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ORIGINAL RESEARCH

The invisible heterogeneity of forests -β-diversity of volatiles

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Abstract
Context Volatile organic compounds (VOCs) create invisible chemical landscapes that influence ecosystem processes. Yet whether VOC β-diversity (i.e., variability in VOC composition between patches) responds to structural heterogeneity and reflects silvicultural habitat management remains unclear.
Objectives In a large field experiment, we quantified how enhanced structural beta complexity (ESBC) affects VOC β-diversity patterns and investigated potential drivers and ecological effects in temperate production forests.
Methods We sampled VOCs in ambient forest air using Tenax/Carboxen adsorbent traps at forest floor and 1 m heights across 234 treatment and control forest patches in six German regions. We analyzed VOCs via thermal desorption-gas chromatography mass-spectrometry (TD-GCMS) and examined environmental drivers including deadwood characteristics, canopy cover, tree species dissimilarity, and herb layer dissimilarity. We tested potential ecological

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relevance by analyzing saproxylic beetle community responses.

Results VOC β-diversity increased significantly at 1 m height in heterogeneous forests compared to homogeneous forests, but we found no significant change at the forest floor. Deadwood volume and deadwood structural diversity, rather than canopy openness, were identified as the main drivers of increasing VOC β-diversity. Dissimilarity in beetle community composition was associated with VOC β-diversity, but only for forest floor VOCs, suggesting these chemical patterns may correlate with variables beetles respond to.

Conclusions Our findings suggest that volatile β-diversity represents an overlooked dimension of habitat heterogeneity, one that creates invisible chemical heterogeneity influencing inter- and intra-species interactions and ecosystem processes. We demonstrate that enhancing forest heterogeneity through deadwood retention increases both structural heterogeneity and volatile β-diversity.

Keywords Volatile organic compounds · β-diversity · Heterogeneity · Deadwood · Forest management · Forest ecology · Chemical ecology · Saproxylic beetles

Introduction

Volatile organic compounds (VOCs) are secondary metabolites released by all living organisms and organic matter as byproducts of metabolic processes. They create an invisible chemical landscape (the volatilome or scentscape) that influences numerous forest ecosystem processes such as inter- and intra-species interactions, multitrophic interactions and the colonization of leaf litter or deadwood by decomposer communities (Holighaus & Schütz 2006; Mäki et al. 2021; Hagiwara et al. 2024; Isidorov et al. 2024). The volatilome represents an environmental niche dimension in Hutchinson's (1957) multidimensional niche framework. As VOC composition varies spatially, this chemical heterogeneity increases the number of niche dimensions. Expansion of niche dimensionality can facilitate species coexistence by increasing the total niche space available (MacArthur 1972), consistent with the habitat heterogeneity hypothesis that environmental heterogeneity promotes species richness (MacArthur & MacArthur 1961). This relationship has been demonstrated across multiple heterogeneity gradients, including vertical and horizontal forest structure, deadwood distribution, topographic, and biotic heterogeneity (Stein & Kreft 2015; Heidrich et al. 2020). The composition of VOCs present in the volatilome of an ecosystem may represent an additional heterogeneity gradient. We used the BETA-FOR experimental framework (Müller et al. 2023), comprising 234 forest patches (50 m × 50 m) across six regions in Germany, to test whether VOC composition varies between forest patches and relates to biodiversity patterns. While alpha (α)-diversity describes the volatilome within individual forest patches and gamma (γ)-diversity represents the total volatilome across all patches, understanding VOC beta (β)-diversity, the dissimilarity in volatilomes between patches, is central to assessing whether VOC heterogeneity influences biodiversity.

Spatial heterogeneity in the volatilome reflects ecosystem-level processes operating across multiple scales (Šimpraga et al. 2019), with VOC emission patterns influenced by plant community composition and its interaction with herbivory (Kigathi et al. 2019), while decomposition processes affect soil microbial communities through VOC-mediated interactions (McBride et al. 2020). VOC patterns are diverse and species-specific (Courtois et al. 2009; Kessler & Kalske 2018), though the relationship between community diversity and volatilome heterogeneity is not always straight forward, with reduced diversity sometimes decreasing VOC diversity (Abis et al. 2020). Recent studies show that the relationship between VOCs and organisms is complex and context-dependent due to environmental conditions, multitrophic interactions, and scale dependencies (Kessler & Kalske 2018; Dixon & Dickinson 2024; Berkum et al. 2025).

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Many VOCs have evolved into chemical communication networks that likely predate auditory and visual systems (Steiger et al. 2011). They serve as carbon sources for microbes (Ramirez et al. 2010) and influence atmospheric chemistry (Dicke & Baldwin 2010; Peñuelas & Llusià, J, 2003). In forests, VOCs serve diverse functions. They act as anti-aggregation pheromones for saproxylic beetles to detect when host trees are sufficiently colonized (Frühbrodt et al. 2023), while other species are attracted to the chemical signatures of decomposing deadwood (Holighaus & Schütz 2006). Structural changes in forests resulting from disturbance, climate change and management may alter VOC emissions, potentially creating chemical changes alongside physical changes. Over the past three decades, canopy dieback in European forests has doubled (Senf et al. 2018), while management practices such as selection cutting (i.e. single tree and group selection) and retention forestry increasingly aim to enhance structural diversity to improve forest resilience (Bauhus et al. 2009; Thom & Keeton 2020; Aszalós et al. 2022). These practices include deadwood retention (Gustafsson et al. 2012; Großmann et al. 2023) and canopy gap creation (Kern et al. 2016, 2014; Tong et al. 2024), both of which could potentially influence VOC β-diversity patterns across multiple spatial scales and through various drivers.

Deadwood may lead to an increase in VOC β-diversity among patches through decomposition processes that create diverse chemical signatures from different decomposer communities (Mäki et al. 2021). Deadwood varies in both volume and structural diversity, with different deadwood structures (e.g. standing vs. lying deadwood) providing distinct microhabitats for plants, animals, fungi and microbes (Krumm et al. 2013; Lachat et al. 2019) that may in turn affect VOC emissions. Canopy gaps alter microclimate (Abd Latif & Blackburn 2010) and understory vegetation composition (Blondeel et al. 2020), potentially driving VOC β-diversity through effects on plant emissions and decomposition processes. As sample organisms, saproxylic beetle communities may respond to VOC patterns by colonizing chemically distinct substrates and contribute to the volatilome as they themselves release VOCs (Graf et al. 2021; Leather et al. 2014). While vertical VOC heterogeneity is well documented in forest canopies (Yáñez-Serrano et al. 2018; Petersen et al. 2023; Schuman 2023; Ringsdorf et al. 2024; Sulzer et al. 2025), the horizontal VOC heterogeneity of forest landscapes has rarely been studied. Saproxylic beetles, which depend on the availability and a diversity of deadwood habitats, are likely to respond to changes in forest heterogeneity and VOC composition. An increase in chemical heterogeneity among patches should therefore be reflected in differences in beetle community composition.

Here, we conducted the first landscape-scale field study of horizontal VOC patterns, sampling ambient air at the forest floor and 1 m height across 234 forest patches. To determine whether forest management interventions that enhance structural heterogeneity also create chemical heterogeneity, we compared VOC β-diversity between treatment and control districts across 11 paired sites. Treatment districts had experimentally enhanced structural heterogeneity through deadwood addition and canopy gap creation, while no experimental interventions were applied in control districts. We further examined drivers of VOC β-diversity across all 234 patches and tested the following hypotheses:

H1: Treatment districts show higher within-district VOC β-diversity than control districts, due to an increase in (H1a) deadwood volume heterogeneity and (H1b) canopy cover heterogeneity.

H2: Deadwood structural diversity (the presence of both standing and lying deadwood) drives higher VOC β-diversity than deadwood volume alone or single deadwood types.

H3: Saproxylic beetle communities become more dissimilar with increasing VOC β-diversity.

Methods

Experimental design and site description

This study was conducted on 234 50 m × 50 m forest patches within the BETA-FOR experimental framework across six regions (Würzburg University Forest, Bavarian Forest, Passau, Hunsrück, Saarland and Lübeck) in Germany (Müller et al. 2023). The study sites cover a broad gradient of environmental conditions typical for Central European forests, from acidic to base-rich soils, and from Atlantic to more continentally influenced climatic conditions. All forest stands were production forests of mature age. The stands were either dominated by European beech (*Fagus sylvatica*), or made up of diverse mixtures dominated by native broadleaf species (primarily *Quercus*, *Fraxinus*, *Acer*, *Carpinus*, and *Tilia* sp.), with some Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*).

The 22 districts (10 to 20 ha each) consisted of 11 treatment districts with enhanced structural β-complexity (ESBC) manipulations and 11 paired control districts, together forming the 11 forest sites. Within each treatment district, nine forest patches received different ESBC treatments: eight patches received different combinations of experimental deadwood removal, deadwood retention, and canopy gap creation, and one patch served as an internal control. Treatments were implemented in either spatially aggregated or distributed fashion between winter 2015 and winter 2018. Each treatment district was paired with a control district containing nine control patches with largely homogeneous canopy cover and minimal deadwood amounts. In the Würzburg University Forest, additional treatments resulted in 14 different patch configurations and one control patch within the treatment district, and 15 corresponding control patches in the control (Fig. 1).

Preliminary analyses showed no effect of aggregated versus distributed implementation on VOC patterns, so this factor was excluded from all subsequent analyses (see Table 3 in supplementary material). This hierarchical design, from patch (0.25 ha) to district (10–20 ha) to region (spanning climatic gradients), represents the first landscape-scale field study of VOC β-diversity in temperate forests.

Although VOC sampling covered all treatments, we used a simplified grouping for analysis.

For this study, forest patches were grouped into four classes:

1 Lying deadwood (logs and stumps),
2 Standing deadwood (snags and habitat trees),
3 Both lying and standing deadwood and.
4 No coarse deadwood structures, including patches with experimental deadwood-removal patches and control patches from treatment and control districts, patches with stumps and patches with crowns.

The treatment "crowns" was equated with "stumps", since crown deadwood had decomposed by the time of VOC sampling. Habitat trees were included in the standing deadwood class, as most artificially created habitat trees had died since implementation.

For the analysis, we focused on the realized structural classes of each patch rather than its designated treatment category. We used continuous variables describing deadwood volume (m^3 ha^{-1}) and canopy cover derived from LiDAR data, which captured the actual structural gradients resulting from the manipulations. Patches subjected to different treatments varied along these gradients (e.g. logs and snags yielded higher deadwood volumes than stump-only or removal patches). From the measured components, we derived a deadwood heterogeneity index (a categorical variable ranging from 0 to 2) representing the number of deadwood types present per patch where 0 indicates no deadwood, 1 indicates either standing or lying deadwood, and 2 indicates both types present.

This approach allowed us to test (i) the effect of the ESBC treatment on VOC β-diversity (treatment vs. control districts; H1) and (ii) the relationships between realized forest structure and VOC β-diversity (H2), using both continuous measures of deadwood volume and canopy cover and the categorical grouping of deadwood types described above.

VOC sample collection

VOCs were collected from all 234 BETA-FOR forest patches throughout July 2023. Sampling was conducted simultaneously at two heights at the center of each forest patch: at 1 m and at the forest floor to capture possible vertical variation in VOC emissions (Fig. 2a). VOC samples were collected using conditioned quartz glass tubes (15 mm × 1.9 mm inner diameter) packed with Tenax and Carboxen adsorbents (1.5 mg each) and secured with glass wool plugs (Fig. 2b). The traps contained an equal mix (1.5 mg each) of Tenax and Carboxen adsorbents. Tenax leads to sample losses for smaller, more volatile compounds but is effective for larger compounds (Pollmann et al. 2005), and Carboxen is especially efficient for sampling smaller VOCs (Schieweck 2018). By combining both, we ensure the sampling of a wider range of compounds in a highly diverse ecosystem setting.

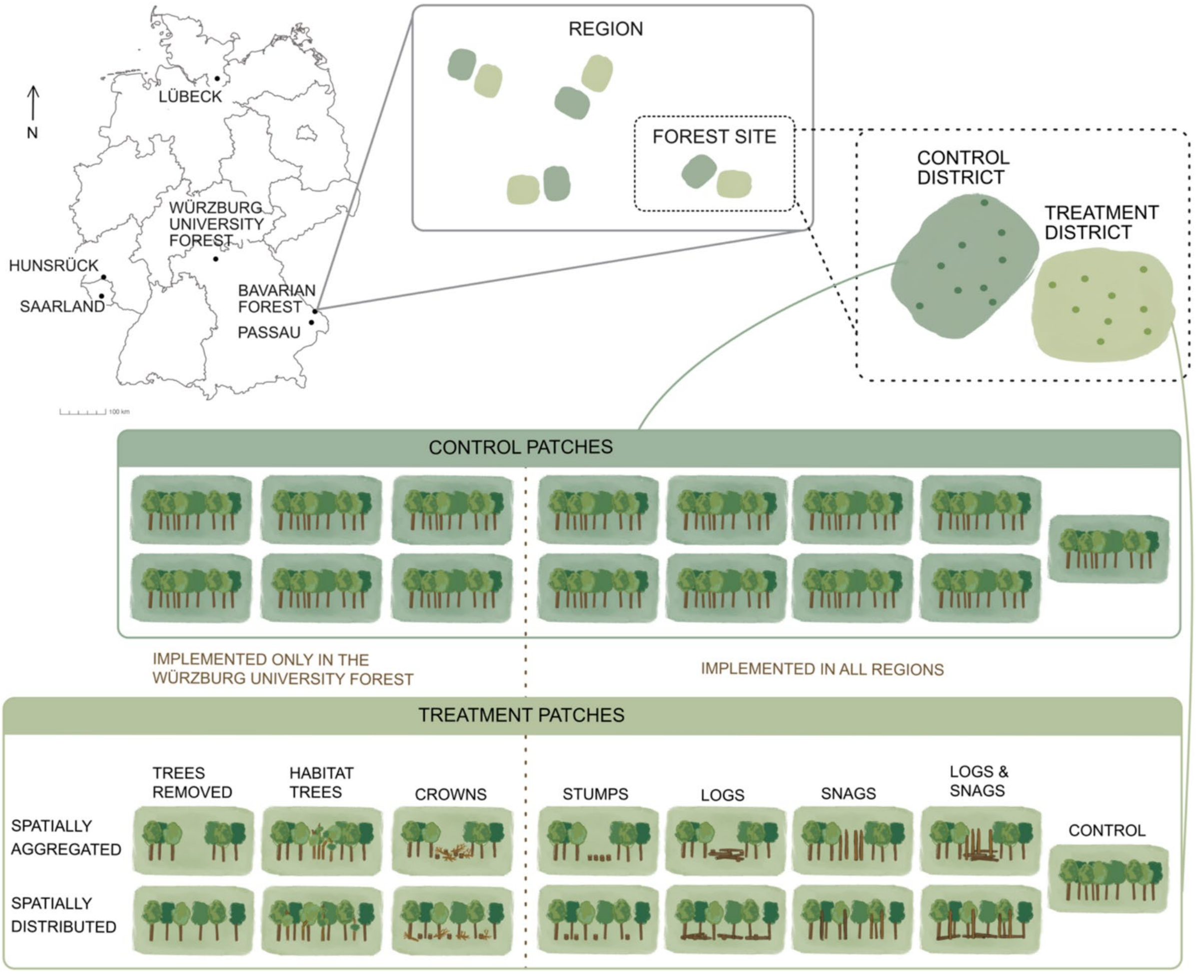


Fig. 1 The BETA-FOR experimental design spans 234 forest patches at 11 forest sites across six regions in Germany: the Bavarian Forest, Passau, Würzburg University Forest, Saarland, Hunsrück and Lübeck. The 11 forest sites each contain one treatment district (9 patches with manipulated canopy and deadwood; 15 patches at Würzburg) and one paired control district (9 or 15 patches with homogeneous structure). The brown dotted line distinguishes treatments implemented only in the Würzburg University Forest (left) from those implemented in all regions (right)

The VOC traps were connected to battery-powered DC pumps (Fürgut, Tannheim, Germany), drawing ambient forest air through the tubes at a flow rate of 1.1 L/min for 30 min per sample. This sampling protocol was adapted from methods described by Otieno et al. (2023). Due to logistical constraints and given the large spatial scale of this study, we prioritized extensive spatial coverage (234 patches across six regions) over within-patch replication, collecting one sample per height per patch. After excluding faulty samples, we analyzed 230 samples from 1 m height and 232 from the forest floor.

Ambient air sampling captures the integrated volatile profile of forest patches—a composite of emissions from multiple sources (e.g., vegetation, decomposing organic matter, soil, microbes, fungi, animals) that have mixed in the forest air. This approach allows us to characterize the overall ‘VOC fingerprint’ or volatilome of each forest patch. The volatilome is the totality of VOCs detected at a defined time and area, in this study referring to the collective VOC profile of forest patches, forest districts, or the broader forest ecosystem. In this study VOCs are the volatile organic compounds detectable by our TD-GC/MS method, encompassing compounds containing 5 to

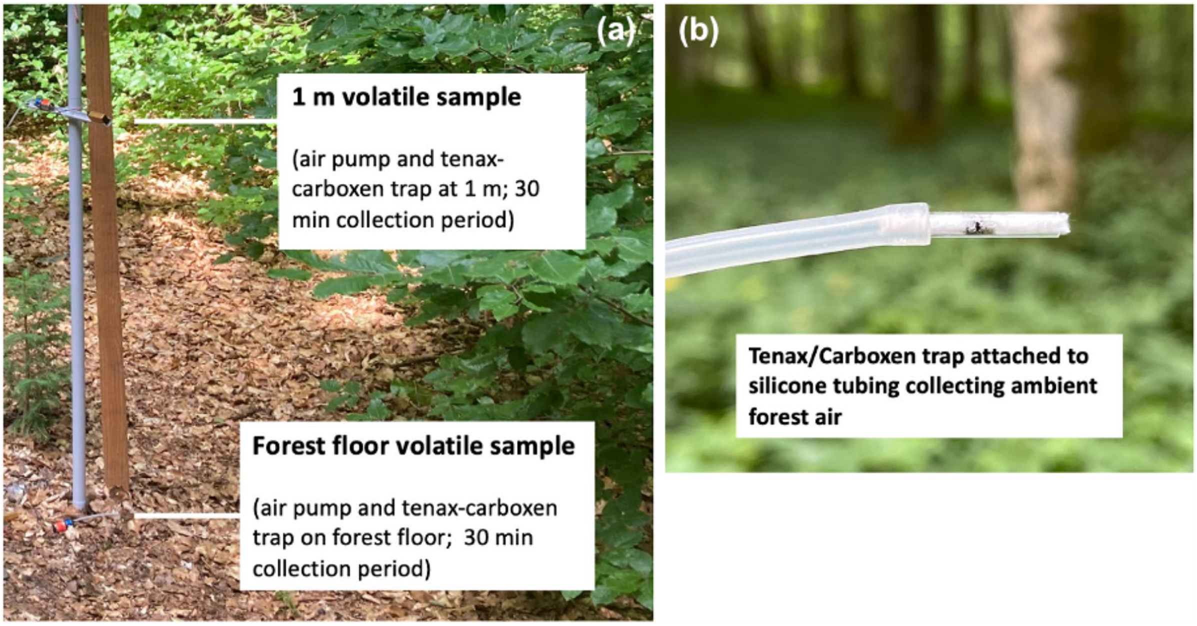


Fig. 2 Volatile organic compound (VOC) sampling set up on BETA-FOR forest patches. (a) VOC samples were collected at 1 m height and at the forest floor using Tenax/Carboxen adsorption tubes connected to portable battery-powered air pumps. Air was sampled for 30 min at a flow rate of 1.1 L min^{-1} from the center of each of the 234 50 m × 50 m forest patches. (b) Close-up of a Tenax/Carboxen tube attached to silicone tubing collecting ambient forest air

40 carbon atoms (i.e., C5 and C40) and eluting up to retention time ≈ 55.

To focus the scope of the study and further minimize variation between the samples, we made an effort to restrict sampling of all experimental patches to one month (July 2023) and collected samples during daylight hours (9:30–17:30) when VOC production is highest. We avoided days with precipitation since rain leads to a short-term increase in VOC emissions (Lappalainen et al. 2009; Greenberg et al. 2012).

Chemical analysis and data processing

The TD-GC/MS methods were adapted from Otieno et al. (2023). VOC samples were analyzed via thermal desorption gas chromatography-mass spectrometry (TD-GC/MS) using a Markes TD100-xr thermal desorption unit (Markes, Offenbach am Main, Germany) coupled to an Agilent 7890B/5977 GC–MS system (Agilent Technologies, Palo Alto, USA). The mass spectrometer was operated in single quadrupole mode with a scanning range of m/z 40–650. For the chemical analysis, each glass tube containing the Tenax/Carboxen sorbent was transferred to sorption tubes, which were then loaded into the thermal desorber. In the thermal desorber, the sorption tubes were heated in a stream of nitrogen carrier gas to release VOCs from the sorbent materials using the following parameters: flow rate 20 ml / min, flow temperature 180°C, minimum delivery pressure 2 psi; pre-desorption with dry purge time 10 min and purge flow 40 ml / min; tube desorption for 10 min at 260°C with trap flow 40 ml/min. The desorbed VOCs were then directed to a 5°C Peltier-cooled focusing trap, which was rapidly heated to 210°C in the counter-current of carrier gas to inject the VOCs into the GC column. Chromatographic separation was achieved using a HP-5MS UI capillary column (30 m × 0.25 ID; df = 0.25 µm, Agilent Technologies, Palo Alto, USA) with helium as the carrier gas (flow rate 1.287 ml/min, at a constant pressure of 1 bar). The temperature program started at 40°C and increased at 5°C/min to 300°C, with a total run time of 56 min per sample.

Raw chromatograms were integrated in MassHunter Qualitative Workstation using the Agile 2 algorithm with the threshold parameter set to 0 to quantify individual VOC peaks, with each peak corresponding to one compound (see Error! Reference source not found. in supplementary material for an example of a chromatogram and corresponding compound classes). Peak alignment across samples was performed using the *GCalignR* package (Ottensmann et al. 2018) to ensure consistent compound quantification across all samples. This processing workflow generated two data outputs for each detected compound: the mean retention time (the average elution time of a compound) and the integrated peak area, which represents the total ion signal, or counts, detected for each compound and is proportional to their relative abundances. Individual compounds were not identified to specific VOC classes. Instead, we focused on VOC β-diversity patterns in forest ecosystems. Experimental procedures were randomized throughout. Siloxane compounds from column bleed and ambient forest background noise were equally present across all samples and were not removed, as they do not bias comparisons of relative VOC composition between patches. The complete VOC dataset contained 724 peaks detected at 1 m height and 727 peaks at the forest floor level. Sampling across 234 forest patches generated highly skewed VOC data with frequent zeros. We therefore analyzed presence/absence data rather than abundance, which proved effective for analyzing β-diversity patterns while avoiding the statistical issues associated with extreme data distributions.

Environmental variables

Average air temperature during sampling was calculated for each sample using temperature data measured with EasyLog EL-USB2 logger (Lascar Electronics, United Kingdom) installed within TX COVER sun shields (Technoline, Germany). The data were recorded at 2 m height at the patch centers within 30 min of the 30 min VOC sampling period, since exact time periods were not available for all sampling periods.

Tree species composition surveys and basal area measurements (Pierick & Ammer 2025), as well as deadwood volume and type (including stumps, logs, snags, and habitat trees) surveys (Junginger et al. 2025) were conducted on all patches. 278 herbaceous and woody species were recorded in the herb layer (i.e. up to 1 m height) on five 4 m radius subpatches per patch during the vegetation period in 2023 (Bradler et al. 2025). For analysis, understory species cover data were averaged per patch and used to calculate Bray–Curtis dissimilarities in herb-layer composition using the *vegan* package (Oksanen et al. 2025). To calculate canopy densities, LiDAR data was collected using a DJI M300 mounted with an L1 sensor. Flight height was set to 90 m and the sensor's triple mode was used. Variables to describe the vertical structure were adapted from Moudrý et al. (2023). Canopy cover was calculated as the proportion of LiDAR points classified as canopy (>7 m height) relative to the total points within each patch, with values ranging from 0 (open canopy) to 1 (closed canopy) (Castañeda-Gómez et al. 2025). Since many fungal sporocarps are closely associated with deadwood, we used data on sporocarp abundance from stumps, logs and snags surveyed on the BETA-FOR patches in autumn of 2023 and 2024 (Lira Dyson & Bässler 2025). Beetles were sampled in the Würzburg University Forest and the Bavarian Forest in 2022 and in 2023 in the Hunsrück, Saarland, and Lübeck, using two non-attracting flight interception traps per patch. Each trap consisted of a crossed pair of transparent hard plastic shields (40 cm × 60 cm), a plastic roof, and a funnel leading to a bottom plastic container filled with a ~ 15% solution of sodium chloride (NaCl) and a drop of odorless detergent to break the surface tension and preserve the caught arthropods. Specimens were subsequently identified by an expert and filtered to include only saproxylic beetles for a total of 448 species (Müller 2025).

Statistical analysis

All statistical analyses were performed in R version 4.4.3 (R Core Team 2025). The *tidyverse* package (Wickham et al. 2019) was used for data handling and visualization. We used two complementary approaches: First, to test whether treatment districts show higher within-district VOC β-diversity (H1), we used generalized linear mixed models (GLMMs) comparing pairwise dissimilarities within control versus within treatment districts. Second, to identify drivers of VOC beta-diversity (H2), we analyzed all 234 patches using Multiple Regression on distance Matrices (MRM), which captures the full range of environmental variation. MRM are designed for analyzing pairwise dissimilarity matrices where observations are not independent. The method uses permutation testing to test whether environmental and ecological predictors explain VOC dissimilarity while controlling for spatial distance (the geographic distance between patches). Positive MRM coefficients indicate that greater differences in predictors between patches correspond to greater VOC dissimilarity.

Analysis of within-district heterogeneity

We compared VOC β-diversity between treatment and control districts. Within-district heterogeneity was calculated using pairwise VOC dissimilarities (True Jaccard distance based on VOC presence-absence profiles) among all patches within each district. We used two GLMMs—one for VOC β-diversity at 1 m height, one for the forest floor—implemented in *glmmTMB* version 1.1.11 (Brooks et al. 2017; McGillycuddy et al. 2025). Ordered beta regression (ordbeta family, logit) was selected because the response variable was continuous and bounded between 0 and 1. We fitted each ordered beta regression GLMM with district type (treatment vs. control) as a fixed effect and crossed random intercepts for site (representing paired treatment and control districts within regions), sampling hour, sampling date, and the two patches in each pairwise comparison to account for the correlation among observations.

Analysis of environmental drivers

We examined which environmental factors drive VOC dissimilarity using MRM analyses (999 permutations) from the *ecodist* package version 2.1.3 (Goslee & Urban 2007). VOC dissimilarity (True Jaccard distance) served as the response matrix, and environmental predictors were calculated as pairwise distance matrices: Euclidean distances for deadwood volume and canopy cover; Bray–Curtis dissimilarity for tree species composition and herb layer composition; Bray–Curtis dissimilarity for fungal sporocarp abundances; and Euclidean distances for air temperature and sampling time. All matrices were standardized (z-transformed) prior to analysis. All predictors were entered into the same MRM model to test their relative importance for explaining VOC β-diversity.

Analysis of deadwood structure and component diversity

In addition to the effect of deadwood volume, we analyzed how different deadwood structures affect VOC β-diversity. Using MRM we tested whether pairwise differences in (i) total deadwood volume, (ii) lying deadwood volume (logs and stumps), (iii) standing deadwood volume (high stumps and habitat trees), and (iv) deadwood component diversity (count of standing and/or lying deadwood present on each patch; range from 0–2) explained VOC dissimilarity (True Jaccard distance). To evaluate whether structural diversity explained VOC dissimilarity beyond the effect of total deadwood amount, we included both total deadwood volume and deadwood type diversity in the same model.

Analysis of saproxylic beetle dissimilarity

To test whether saproxylic beetle community composition relates to VOC β-diversity patterns, we calculated beetle community dissimilarity using the vegdist function in the *vegan* package (Oksanen et al. 2025) and three metrics: We used Jaccard dissimilarity on presence-absence data, Bray–Curtis dissimilarity on abundance data, and Bray–Curtis dissimilarity on square-root-transformed abundance data to down weight dominant species. We then used MRM analyses to test whether spatial distance between patches, canopy cover, deadwood and VOC dissimilarity at 1 m height and at the forest floor influence beetle community dissimilarity.

VOC samples were analyzed separately by sampling height (1 m and forest floor) to capture possible height-specific responses, as differences in forest air composition have been found particularly in the forest canopy and close to the soil (Noe et al. 2012; Mäki et al. 2019), though few studies have been conducted on ambient understory air (Jüttner 1986; Isidorov & Jdanova 2002).

Results

Our findings show that the enhancement of structural heterogeneity among patches significantly increased within-district VOC β-diversity at 1 m height (ordered beta regression GLMM; effect size = 0.220, SE = 0.034, $p < 0.001$) but not at the forest floor (beta regression GLMM; effect size = 0.026, SE = 0.016, p = 0.116) (Fig. 3). All model parameters are provided in supplementary material Tables S1 and Tables S2

Deadwood volume emerged as the strongest treatment-related driver of VOC heterogeneity at both sampling heights (1 m: effect size = 0.015, $p < 0.005$; forest floor: effect size = 0.014, $p < 0.001$), while canopy cover showed no significant effects (Fig. 4). Herb layer dissimilarity significantly influenced VOC patterns at both heights (1 m: $p < 0.004$; forest floor: $p < 0.001$). Tree species dissimilarity had no effect at 1 m height but a significant negative effect on VOC dissimilarity at the forest floor ($p < 0.003$). Fungal sporocarps, temperature and time of day showed no significant effects on VOC patterns, whereas spatial distance between patches showed the strongest overall effect across both heights (1 m, $p < 0.001$; forest floor, $p < 0.001$). The MRM explained more variance at the forest floor ($R^2 = 0.071$) than at 1 m height ($R^2 = 0.05$).

To disentangle the effects of deadwood quantity versus deadwood structural diversity (lying vs. standing vs. both), we tested whether total deadwood volume or the presence of standing deadwood only, lying deadwood only or both, explained VOC dissimilarity (Fig. 5). When deadwood volume and structural diversity were tested together, the effect of volume was no longer significant at either height. However, the presence of both standing and lying deadwood significantly affected VOC dissimilarity at both 1 m height ($p < 0.001$) and the forest floor ($p < 0.001$). This means that patches differing in whether they had both deadwood types showed greater VOC dissimilarity than expected from volume differences alone. Individual deadwood types tested separately showed no significant effect, indicating that having both structural types creates chemical complexity beyond what either type alone can provide. The model explained little variance in VOC dissimilarity (forest floor $R^2 = 0.025$; 1 m height $R^2 = 0.015$).

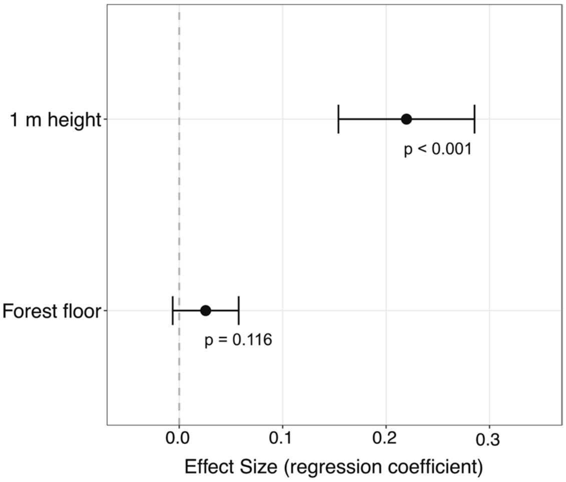


Fig. 3 Effect of treatments on district-level VOC β-diversity (Jaccard dissimilarity) at 1 m and the forest floor from ordered beta regression GLMMs (logit). Treatment districts show higher VOC β-diversity at 1 m ($p < 0.001$) but not at forest floor (p = 0.116). Error bars are 95% confidence intervals

Forest floor VOC β-diversity significantly influenced saproxylic beetle composition (Jaccard, $p < 0.02$) but had no significant effects on dominant or rarer species (Fig. 6). In contrast, 1 m height VOCs showed no significant effects on saproxylic beetle communities across any diversity order. Structural variables consistently drove beetle community patterns across all diversity measures. Spatial distance showed the strongest effects ($p < 0.001$), followed by canopy cover ($p < 0.001$) and deadwood volume ($p < 0.001$).

Discussion

Using a landscape-scale framework, this study provides clear evidence that forest management can create structural gradients that, in turn, modulate the forest volatilome. By comparing VOC heterogeneity between 11 treatment and 11 control districts across Germany, we show that structurally enhanced forests create detectable VOC β-diversity patterns at 1 m height. This expands on vertical VOC heterogeneity findings in forest canopies (Yáñez-Serrano et al. 2018; Petersen et al. 2023; Ringsdorf et al. 2024; Sulzer et al. 2025) and horizontal VOC heterogeneity patterns within a beech forest (Hagiwara et al. 2024) to demonstrate that management creates VOC heterogeneity within and among forest districts.

Despite sampling for only 30 min per patch, we detected treatment effects, indicating that treatments create measurable changes in volatilomes. Treatment districts exhibited higher VOC β-diversity than control districts only at 1 m height, partially supporting H1. The height-specific response likely results from differences in emission sources and vertical mixing.

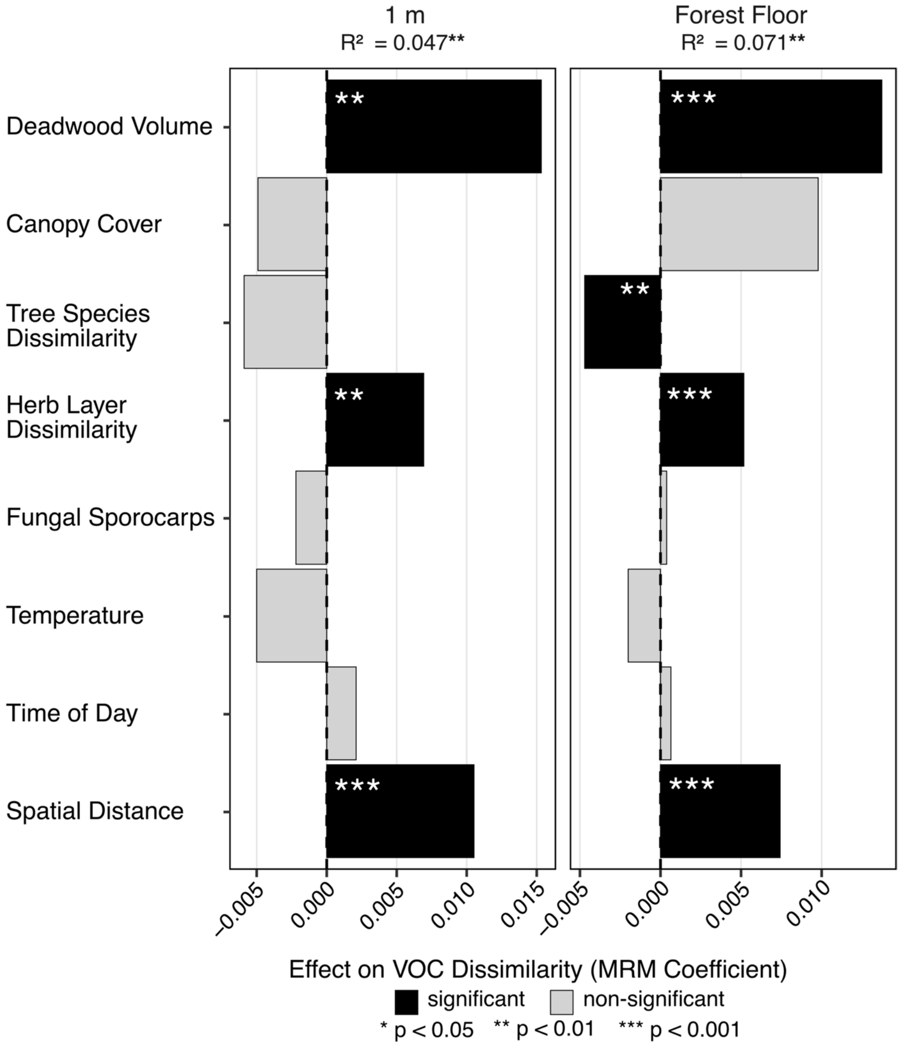
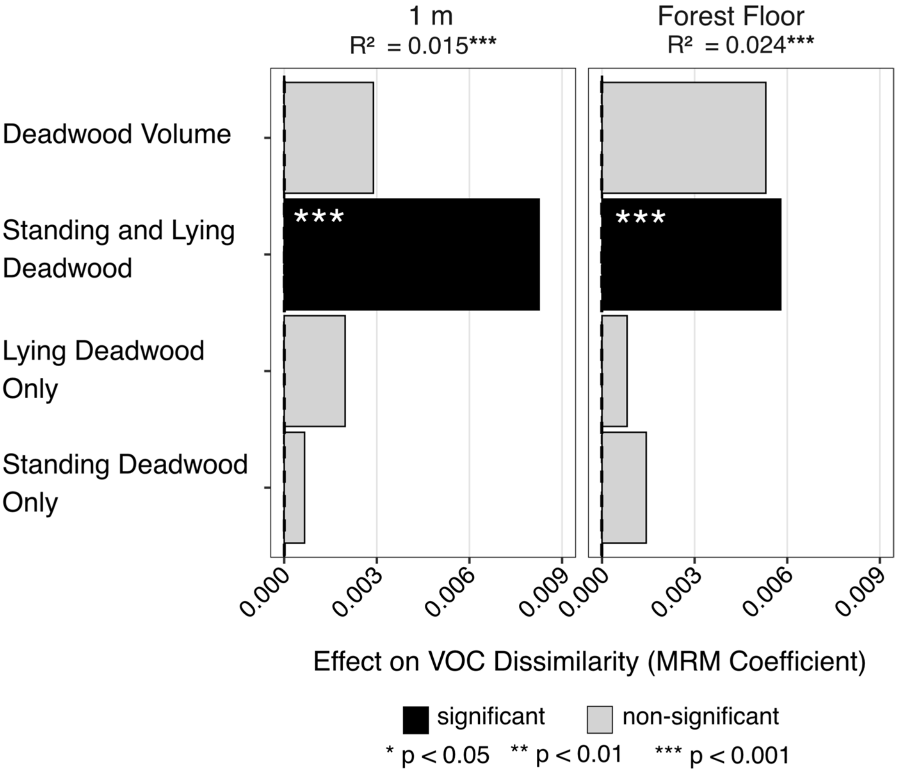


Fig. 4 Effects of structural and environmental Drivers on VOC β-Diversity at 1 m height and the forest floor. Bars show MRM coefficients; larger coefficients indicate stronger effects on VOC dissimilarity. R^2 values show the proportion of variance explained by the model at each height

At 1 m height, VOC profiles were primarily driven by deadwood structural diversity, with emissions from standing deadwood components and vegetation creating detectable spatial patterns across treatment districts. At the forest floor, VOC emissions from multiple sources (soil respiration, litter decomposition, deadwood, root exudates, and microbial activity) may have created greater spatial and temporal heterogeneity (Trowbridge et al. 2020a). The combination of reduced air movement at ground level, our relatively brief sampling period (30 min per patch), and greater temperature and moisture fluctuations at the forest floor (Blondeel et al. 2020) may have been insufficient to detect treatment-level patterns where fine-scale variation is high. Under the dry and warm summer conditions during our sampling, litter and soil may have acted as a sink for some VOCs (such as sesquiterpenes) rather than a source (Trowbridge et al. 2020b; Legros et al. 2025; Rocco et al. 2025), potentially reducing overall volatilome heterogeneity at the forest floor. Vegetation VOC dynamics and VOC mixing through additional environmental factors may be more prominent at 1 m height when various plant species with different emission profiles are involved. Plant species in the forest understory can also be a significant source of VOCs (Šimpraga et al. 2019). Together, these factors could lead to more heterogeneous volatilomes among treatment districts. Neither sampling time nor temperature significantly affected our results. VOC emissions typically vary with light, humidity, and temperature (Owen et al. 2002; Karl et al. 2008; Schade et al. 2011; Spinelli et al. 2011;

Fig. 5 Effects of deadwood volume and diversity of deadwood type on VOC β-diversity at 1 m height and the forest floor. Bars depict MRM effect sizes (coefficients), where larger values indicate stronger effects on VOC dissimilarity. R^2 values show the proportion of variance explained by each model



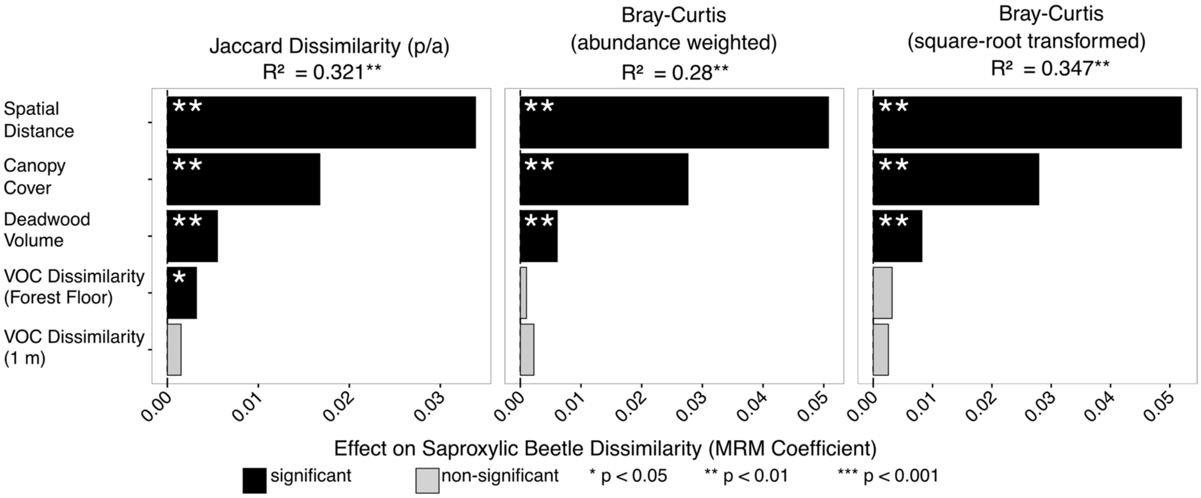


Fig. 6 Effects of VOC β-diversity and structural variables on the saproxylic beetle community dissimilarity using Jaccard dissimilarity (presence/absence), Bray–Curtis dissimilarity (abundance-weighted), and Bray–Curtis dissimilarity on square-root transformed data (more weight to rare species). Bars depict MRM coefficients; larger values indicate stronger effects. R^2 values show the proportion of variance explained by each model

Rinnan et al. 2020; Trowbridge et al. 2020a), but, contrary to our expectations, did not directly impact our findings. Treatment effects were documented for fauna, flora, and fungi surveyed in the same experimental design (Lira Dyson et al. 2024; Bradler et al. 2025; Massó Estaje et al. 2026; Rothacher et al.

2025), indicating that the structural manipulations influencing biological communities also extend to the invisible volatilome.

Having established that treatments create VOC β-diversity at 1 m we then examined which structural drivers explain this pattern. β-diversity responses to the ESBC treatments varied among taxa. Bat assemblages showed increased β-diversity associated with variation in light and deadwood, while bird declined despite local diversity gains (Wild et al. 2025), and hoverflies had weak and regionally variable β-diversity responses (Massó Estaje et al. 2026) For VOCs, deadwood diversity emerged as the main driver of β-diversity at 1 m height, suggesting that decomposition processes associated with deadwood create chemical heterogeneity among forest patches. This pattern remained consistent across both heights, while canopy cover showed no significant effects despite creating microclimatic changes in temperature and light. The importance of deadwood over canopy cover suggests that decomposition and microbial processes, rather than treatment-caused changes in light availability, primarily shape volatilome heterogeneity at 1 m. This aligns with recent work identifying microbial activity as a key regulator of forest VOC dynamics (Weisskopf et al. 2021; Ali et al. 2025; Lee et al. 2025; Murata 2025). The strong effect of deadwood indicates that decomposition-derived VOCs are key contributors to chemical heterogeneity. Canopy effects may act indirectly by influencing herb layer composition which significantly influenced VOC patterns at both heights.

Several mechanisms likely contribute to chemical heterogeneity. Different dead tree species harbor distinct volatile profiles (Mäki et al. 2021; Isidorov et al. 2024). Decay stage and type alters both substrate chemistry and fungal community composition, producing distinct VOC signatures (Mäki et al. 2021; Mali et al. 2019). Saproxylic beetles associated with deadwood may add to VOC variation through interactions with fungi and their own metabolic activity (Sbaraglia et al. 2025). Although fungal sporocarp abundance (Bray–Curtis) did not significantly affect VOC patterns in our models, this may reflect a temporal mismatch between sporocarp surveys (fall 2023 and 2024) and VOC sampling (July 2023). Fungal sporocarps represent brief fruiting events, separate of underlying mycelial activity that may emit different VOCs (Berger et al. 2022). Although we did not measure deadwood decay stage or identify individual compounds, these mechanisms provide a basis for interpreting the observed β-diversity patterns. Additionally, temperature was measured at 2 m rather than at exact VOC sampling heights (the forest floor and 1 m), which, while a relatively small difference, may not fully capture microclimate conditions directly influencing VOC emissions at these heights and may explain why temperature did not have a significant influence on VOC patterns in our results.

We found partial support for hypothesis two (H2). Patches differing in deadwood structural diversity showed greater VOC dissimilarity, particularly when comparing patches containing both standing and lying deadwood to those with one type or none. The deadwood diversity index (0–2) significantly predicted β-diversity at both heights, while neither standing nor lying deadwood volume alone explained VOC patterns. Deadwood structural diversity, rather than total volume, drives chemical heterogeneity. Patches containing both standing and lying deadwood generate distinct volatilomes beyond what total volume explains. Neither deadwood type alone significantly affected VOC patterns. This may reflect small effect sizes that are difficult to detect statistically in VOC data (Kempraj 2025). However, the combined presence of both types likely increases organismal diversity by providing a range of microhabitats. Standing deadwood offers drier, sun-exposed conditions, while lying deadwood retains moisture and supports different decomposers (Graf et al. 2021; Löfroth et al. 2023). Patches containing both forms of deadwood support a greater diversity of microbes, fungi, and beetles, producing more heterogeneous volatilomes (Holighaus & Schütz 2006; Bauhus et al. 2018).

Hypothesis three (H3) was also partially supported. Saproxylic beetle community dissimilarity increased with VOC dissimilarity between patches. This relationship was significant for presence/absence (Jaccard) but not for abundance-weighted (Bray–Curtis) beetle data, and only at the forest floor. We used beetles as a test community because they rely on chemical cues to locate deadwood and fungi (Holighaus & Schütz 2006; Holighaus et al. 2014; Leather et al. 2014; Sbaraglia et al. 2025) and respond to our treatments (Rothacher et al. 2023). Forest floor VOC β-diversity significantly predicted beetle community dissimilarity (Fig. 6), suggesting that these chemical patterns may have ecological relevance. However, the structural variables deadwood volume, canopy cover, and spatial distance predicted beetle community dissimilarity more strongly, indicating that physical habitat structure dominates distributions even when chemical gradients are present. While these results are based on correlative MRM analyses, the significant beetle and VOC relationship supports the idea that volatilomes act as ecological information.

Other environmental and structural factors also shaped VOC heterogeneity. Herb layer composition significantly influenced VOC patterns, indicating that understory vegetation contributes to VOC β-diversity. This influence may be an indirect consequence of canopy openness affecting light and herb layer growth. Unexpectedly, tree species diversity had a negative effect at the forest floor level. This negative effect may be a confounding effect of regional differences in tree species richness rather than a true ecological pattern. At canopy levels, distinct species emit unique VOC profiles (Antonelli et al. 2020). Near the forest floor, however, litter and soil influences may dominate in summer months (Borsdorf et al. 2023). The significant effect of spatial distance confirmed that VOC dissimilarity increases with geographic distance. Our study spanned six regions and variation among regions likely introduced additional chemical variability as supported by the significant effect of spatial distance across MRMs.

Our results demonstrate that structural management interventions create chemical heterogeneity within and between districts (both β-diversity), resulting in an invisible heterogeneity gradient. These volatilome-level gradients operate alongside established structural and biotic gradients, extending the habitat-heterogeneity hypothesis into the chemical domain. Although our models generally explained little variance, as expected in large-scale ecological studies, especially chemical ecology (Kempraj 2025), the consistent detection of treatment effects demonstrates that this pattern is ecologically meaningful. Our findings complement documented effects of structural heterogeneity on multiple taxa, from beetles, hoverflies and nematodes to bats, birds and understory vegetation (Rothacher et al. 2023; Kacic et al. 2024; Asch et al. 2026; Bradler et al. 2025; Wild et al. 2025; Massó Estaje et al. 2026; Schwarz et al. 2026) demonstrating that structural heterogeneity affects different aspect of forest ecosystems at multiple spatial scales. By focusing on volatilome-level patterns rather than individual compounds, we captured the complex chemical environment that organisms experience, revealing that management modifies both the visible habitat structure and the invisible volatilome influencing species interactions.

Conclusion

Our findings indicate that increasing structural heterogeneity affects temperate forest volatilomes with ecological consequences, extending the habitat heterogeneity hypothesis to include the invisible dimension of the forest volatilome. Future research should aim to identify specific mechanisms, compound classes, and compounds driving these responses, and link individual VOC sources, from microbial and fungal to plant or animal, to ecosystem processes. Expanding this approach to other forest systems and management regimes will build a broader understanding of how structural change shapes landscape-scale chemical diversity. Although much additional research is necessary to increase our understanding of the roles of VOCs at the ecosystem level, our results highlight that deadwood structural diversity, rather than volume alone, shapes volatile β-diversity patterns in beech-dominated production forests, adding an invisible but ecologically relevant dimension to habitat heterogeneity in forests.

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Author contributions T.S., J.M., O.M., and L.C. conceived the study and designed the methodology. L.C. performed the analyses, prepared the figures, and wrote the first draft. O.M. and J.M. provided statistical support. L.C., M.B., P.M.B., A.J.C.G., B.L.D, L.F., K.P., J.R., J.S.W., M.W., C.W. contributed data. J.M., C.A., P.M.B., B.M.D, B.L.D., A.F., O.M., G.v.O., K.P., J.R., M.S.L., C.W., and T.S. provided revisions. All authors reviewed the manuscript.

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Data availability The datasets generated and analyzed in this study are available in the Zenodo repository: https://doi.org/10.5281/zenodo.14975137. R code for statistical analyses is available from the corresponding author upon request.

Declarations

Conflict of interest The authors declare no competing interests.

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