhabitat variables, including vegetation structure and dead wood availability, can predict the occurrence of small mammal species acting as fungal spore dispersers, yet it remains unclear how these habitat features affect both the quantity and diversity of dispersed spores.

Linking fine-scale habitat structure to animal-mediated fungal dispersal can therefore provide mechanistic insights directly relevant to forest management. To address this knowledge gap, we conducted a two-year study in the Italian Eastern Alps across six stands representing three different forest management regimes: a conifer reforestation, a logged beech forest, and an unmanaged mixed beech forest. These stands differ in canopy cover, dead wood volume, and tree community composition, creating distinct microhabitats that can influence the production of mycorrhizal fungal sporocarps as well as small mammal abundance and activity (Carey and Johnson, 1995; Tomao et al., 2020).

We collected scat samples from two European ground-dwelling small mammals, *Apodemus flavicollis* (yellow-necked mouse) and *Clethrionomys glareolus* (bank vole). Both species consume mycorrhizal fungi and may therefore contribute to spore dispersal within their home ranges (measured in the study areas as 1.31 ha and 0.33 ha, respectively; Capitani, 2026), although *C. glareolus* shows stronger mycophagous behaviour (Schickmann et al., 2012; Komur et al., 2021). We investigated differences in the richness and quantity of dispersed fungal spores, hypothesizing that *C. glareolus* disperses a greater diversity and abundance of mycorrhizal spores than *A. flavicollis* (Fig. 1 A), past work has shown that *C. glareolus* is a preferential mycophagous species, relying more consistently on fungi as a dietary component (Urban, 2016; Zambonelli et al., 2018; Komur et al., 2021).

We further assessed the effects of forest management and microhabitat characteristics on both the taxonomic richness and abundance of spores dispersed by the two species. Following Rajala et al. (2011) and Tomao et al. (2020), we hypothesized that mixed beech stands would support greater richness and higher spore loads due to higher volumes of dead wood, higher canopy cover, and increased tree species diversity, including both broadleaved and coniferous species that enhance the diversity of mycorrhizal fungal communities. This combination of habitat features is expected to increase fungal availability and niche heterogeneity, thereby favouring more diverse and abundant spore loads in rodent scats (Fig. 1B). We also expected species-specific responses linked to differences in feeding ecology and habitat use. We expected *C. glareolus* to respond more strongly to microhabitat variation in both spore richness and abundance, reflecting its reliance on fungal resources and its sensitivity to habitat features associated with fungal availability (e.g. dead wood and structural complexity; Gasperini et al., 2016; Zambonelli et al., 2018; Komur et al., 2021). In contrast, we expected *A. flavicollis* to exhibit weaker and less consistent responses, reflecting its broader diet and less specialized microhabitat use (Hansson, 1985; Abt and Bock, 1998).

2. Methods

2.1. Study area

The study was conducted in the Val Alba Regional Nature Reserve (Prealpi Giulie Natural Park, Friuli-Venezia Giulia, Italy; Fig. 2A). The area lies in the eastern Southern Carnic Alps at the transition with the Julian Alps and Prealps, with elevations ranging from 450 to 2197 m above sea level. This area is part of the inner subalpine climatic district, characterized by high annual precipitation (~1900 mm) and mean monthly temperatures from −1 °C (January) to 16 °C (July), with an annual mean of 10–11 °C. In the study area, snow cover is discontinuous during the winter season (December–April), with depths > 10 cm occurring for ~24 days annually.

Most soils in the study area are classified as “A–C soils” (Soil Conservation Service, 1975), with an organic horizon overlying a mineral horizon. Developed on calcareous bedrock under subalpine conditions, they are deep, well-drained, and rich in organic matter. The organic horizon contains leaf litter and partially decomposed plant material, forming an intermediate humus type primarily decomposed by saprotrophic fungi (Cassol et al., 2012).

Sampling grids (0.81 ha) were established at an average elevation of 1168 m above sea level across three forest management regimes

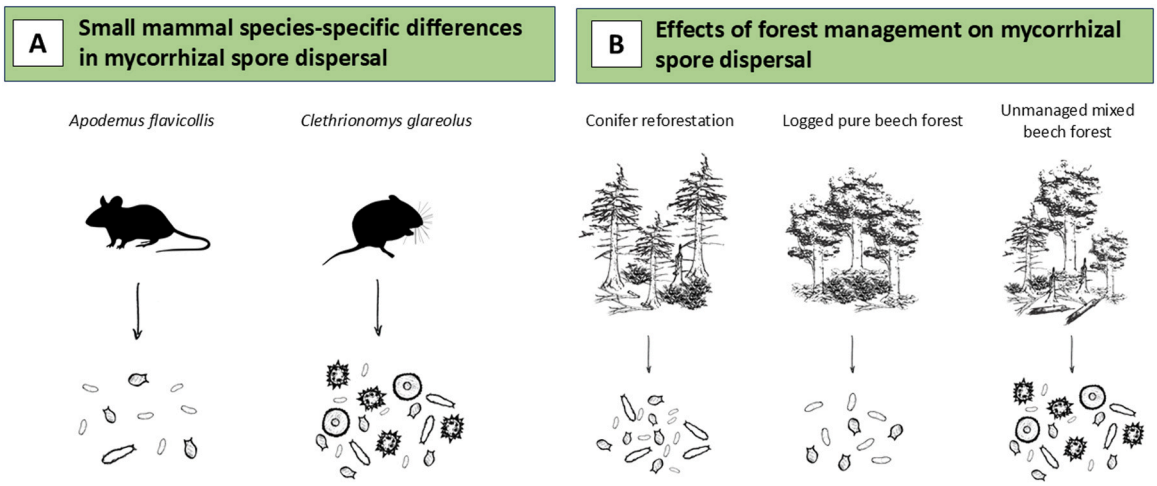

Fig. 1. (A) Graphical representation of hypothesis 1: *Clethrionomys glareolus* faeces are expected to show higher fungal spore abundance and taxonomic richness than *Apodemus flavicollis*; (B) hypothesis 2: higher fungal spore abundance and richness are expected in samples from mixed beech forest than pure beech and conifer reforestation.

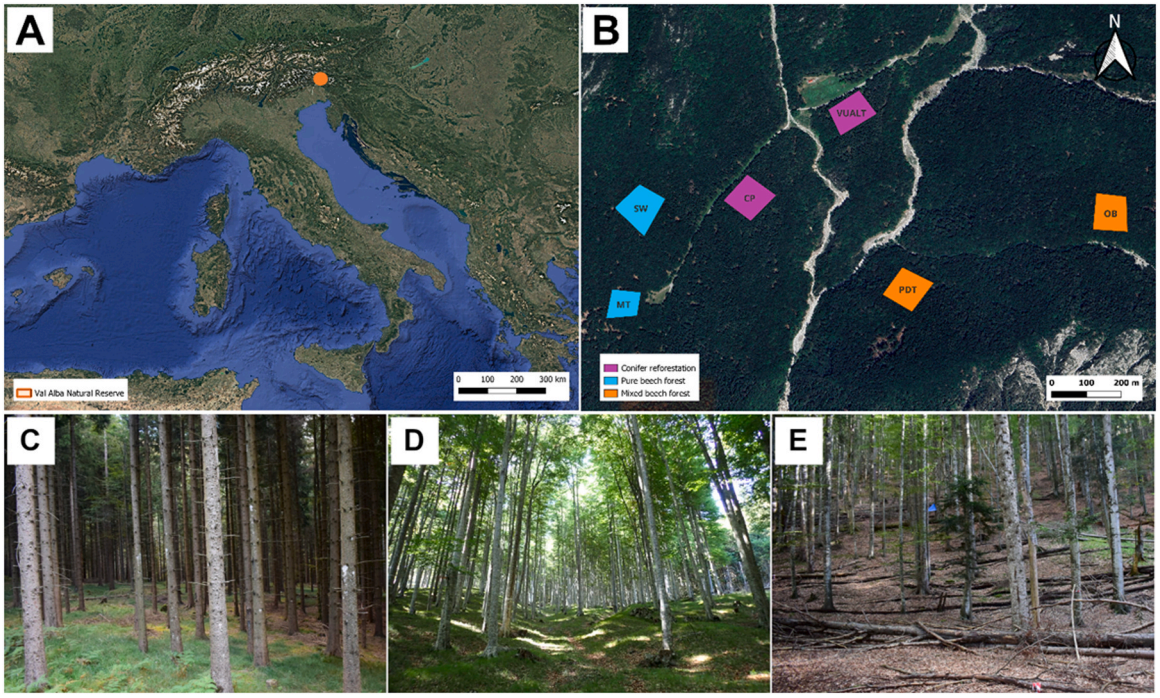

Fig. 2. Val Alba Nature Reserve (Friuli-Venezia Giulia, Italy): (A) study area location; (B) sampling grid distribution by forest type—conifer reforestation (purple), pure beech (blue), mixed beech (orange). (C–E) Representative stands: conifer reforestation (C), pure beech (D), mixed beech (E), differing in tree composition, canopy cover, and dead wood volume. Maps produced with QGIS 3.34.11.

(Fig. 2B), with two independent replicates per forest type (mean inter-grid distance = 741 m; range = 291–1465 m). Replication across independent forest stands is generally recommended to avoid confounding local environmental conditions with broader ecological patterns and account for spatial heterogeneity in fungal availability and foraging behaviour (e.g. Schickmann et al., 2012; Komur et al., 2021; Stephens et al., 2021). In this study, spatial replication (i.e., 2 grids per forest types) was constrained by the availability of forest management units. The selected forest types included four managed stands and two unmanaged stands used as control. Managed stands consisted of (i) two conifer reforestation sites (Fig. 2C) and (ii) two pure alpine beech forests (Fig. 2D), while unmanaged stands comprised mixed alpine beech forests (Fig. 2E; more details are provided in Supplementary Materials – Forest type descriptions). The average stand area of forest type was 14.77 ha (range: 3.57–22.60 ha). Importantly, all forest management regimes have been in place for several decades, capturing long-term effects of management on small mammal–mediated fungal spore dispersal rather than short-term responses directly following cutting. This temporal scale is particularly suitable for ectomycorrhizal fungi, whose communities develop slowly and reflect long-term forest structure and management history (Tomao et al., 2020).

A preliminary, non-systematic survey of epigeous fungi present in the study area was conducted from May to October 2025.

2.2. Forest structure sampling and meteorological variables

We calculated mean deadwood volume and canopy cover for each trapping grid. We conducted deadwood sampling (May 2024) within each grid using two 20 × 20 m sampling units at opposite corners to capture within-grid compositional and structural variability, for a total of 12 units across the six grids. We recorded all deadwood elements ≥ 10 cm in diameter, classifying them as coarse woody debris (CWD), standing deadwood (snags), or stumps (Hunter, 1990), and calculated volume as follows: for downed deadwood, we measured diameters at both ends and total length; for stumps, diameter of the cut surface and stump height; and for standing dead trees, diameter at breast height (1.37 m; DBH) and total height using a Vertex. Canopy cover was assessed in August 2024, when it reached its maximum, at 100 trap sites per grid (600 sites total), estimating cover as the mean of four densiometer readings in the cardinal directions.

Meteorological data (temperature and precipitation) were obtained from ERA5 (Hersbach et al., 2023), and 14-day averages prior to each sampling session were used in analyses. This timeframe is biologically meaningful because fungal sporulation and spore availability are driven by recent moisture and temperature conditions, typically over days to weeks (Krah et al., 2023; Tsunoda et al., 2025), while small mammal foraging responds to contemporaneous resource pulses.

2.3. Small mammal and scat sampling

We conducted small mammal sampling on six mark-recapture grids, each consisting of 100 live-trap stations (10 × 10 array, 10 m spacing) covering 0.81 ha, sufficient to encompass multiple individual home ranges (Amori et al., 2008). Trapping was conducted from July to October 2024 and from May to October 2025 for three consecutive nights in each site, using a combination of Longworth and Heslinga traps, baited with a mixture of peanut butter, flour, and sunflower seeds and provisioned with polyester batting for insulation. Captured individuals were marked with PIT tags (passive integrated transponders; 7 mm), ear tags, and unique fur mark before release at the capture site (Brehm and Mortelliti, 2022; Gurnell and Flowerdew, 2006). We focused on two small mammal species, *A. flavicollis* and *C. glareolus*, which are widespread in European forests, including Alpine environments (Amori et al., 2008), and together accounted for the majority (70%) of unique captures in our study. Ear biopsies were collected from *Apodemus* individuals for genetic confirmation to distinguish *A. flavicollis* from the cryptic species *A. sylvaticus* (Bartolommei et al., 2016; see Supplementary Materials for a detailed description of the genetic analyses). In total we found 73 *Apodemus flavicollis* and 1 *Apodemus sylvaticus*, which was removed from the scat analyses. Scat samples were collected from each individual at its first capture within a sampling session (i.e., month), thereby avoiding pseudoreplication. Samples were then dehydrated in open vials under a laboratory hood for 2–3 days, and then stored at 4 °C (Stephens and Rowe, 2020). Traps were washed with 70% ethanol prior to redeployment.

2.4. Fungal spore analyses

Scat samples were processed following Stephens et al. (2017). Approximately 20–25 mg of each dehydrated sample was crushed in 1 ml of 5% KOH, rinsed through a 125 µm sieve, and allowed to settle for 36 h. The spore suspension was then mixed with 95% ethanol, allowed to settle, and 75 µl was mounted on a glass slide with glycerin and sealed with a cover slip. Slides were gridded into 25 cells (5 × 5 mm) to facilitate counting. Mycorrhizal fungal spores were quantified in nine randomly selected cells at 400 × magnification, with additional scanning at 200 × to detect less abundant or larger spores. Fungal spore identification was performed to the genus level when possible; otherwise, identification was carried out to the lowest possible taxonomic level, based on Castellano et al. (1989), Montecchi and Sarasini (2000), and a reference collection from a national mycological association (Associazione Micologica Bresadola, Gruppo di Muggia e del Carso). Mycorrhizal fungal spore abundance per sample was summarized as a spore load index, calculated by scaling abundances of each taxon and summing across taxa (Stephens et al., 2021).

2.5. Statistical analyses

To compare fungal spore dispersal by *A. flavicollis* and *C. glareolus*, we first assessed sampling completeness using Mao's tau rarefaction (Colwell et al., 2004), implemented in the R package *vegan* (Oksanen et al., 2013). Differences in mean fungal taxa richness and spore load between the two species were tested using the non-parametric Wilcoxon rank-sum test (Wilcoxon, 1945), and effect sizes were calculated as Cohen's d (Cohen, 1988) using the *effsize* package (Torchiano, 2020).

We analyzed differences in the composition of dispersed fungal communities using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) with Bray-Curtis dissimilarity and 999 permutations, followed by pairwise post-hoc tests with Bonferroni correction. Spore abundance data were square-root transformed and scaled, excluding samples with no spores. Multivariate dispersion was assessed with the *betadisper()* function and quantified via Tukey's post-hoc test. Patterns of similarity in spore communities were visualized through non-metric multidimensional scaling (NMDS), while similarity percentage (SIMPER) analysis (Clarke, 1993) identified the taxa contributing most to differences between species.

We used analysis of variance (ANOVA) followed by Tukey's HSD post-hoc tests to assess differences in spore richness and spore load among forest management regimes. To evaluate environmental predictors of fungal taxa richness, we fitted generalized linear models (GLMs) separately for each rodent species (*lme4* package Bates et al., 2015), including individual PIT tag as a random intercept to account for repeated measures. Fungal taxa richness was analyzed on its original scale using a Gaussian error distribution. We constructed a set of candidate models with different combinations of environmental and meteorological predictor variables and used Akaike's information criterion corrected for small sample size (AICc; Burnham and Anderson, 2004) to select the top ranking model. Model diagnostics were calculated using the DHARMa package (Hartig, 2026). Collinearity among predictors was assessed using Pearson correlation coefficients and variance inflation factors (VIF; (Fox et al., 2019). Similarly, environmental and meteorological predictors of fungal spore abundance were evaluated using generalized linear mixed models (GLMMs; Gaussian family), with model selection and diagnostic procedures following the same framework. Predicted values from the selected models were obtained using the *ggeffects* package (Lüdecke, 2017).

Finally, we analyzed differences in small mammal community composition among forest types using PERMANOVA (Anderson, 2001) based on Bray–Curtis dissimilarity matrices with 999 permutations.

3. Results

3.1. Small mammal and scat sampling

We collected 211 scat samples over 18,000 trap-nights. In 2024, these included 59 samples from 41 *Apodemus flavicollis* (yellow-necked mouse) individuals and 22 from 15 *Clethrionomys glareolus* (bank vole), while in 2025 we obtained 46 samples from 32 *A. flavicollis* and 84 from 53 *C. glareolus*. Sample numbers varied among forest types, with 81 individuals collected in conifer reforestations, including 35 *Apodemus flavicollis* in 2024 and 46 individuals in 2025 (15 *A. flavicollis* and 17 *Clethrionomys glareolus*). Mixed beech forests accounted for 100 individuals, including 36 individuals in 2024 (14 *A. flavicollis* and 14 *C. glareolus*) and 64 individuals in 2025 (7 *A. flavicollis* and 30 *C. glareolus*). Pure beech forests yielded 30 individuals, including 10 individuals in 2024 (7 *A. flavicollis* and 1 *C. glareolus*) and 20 individuals

in 2025 (10 *A. flavicollis* and 6 *C. glareolus*). Overall, the percent of captures across forest types differed for *A. flavicollis* and *C. glareolus*, respectively: conifer reforestations (57%, 43%), mixed beech (21%, 50%), and pure beech (57%, 23%).

A PERMANOVA analysis based on Bray–Curtis dissimilarity revealed significant differences in small mammal community composition among forest types ($R^2 = 0.281$, $F = 14.493$, $p = 0.001$), indicating that habitat type significantly influenced species abundance patterns.

3.2. Forest structure sampling

We found that the three forest types exhibited comparable average structural conditions, but differed more markedly in deadwood composition. Canopy cover was highest in pure beech forest (mean = 49.62%), intermediate in mixed beech forest (mean = 38.69%), and lowest in conifer reforestation (mean = 24.3%).

Deadwood composition differed markedly among forest types and sampling grids. Conifer stands exhibited the highest stump volume (mean = 675.06 dm^3), followed by pure beech (mean = 220.59 dm^3) and mixed beech forests (mean = 67.25 dm^3). In contrast, coarse woody debris (CWD) was most abundant in mixed beech forests (mean = 3542.36 dm^3), while considerably lower volumes were observed in conifer stands (mean = 237.49 dm^3) and pure beech forests (mean = 141.63 dm^3). Standing deadwood occurred predominantly in conifer (mean = 1464.3 dm^3) and mixed beech forests (mean = 1373.14 dm^3) while it was not recorded in pure beech stands.

3.3. Fungal spores in small mammal scats

Fungal spores occurred in 95% of the samples, with an average of 3.44 fungal taxa per sample (SD = ±1.85). We identified 21 fungal taxa, 76% at genus level and 24% at family level. Among the genera, 94% were mycorrhizal and 6% saprotrophic (Fig. 3, Table S1). Our sampling captured most of the dispersed fungal taxa, as shown by the rarefaction curves for *A. flavicollis* and *C. glareolus* (Fig. S1).

A higher number of fungal taxa was recorded in bank vole scats (23 taxa in *C. glareolus*) than in *A. flavicollis* (17 taxa). *Melanogaster* spp. was the most frequent taxon in both species, occurring in 60% of *A. flavicollis* samples and 83% of *C. glareolus* samples. Several fungal taxa showed marked differences in frequency between rodent species, particularly *Elaphomyces* spp. (49.1% in *C. glareolus* vs. 11.4% in *A. flavicollis*) and *Gymnomyces* spp. (4.7% in *C. glareolus* vs. 16.2% in *A. flavicollis*; Fig. 4).

Spore load and fungal taxonomic richness differed between rodent species and showed consistent seasonal dynamics. *C. glareolus* dispersed higher spore loads (mean = 1.11) and hosted significantly higher richness (mean = 4.24) than *A. flavicollis* (mean spore load = 0.62; richness = 2.64; Wilcoxon rank-sum tests: spore load $W = 3110.5$, $p < 0.001$; richness $W = 2775$, $p < 0.001$; effect sizes were relatively large: Cohen's $d = 0.74$ and 0.96, respectively). The only exception occurred in October 2025, when scats of *A. flavicollis* showed a spore load (0.78 ± 0.38) comparable to that of *C. glareolus* (0.68 ± 0.51). For both species, spore richness and spore load increased from May to August, peaked in August, and declined thereafter (Fig. 5), in line with temperature patterns until September (Fig. S2).

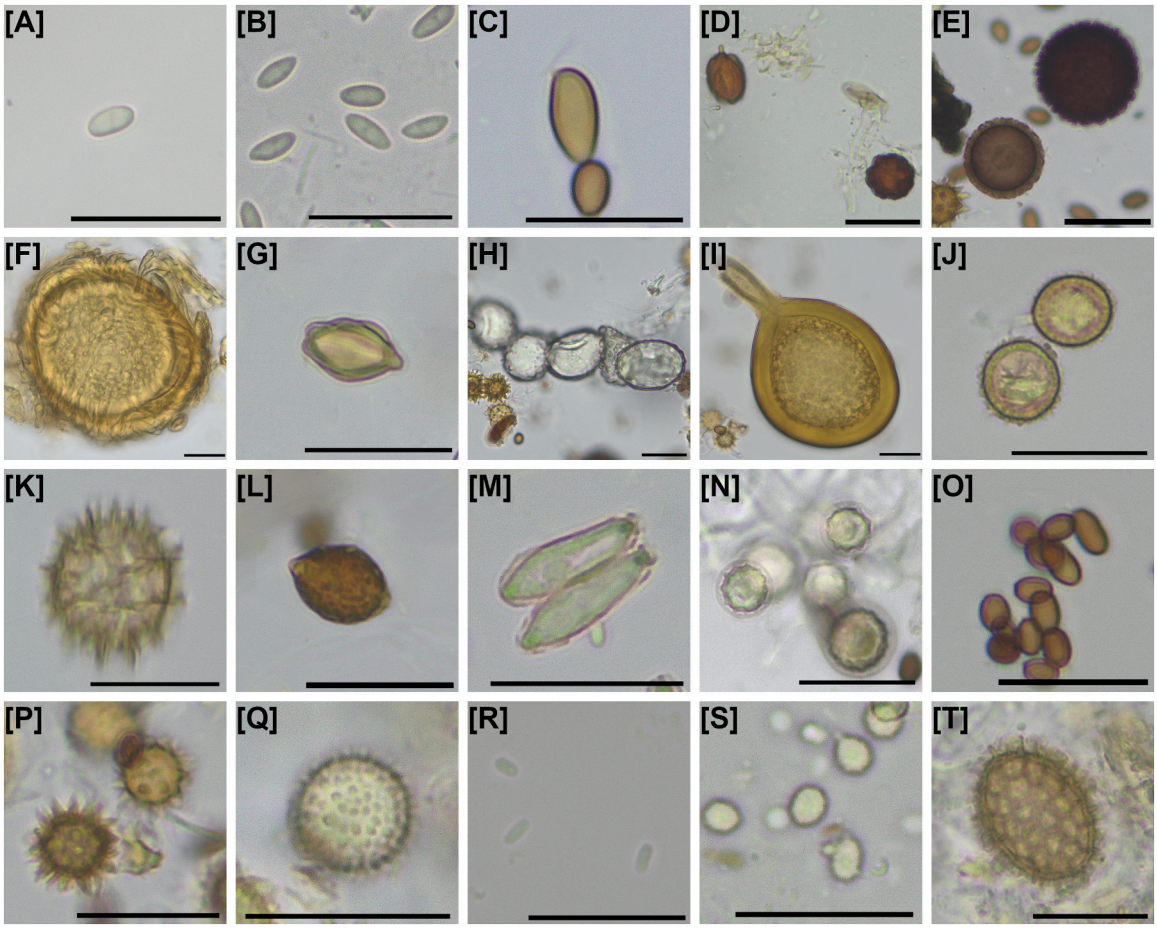

Fig. 3. Some of the most representative fungal spore morphotypes at 400x magnification found in small mammal scat samples collected in the Val Alba Nature Reserve (Friuli-Venezia Giulia, Italy). (A) Boletales morphotype A, (B) Boletales morphotype B, (C) Boletaceae, (D) *Chamonixia* spp., (E) *Elaphomyces* spp., (F) *Endogone* spp., (G) *Gautieria* spp., (H) *Genea* spp., (I) *Glomus* spp., (J) *Gymnomyces* spp., (K) *Hydnobolites* spp., (L) *Hymenogaster* spp., (M) *Hysterangium* spp., (N) *Leucogaster* spp., (O) *Melanogaster* spp., (P) *Octavianina* spp., (Q) *Pachyphlodes* spp., (R) Phallales, (S) Russulaceae, (T) *Tuber* spp. Scale bars: 20 μm.

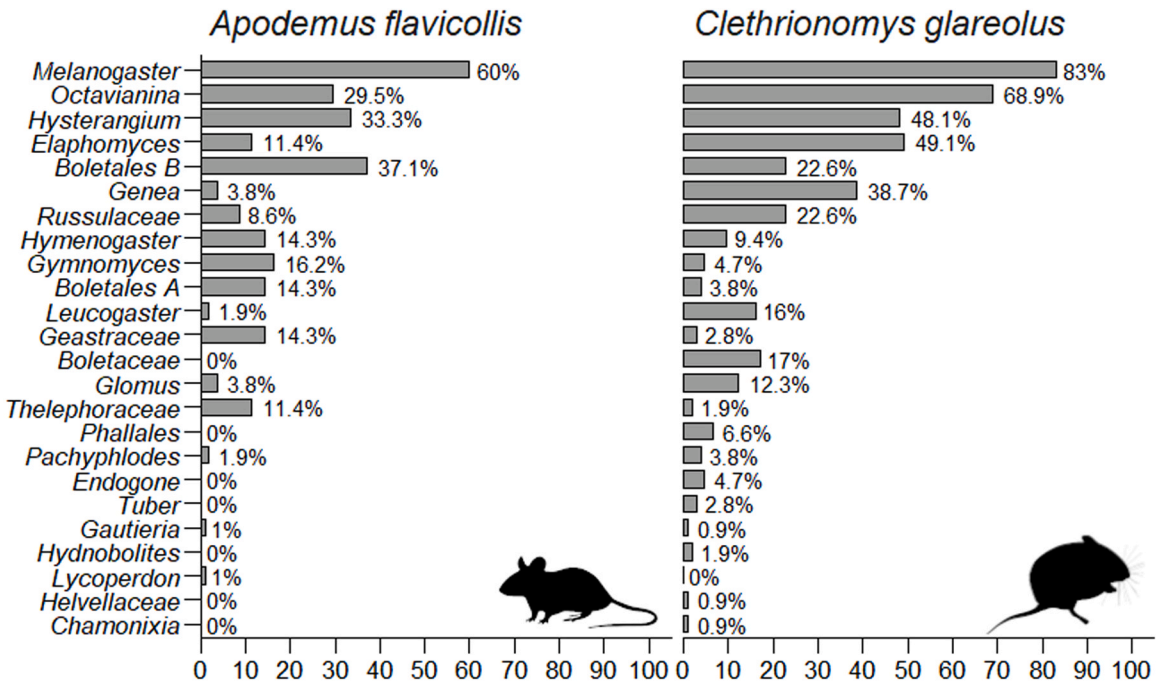

Fig. 4. Frequency of occurrence of fungal taxa across *Apodemus flavicollis* and *Clethrionomys glareolus* in the scat samples collected in the Val Alba Nature Reserve (Italy).

The analysis of spore abundance revealed small but significant differences in dispersed fungal communities between *A. flavicollis* and *C. glareolus* (PERMANOVA, Bray–Curtis distance: $R^2 = 0.051$, $F = 10.62$, $p = 0.001$, Bonferroni corrected; Table S3). Small mammal species explained 5.1% of the variability in the spore community.

Multivariate dispersions were heterogeneous (betadisper: $p < 0.001$). Through Tukey's post hoc test, we found that *A. flavicollis* samples were significantly more dispersed than those of *C. glareolus* (mean difference = −0.074, 95% CI [−0.106, −0.042], $p < 0.001$), indicating higher within-species variability. Non-metric multidimensional scaling (NMDS, Bray–Curtis dissimilarity; stress = 0.167) confirmed partial overlap between species and greater within-group dispersion in *A. flavicollis* compared to *C. glareolus* (Fig. S3).

Through SIMPER analysis, we identified the main drivers of dissimilarity in the fungal spore community. *Melanogaster* spp. (19.56%, $p = 0.002$), *Elaphomyces* spp. (9.53%, $p = 0.001$), and *Octavianina* spp. (9.21%, $p = 0.001$) together accounted for ~40% of total similarity. Additional taxa contributed to cumulative dissimilarity, with *Glomus* spp. providing the strongest contribution (4.87%, $p = 0.042$; Fig. S4). All taxa were more abundant in *C. glareolus* than in *A. flavicollis*.

3.4. Effects of forest management on fungal spore dispersal

Samples from the conifer reforestation contained 21 fungal taxa, those from the mixed beech forest contained 22, and samples from the pure beech forest contained 15 (Table S4). *Melanogaster* spp. was the most frequent taxon across all forest types. Fungal taxonomic richness per sample differed significantly among forest types (one-way ANOVA: $F_{2,208} = 5.87$, $p < 0.01$), with higher values in mixed beech forests compared to pure beech forests (Tukey HSD, $p < 0.01$). Spore load did not differ significantly among forest types (one-way ANOVA: $F_{2,208} = 2.82$, $p = 0.06$).

We found that the null model best described fungal taxonomic richness in *A. flavicollis* (Gaussian GLM with intercept only; AIC = 286.08; $R^2 = 0.00$; Table S5) and spore load in the same species (Gaussian LMM with intercept only and individual as a random effect; AIC = 203.96; marginal $R^2 = 0.000$; conditional $R^2 = 0.14$; Table S6).

By contrast, the top-ranked model for fungal taxonomic richness in spore communities dispersed by *C. glareolus* was a Gaussian GLM including stump volume, mean temperature, and their interaction (Table S5), explaining 17.8% of the variance ($R^2 = 0.178$). All predictors showed positive estimated effects, with stronger support for stump volume and the interaction term, while the effect of mean temperature was more uncertain (Table 1; Fig. S5A). Overall, the interaction suggests that the influence of stump volume varies with temperature, peaking under warmer conditions and weakening as temperatures decrease.

Similarly, for spore load in *C. glareolus*, the top ranked model was a Gaussian LMM including stump volume, mean temperature, and their interaction, with individual as a random intercept (conditional R^2 = 0.30; Table S6). Spore load increased with both predictors, and their interaction suggested a stronger combined effect (Table 2; Fig. S5B), with the positive effect of stump volume being strongest under warm conditions, weaker at intermediate temperatures, and turning negative in colder conditions.

4. Discussion

Through our field study we found that forest management affects small mammal–fungal interactions, with direct consequences for the dispersal of mycorrhizal fungi. *Clethrionomys glareolus* dispersed a greater taxonomic richness of fungi and higher spore loads, likely reflecting its stronger dependence on fungal resources compared to the more opportunistic *Apodemus flavicollis*, which exhibited greater individual variability in diet and dispersal patterns.

We found a higher richness of dispersed fungal taxa in mixed beech stands compared to pure beech stands likely due to their greater structural complexity. Similarly, stump availability emerged as a key predictor of spore dispersal, particularly for *C. glareolus*, suggesting that deadwood enhances foraging opportunities and consequently fungal spore dispersal.

Overall, these results highlight that tree species composition and deadwood presence act as critical structural drivers of animal-mediated fungal dispersal, with important implications for the maintenance of belowground biodiversity and ecosystem functioning.

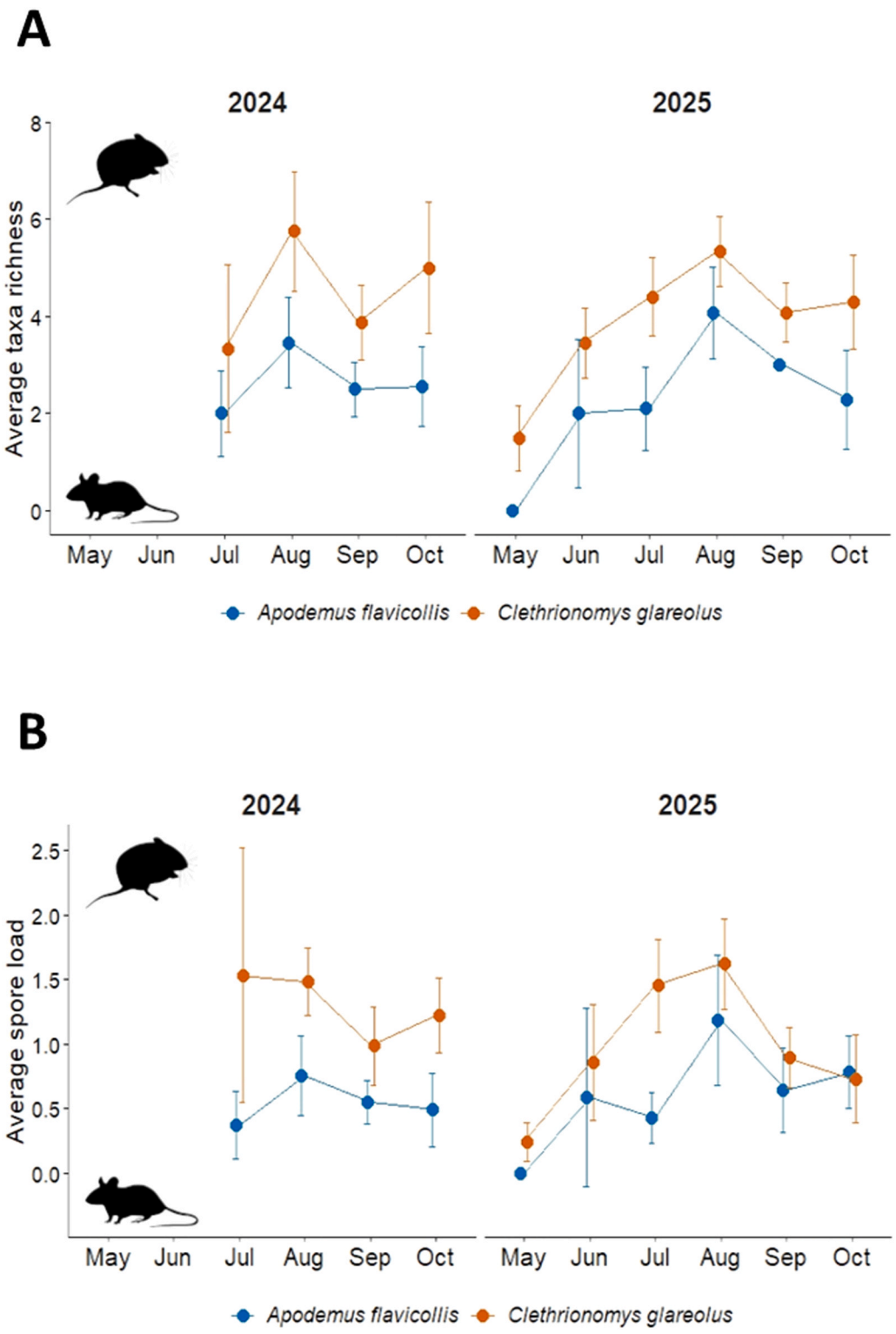

Fig. 5. (A) Average fungal taxa richness and (B) spore load in scat samples collected from *Apodemus flavicollis* (blue) and *Clethrionomys glareolus* (orange) across sampling sessions in the Val Alba Nature Reserve, Italy.

4.1. Small mammal species-specific differences in fungal spore dispersal

C. glareolus dispersed significantly more fungal species and higher spore loads than *A. flavicollis* (Fig. 5). This pattern was consistent across months and aligns with previous studies (Schickmann et al., 2012; Komur et al., 2021), highlighting a stronger contribution of *C. glareolus* to the fungal dispersal processes, although *A. flavicollis* appears to promote higher hetereogeneity in dispersed spore community.

Spores of hypogeous fungi dominated the collected samples, while spores of epigeous taxa were comparatively underrepresented (Table S1). This pattern, also reported by other European studies (Schickmann et al., 2012; Komur et al., 2021), occurred despite the high availability of epigeous fungi in the study area (>40 taxa recorded, including commonly recorded ectomycorrhizal genera such as *Russula*,

Table 1
Results of the GLMM analysis with fungal taxonomic richness (SPDIV) as the response variable and stump volume (stump_dm3_sc), 14-day mean temperature (mean_temp_14d_sc), and their interaction as predictors. Parameter estimates refer to fungal taxa richness in scat samples of *Clethrionomys glareolus*. The selected model was: SPDIV ~ stump_dm3_sc * mean_temp_14d_sc.

Parameter	Estimate (β)	Standard Error (SE)	95% CI
Intercept	4.404	0.245	(3.92, 4.88)
Stump volume	0.760	0.316	(0.14, 1.38)
Mean temperature (14 days before sampling)	0.971	0.346	(0.29, 1.65)
Stump volume: Mean temperature (14 days before sampling)	1.344	0.509	(0.35, 2.34)

Table 2
Results of the GLMM with spore load index (SPLI) as response variable and stump volume and 14-day mean temperature (and their interaction) as predictors. The model was fitted to fungal spore load in scat samples of *Clethrionomys glareolus*: SPLI ~ stump_dm3_sc * mean_temp_14d_sc + (1 | PIT).

Parameter	Estimate (β)	Standard Error (SE)
Intercept	1.222	0.079
Stump volume	0.275	0.100
Mean temperature (14 days before sampling)	0.531	0.112
Stump volume: Mean temperature (14 days before sampling)	0.586	0.160
Groups	Variance	
PIT	0.042	
Residual	0.360	

Lactarius, *Boletus* and *Suillus*; Table S2). Although hypogeous fungi represent only a subset of the overall ectomycorrhizal community, our findings suggest a substantial role of small mammals in maintaining belowground fungal communities (Zambonelli et al., 2018). In line with Borgmann-Winter et al. (2023), our results further suggest that wind- and small mammal-mediated dispersal operate in a complementary way: while abiotic vectors such as wind and water primarily facilitate the spread of epigeous fungi, small mammals play a key role in the dispersal of hypogeous taxa.

We observed that Basidiomycetes spores were more abundant and diverse than Ascomycetes spores in rodent scats (Table S1; Fig. 4). Notably, Ascomycetes spores, particularly those of *Elaphomyces* spp., occurred more frequently in *C. glareolus* samples (Fig. 4). These patterns align with previously reported differences in fungal spore dispersal, suggesting the potential for selective foraging by small mammals at higher taxonomic levels (Schickmann et al., 2012; Komur et al., 2021). Collectively, our results indicate non-random interactions between small mammals and fungal communities, likely influenced by both fungal traits, such as nutritional content, volatile organic compound emissions, and fruiting strategies, and consumer behavior (Stephens and Rowe, 2020; Komur et al., 2021). Future research integrating sporocarp availability and taxon-specific spore production will be critical to confirm the ecological mechanisms underlying these patterns.

Consistent with this interpretation, spore community composition also varied between rodent species, although the overall effect was modest (5.2%; Table S3). *A. flavicollis* showed higher inter-individual variability, likely reflecting its more generalist diet and weaker specialization on hypogeous fungi (Schickmann et al., 2012; Urban, 2016; Zambonelli et al., 2018; Komur et al., 2021).

Overall, the two rodent species appear to play complementary roles in fungal dispersal, with *C. glareolus* contributing to more consistent dispersal of selected high-nutritional fungi (Orczán et al., 2012), while *A. flavicollis* disperses a more heterogeneous spore community.

Although broadly consistent with previous studies, dominant hypogeous fungal taxa vary among study sites (Schickmann et al., 2012; Komur et al., 2021), likely due to strong effects of geographic context and forest structure on community composition (Fogel and Trappe, 1978; Claridge et al., 2000; Meyer and North, 2011). These factors may interact with species-specific foraging behaviour of small mammals to influence spore dispersal patterns. Moreover, fungal spores detected in scats likely reflect both the availability of hypogeous fungi in the environment and selective consumption by different rodent species, which may have distinct preferences for fungal taxa (Schickmann et al., 2012; Komur et al., 2021). Direct assessments of sporocarp availability through field surveys would help disentangle these effects.

4.2. Effects of forest management on mycorrhizal fungal spore dispersal

In *C. glareolus*, variation in both fungal taxonomic richness and spore abundance was significantly influenced by the interaction between stump volume and mean temperature during the 14 days preceding sampling. Although gut passage times mean that spores detected in scats may originate from locations other than the capture site, the spatial context of our study limits the source of confounding factors: sampling grids (0.81 ha) were embedded within homogeneous forest stands (average 14.77 ha), whereas *C. glareolus* home ranges are much smaller (0.33 ha; Capitani, 2026). This indicates that individuals predominantly forage within uniform habitat patches, suggesting that both stump availability and short-term thermal conditions contribute to sporocarp production (Fogel, 1976; Luoma et al., 1991; Claridge et al., 1993). Importantly, the recurrent presence of spores in forests rich in stumps suggests that voles act as effective dispersal agents for fungal propagules. Given the role of stumps as nurse logs providing moisture, nutrients, and mycorrhizal inoculum, such dispersal may influence local fungal community structure and potentially facilitate forest regeneration (Amaranthus et al., 1994; Claridge et al., 2000, 2009; Danks et al., 2013). Future studies quantifying fungal biomass alongside small mammal foraging behavior will be essential to directly link resource availability, consumption, and the ecological consequences of this dispersal pathway.

Stump volume emerged as a significant driver of fungal spore dispersal, more so than other classes of dead wood. This effect may be explained by the high moisture retention capacity of stumps, which act as reservoirs and gradually release water and nutrients into the soil (Tomao et al., 2020). Such conditions create microhabitats favorable for the development of many hypogeous fungi and can prolong fruiting periods, which may explain the observed positive effect on spore abundance (Amaranthus et al., 1994; Claridge et al., 2000, 2009; Danks et al., 2013). Higher moisture levels may also enhance scent emission and thus sporocarp detectability by small mammals, which have been reported to increase seed pilfering in more humid sites (Vander Wall, 2000; Humphreys and Mortelliti, 2025). Additionally, decayed stumps provide shelter and predator cover, increasing small mammal activity and thereby promoting sporocarp consumption and fungal spore dispersal (Bowman et al., 2000; Carey et al., 2002; Sullivan et al., 2011).

The interaction between stump volume and mean temperature indicates that the effect of dead wood on fungal spore load and taxa richness is strongly context-dependent (Fig. S5). Specifically, increasing stump volume is associated with higher spore loads under warm conditions, a weaker positive response at intermediate temperatures, and a negative trend under colder conditions. This pattern suggests that stump-mediated improvements in microhabitat conditions (i.e., enhanced moisture retention, nutrient availability, and suitability for sporocarp development) are most effective when thermal conditions are favourable for fungal growth and fruiting. Conversely, under low temperatures, reduced fungal metabolic activity and slower sporocarp production may decrease sporocarp availability and detectability (Fogel, 1976; Claridge et al., 1993; Luoma et al., 1991), leading to a negative effect of stump volume. Overall, these results highlight that dead wood

does not act as a uniform driver of fungal resource availability, but rather amplifies or constrains sporocarp production depending on short-term thermal conditions, thereby affecting spatial and temporal variation in fungal spore loads.

Consistent with this interpretation, stump-associated conditions had a stronger effect on spore abundance than on fungal taxonomic richness (Tables 1, 2), indicating that these drivers primarily regulate fruiting intensity rather than community composition. In contrast, fungal richness appears to be more strongly related to broader stand-level factors, such as balanced composition of broadleaved and coniferous species, as observed in mixed beech forests supporting a higher diversity of mycorrhizal taxa. This coexistence likely promotes mycorrhizal fungal diversity by increasing host availability and structural heterogeneity, thereby enhancing niche differentiation (Tomao et al., 2020).

None of the environmental or meteorological variables considered here explained variation in fungal spore abundance or taxonomic richness in *A. flavicollis* scats. This likely reflects its more opportunistic diet and a weaker coupling between its foraging behaviour and resource availability (Schickmann et al., 2012; Urban, 2016; Zambonelli et al., 2018; Komur et al., 2021). Consequently, generalist species such as *A. flavicollis* maintain relatively stable dispersal functions across environmental gradients, whereas forest management practices may exert a stronger influence on more specialised mycophagous species. Accordingly, while specialists likely drive variation in abundant and diverse mycorrhizal spore loads, generalists may represent a more consistent but underappreciated component of fungal dispersal dynamics in managed or disturbed forests, consistent with Stephens and Rowe (2020). Further studies incorporating a higher number of independent replication units would improve the generalizability of these findings.

4.3. Managing forests for small mammal-mediated fungal diversity

Mycorrhizal fungi affect forest productivity and resilience by supporting nutrient cycling and tree growth, and small mammals act as key vectors for their dispersal (Fogel and Trappe, 1978; Maser et al., 1978, 2008). Forest management strongly influences the interactions between fungi and small mammals, therefore promoting environmental conditions that maximise fungal spore dispersal is crucial for maintaining belowground connectivity and ecosystem functioning. This is particularly important in Alpine forests, which are highly vulnerable to climate and land-use change. Based on our findings we suggest two main forest management strategies to promote small mammal-mediated fungal spore dispersal:

1. Retain deadwood, especially stumps, to provide moist, nutrient-rich microhabitats that boost sporocarp production and are actively used by small mammals, enhancing mycorrhizal spore dispersal.
2. Maintain mixed-species stands combining broadleaves (*Fagus sylvatica*, *Acer pseudoplatanus*) and conifers (*Abies alba*, *Picea abies*, *Larix decidua*) to support more diverse mycorrhizal dispersal networks.

By preserving these structural features, forest managers can safeguard not only fungal diversity but also the dispersal networks that connect belowground communities, which are critical for sustaining forest productivity and resilience.

CRediT authorship contribution statement

Marino Zugna: Methodology, Investigation. **Giovanni Zanfei:** Writing – review & editing, Investigation. **Alessio Mortelliti:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Lucia Muggia:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Sara Savazza:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lorenzo Ferdinando Campaner:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Ryan B. Stephens:** Writing – review & editing, Methodology. **Chiara Manfrin:** Writing – review & editing, Methodology, Investigation.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.124054.

Data availability

Data will be made available on request.

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