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RESEARCH ARTICLE

Regulating bark beetles with mechanical bark treatments: Trade-offs among pest control, operational efficiency and biodiversity

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Abstract

1. Natural disturbances have increasingly shaped global forests in recent decades. Coniferous forests in the Northern Hemisphere are facing intensifying disturbance regimes, exacerbating the conflict between traditional management objectives and the role of disturbance-driven dynamics for biodiversity conservation. In Europe, unprecedented amounts of Norway spruce (*Picea abies*) have been damaged in recent years by hot droughts accompanied by outbreaks of the European Spruce Bark Beetle (*Ips typographus*).
2. To meet the demands of forest protection and secure timber production, *P. abies* trees colonized by *I. typographus*, or suitable for colonization due to abiotic stress, are either extracted by salvage logging or made unsuitable for breeding using debarking techniques. Manual techniques are inefficient for large quantities and the extraction of deadwood can compromise biodiversity. We investigated mechanical bark treatments as potential alternatives to salvage logging for bark beetle regulation in Central Europe. Our study quantified bark beetle regulation efficacy, operational efficiency, wood properties and effects on biodiversity of saproxylic beetles, fungi and bacteria, as well as woodpeckers.
3. Processing Norway spruce logs three times with a harvester to remove bark substantially reduced bark beetle emergence, demonstrating a scalable method that may contribute to the management of pest outbreaks and disturbances at landscape scales. Motor-manual bark gouging and debarking are flexible alternatives and effective methods for small wood quantities.
4. With increasing bark removal intensity, species richness of saproxylic beetles and bacteria decreased, while fungi species richness increased. In all three groups, species assemblages were affected by bark treatments. Differences in moisture content between treated and control logs were the main driver for changes in fungi and bacteria community assemblages. Bark treatments did not affect net

calorific value over the first 2 years, blue-stain fungi colonization and elemental composition (H, C and N).

5. *Synthesis and applications*. Three times harvester processing and motor-manual bark gouging effectively reduce bark beetles, enabling two options: permanent on-site retention for biodiversity conservation, or up to 2 years of intermediate on-site storage with no treatment effect on blue-stain fungi colonization or energy content, thereby buffering operational bottlenecks during landscape disturbances.

KEYWORDS
ecological value, economic value, forest conservation, forest disturbance management, forest protection, fungi and bacteria, net calorific value, saproxylic beetles

1 | INTRODUCTION

In the context of rapid climate change, the forestry sector is facing more natural disturbances, with an increase in storms, droughts and insect outbreaks (Patacca et al., 2022; Seidl et al., 2017; Senf et al., 2020). These disturbances are causing severe and widespread forest diebacks, posing significant challenges to the economic and ecological sustainability of forest management. However, disturbances and the subsequent canopy dieback are inherent components of forest dynamics, particularly in coniferous ecosystems (Franklin et al., 2002; Kulakowski et al., 2017). Increased light availability on the forest floor, greater spatial heterogeneity in stand structure, and deadwood accumulation can improve conditions for forest regeneration and biodiversity, especially in managed but also in unmanaged forests (Busse et al., 2022; Hilmers et al., 2018; Sommerfeld et al., 2021).

Since 2018, unprecedented volumes of unplanned wood harvests and significant financial losses have resulted from landscape-scale European Spruce Bark Beetle (*Ips typographus*) infestations in Central European Norway spruce (*Picea abies*) forests (Hlásny et al., 2021; Patacca et al., 2022). This dynamic is predicted to persist and intensify under future climate change scenarios (Grünig et al., 2026; Mohr et al., 2025; Seidl et al., 2017). With 23% of the growing stock, *P. abies* represents an important component in European forestry (Köhl et al., 2020), yet it is increasingly susceptible to natural disturbances and the changing climate (Biedermann et al., 2019; Marini et al., 2017). Moreover, a significant proportion of *P. abies* forests have been planted outside of their natural ecological range, where increased climatic stress may further exacerbate vulnerability (Jansen et al., 2017). Landscape-scale outbreaks are often accompanied by logistical challenges, labour shortages and low timber prices, which can limit the economic viability and timely implementation of pest control interventions (Hlásny et al., 2021). Consequently, on-site wood storage can be costly (Costa & Ibanez, 2005) and may reduce marketable timber value due to colonization by staining fungi (e.g. blue-stain and brown-rot) and mechanical damage caused by wood-boring insects. In addition, subsequent decomposition can further reduce the energy content of the wood (Barrette et al., 2015; Böhm et al., 2023). Economically, blue-staining fungi are of highest relevance for bark beetle-infested wood, since they are vectored by bark beetles and cause relevant discoloration to the sapwood (Leonhardt et al., 2019; Wingfield et al., 2017). The aesthetic alterations lead to significant timber devaluations and quality downgrading on the timber market (Barrette et al., 2015; Böhm et al., 2023). In temperate forests, microbes (fungi and bacteria) have a key role in wood decay (Seibold et al., 2021) and shifts in their assembly can influence elemental cycling and thus timber and habitat quality (Fukami et al., 2010; Herrmann & Bauhus, 2018). Bark shapes the microbial colonization process and influences the decomposition rate, as it protects the wood against biotic and abiotic impacts and logs dry out faster without it (Dossa et al., 2018; Ulyshen et al., 2016). Consequently, bark presence also may affect the colonization and growth of blue-stain fungi and impact timber value.

While fuel wood may represent a secondary assortment in established forest management strategies, the sheer volume generated during mass mortality events necessitates a deeper understanding of its energetic potential for the bioenergy sector (Barrette et al., 2015; Camia et al., 2021). The net calorific value as well as elemental composition (carbon, hydrogen and nitrogen) of the wood are key factors to evaluate impacts on energy density (e.g. fuel wood), decomposition rates and changes in deadwood habitat quality (Barrette et al., 2015; Gendek et al., 2023; Stokland et al., 2012).

To protect susceptible forest stands from high *I. typographus* densities and minimize beetle dispersal, infested logs or suitable breeding material (e.g. windthrown and damaged trees) are transported away from host trees before beetle emergence (Hoch et al., 2020). Simulation studies suggest that, within the first 5 weeks of colonization, eliminating at least 80% of the beetles (Fahse & Heurich, 2011) or removing 95% of infested or damaged trees outside the dispersal range (~500 m) could potentially prevent outbreaks (Dobor et al., 2020). Empirical observations after a storm event in Switzerland indicate that higher levels of damaged and/or infested tree removal—hereafter referred to as salvage logging—were associated with reduced bark beetle damage in the following years (Stadelmann et al., 2013), whereas similar

interventions in the Western Carpathians showed limited effects on the population dynamics (Vanická et al., 2020).

However, salvage logging cannot always achieve such intensive wood extraction rates, reduces saproxylic (deadwood-dependent) biodiversity (Georgiev et al., 2020; Thorn et al., 2018; Thorn, Chao, et al., 2020) and may compromise forest resilience to future disturbances by removing important structural and ecological legacies essential for regeneration and ecosystem stability (Leverkus et al., 2021; Lindenmayer et al., 2017). Mechanical bark treatments offer an alternative method to existing bark beetle regulation methods like salvage logging, pesticide application and wet storage (artificial irrigation of logs to displace air in the wood). The removal or manipulation of bark destroys the breeding habitat of *I. typographus* and causes the existing larvae to dry out, allowing for intermediate on-site storage or permanent retention of wood on site (Hagge, Leibl, et al., 2019). This method can primarily be applied in forests where tree removal is restricted (e.g. protective or conservation forests), where transport is challenging (e.g. steep terrain or forest mires), and during logistical bottlenecks when temporary storage of logs is required within the supply chain (Fettig et al., 2022; Hlásny et al., 2021; Wermelinger, 2004). Manual and motor-manual debarking techniques, such as the debarking spud and chainsaw attachment, effectively reduce *I. typographus* emergence (Hagge, Leibl, et al., 2019; Thorn et al., 2016; Zarges et al., 2023), but complete bark removal negatively impacts saproxylic species richness, its community assembly and ultimately higher trophic levels like woodpeckers (Hagge, Leibl, et al., 2019; Thorn et al., 2016). Compared to complete debarking, a novel chainsaw attachment that gouges the bark off in regular stripes (Figure 1, Figure S1), reduces *I. typographus* emergence with less effort, while the remaining intact bark benefits non-target biodiversity (Hagge, Leibl, et al., 2019; Thorn et al., 2016; Zarges et al., 2023). Rapid intervention is critical for addressing landscape-scale disturbances involving large volumes of wood, for which bark treatments with harvesters represent an effective solution by removing and perforating bark with delimbing knives and multiple passes over the logs (Delb et al., 2021). Conventional harvester processing (harvester normal), three successive passes through the harvester aggregate (harvester triple), and modified aggregates for debarking (debarking heads) have each indicated promising results to regulate bark beetles (Delb et al., 2021; Zarges et al., 2024). Yet, experimental validation across multiple sites accounting for different site conditions is still lacking, making it unclear whether the observed effects are generalizable across broader geographic scales.

Overall, our objective of this study was to identify suitable treatments, as alternatives to salvage logging, that effectively balance operational and ecological trade-offs. We specifically evaluated mechanical bark treatments suitable for different volumes of bark beetle-infested wood while accounting for the variability of German *P. abies* forests. This will provide the necessary information for two management objectives: temporary wood storage in commercial forests and long-term dead wood retention to support biodiversity conservation goals. We use bark beetle emergence reduction (pest control efficacy), operational efficiency, wood properties and effects on biodiversity of saproxylic beetles, fungi and bacteria to compare five mechanical bark treatments and a control. We quantify changes in wood moisture and chemical composition—using calorific value and elemental composition (Carbon, Hydrogen, Nitrogen) as indicators of energy density and decomposition speed (Gendek et al., 2023)—to determine the recovery potential for bioenergy after 2 years on-site. Additionally, we assessed blue-stain fungi colonization intensity to determine potential impacts of bark removal on timber quality. For the ecological assessment we aimed to evaluate how bark cover influences the assembly of saproxylic beetle, fungal and bacterial communities and subsequent changes in wood chemistry and moisture.

We hypothesize that: (i) although harvester-based techniques are better suited for processing larger wood volumes than

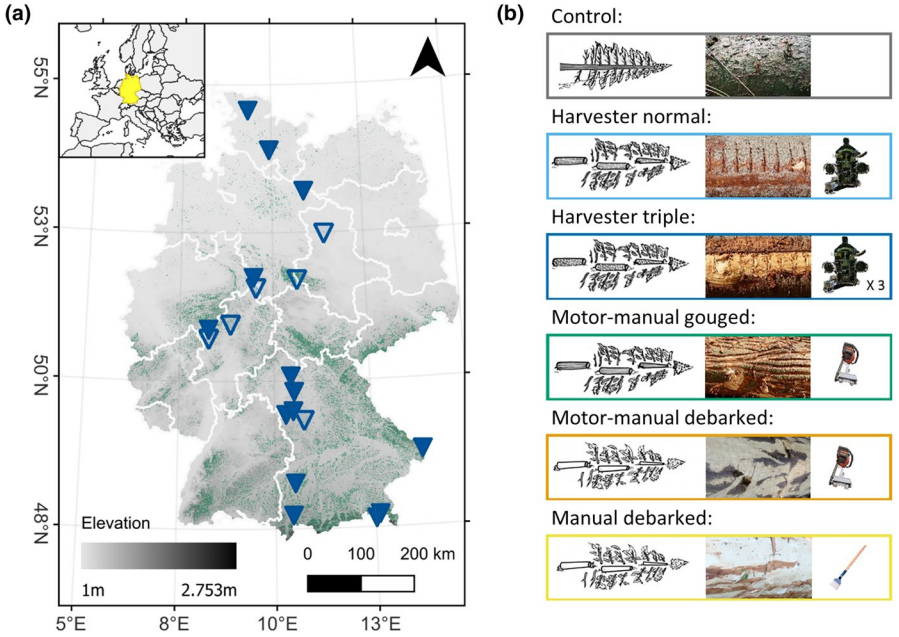

FIGURE 1 Experimental design to test the different bark treatments for *I. typographus* regulation in *P. abies* logs. (a) Distribution of the 20 study sites in Germany (empty markers without time study) with grey shading for altitude (NASA JPL, 2013) and green areas for forests dominated by *P. abies* (Blickensdörfer et al., 2024), © EuroGeographics for the administrative boundaries. (b) The control and five applied bark manipulation treatments with the respective log surfaces and tools used.

motor-manual treatments, conventional harvester handling will not manipulate and remove enough bark to regulate numbers of emerging *I. typographus*; (ii) compared to conventional harvester processing, three passes through the harvester aggregate accomplish bark beetle emergence reduction but decrease the volume which can be treated per machine hour; (iii) management treatments with higher bark removal are anticipated to decrease woodpecker activity, alpha and gamma diversity of saproxylic beetles and bacteria independent of climatic variation between sites, whereas fungi diversity will increase with bark removal. Further, we hypothesize that: (iv) the community assembly for saproxylic beetles, fungi and bacteria will be affected by bark treatments, related wood properties and climate variation between sites; (v) bark removal will reduce moisture content and blue-stain fungi colonization intensity; the net calorific value is predicted to decrease with decomposition over time, while decomposition alters the elemental wood composition of carbon, hydrogen and nitrogen content.

2 | MATERIALS AND METHODS

2.1 | Study area and bark treatments

At 20 study sites distributed across the climatic range of *P. abies* (Norway spruce) dominated forests in Germany (Figure 1a, Figure S2), six healthy *P. abies* trees were felled directly before the first regional swarming periods of *I. typographus* in spring 2022. After first signs of bark beetle colonization (brown sawdust and bore holes), logs were treated within 3 weeks to ensure treatment during the larval stage. Per site, one control log was only felled, without delimbing or cutting, while the other five logs were treated by professional forest workers (harvester normal, harvester triple, motor-manual gouging, motor-manual debarking, manual debarking; see Table S1). For (motor-) manual gouging and debarking, the logs were first delimbed and cut into 5 m sections. A debarking spud (flat blade affixed to a wooden handle) was used for manual debarking and motor-manual debarking was performed using a chainsaw-mounted debarking attachment (EDER Maschinenbau GmbH, Wolfenbüttel, Germany; Figure 1b). The same device, with a different blade configuration, was used to gouge regularly spaced longitudinal grooves in the bark (Figure 1b, Figure S1). For the normal harvester treatment, the trees were processed through the aggregate and cut directly to length. In the harvester triple treatment, the aggregate went first up and down the log, before passing it through a third time and cutting it to length. We measured the volume of treated wood per hour at 14 sites during the setup of the experiment and used it as a proxy for operational efficiency. For (motor-) manual treatments, times for debranching and cut-to-length were excluded, whereas these steps were included in harvester-based treatments because they are integral to the operation and added minimal additional time. The percentage of intact bark was assessed after treatment as a continuous variable of treatment intensity (Figures S3 and S4).

2.2 | Sampling

To evaluate bark beetle regulation efficacy and saproxylic beetle diversity, 30 cm-wide stem emergence traps with a saltwater trapping solution were installed 2 m from the base of the experimental logs. Each trap covered an area of $1.995 \pm 0.331\ m^2$ (SD) and was operated for three sampling seasons (April–October, 2022–2024). After each year, the traps were relocated 50 cm upward to ensure the inclusion of insects colonizing before (Figure S3). All saproxylic beetles (sensu Schmidl & Bußler, 2004) were morphologically identified to species level by a taxonomic expert. Woodpecker foraging holes in the bark and xylem of the experimental logs were counted on the whole log surface after 1 year as a proxy of activity (Aszalós et al., 2020; Thorn et al., 2016). One log was removed from the analysis due to incomplete gauging at one site and one entire site was excluded from the *I. typographus* and biodiversity analysis due to incomplete data, resulting in 19 sites.

We identified the molecular operational taxonomic units (OTUs) for the fungi and bacteria communities from sawdust samples collected in April and October 2022 and 2023 using DNA metabarcoding. We drilled through the full horizontal cross section of the stems, sampling at the base, middle and top tree section (Figure S3) and pooled the samples to represent the whole log (Naranjo-Orrico et al., 2025). The drill was cleaned with isopropanol and sterilized with a propane gas torch between each treatment to prevent cross-contamination. For DNA metabarcoding, subsamples of the directly frozen sawdust (−20°C) were sequenced with specific gene markers for fungi (ITS) and bacteria (16S) (see Text S1). From the fungi dataset we additionally analysed colonization intensity of blue-stain fungi (*Ophiostomataceae* and *Ceratocystidaceae*) to assess possible effects on the timber utilization potential. For this, fungal OTUs were classified with the UNITE v8.3 database (Abarenkov et al., 2024) at a confidence level of 95% and read counts were used as a proxy for colonization intensity. Read counts represent a relative, semi-quantitative measure of fungal abundance and may be influenced by variation in sequencing depth and PCR amplification efficiency across samples. Results should therefore be interpreted as indicative of differences in blue-stain colonization intensity among treatments rather than absolute fungal biomass.

To evaluate energy density (net calorific value) and wood properties (moisture, carbon, nitrogen, hydrogen content), the remaining sawdust was homogenized and assessed according to established procedures by an external laboratory (see Text S2).

2.3 | Analysis

Bark beetle regulation efficacy was quantified as the total abundance of adult *I. typographus* beetles—the most destructive bark beetle species for *P. abies* forests (Marini et al., 2017)—collected in the emergence traps over the three-year sampling period and standardized by sampling area (density per m^2). To homogenize data formats across morphological identification and metabarcoding

datasets, all biodiversity analyses were performed using presence–absence data. To focus on colonization after treatment, the OTUs of fungi (including blue-stain) and bacteria detected in the initial drill samples were excluded from each log. For each site and treatment, the detections of saproxylic beetle species and fungal and bacterial OTUs were pooled across their respective sampling periods. Alpha diversity was defined as the mean number of detected species or OTUs per treatment, averaged across sites. Finally, wood properties were included in the analyses as the difference between initial and final measurements (Δ).

All analyses were performed in R version 4.5.1 (www.r-project.org). *I. typographus* density and blue-stain fungi colonization intensity were modelled with generalized mixed-effects models with negative binomial distribution using the glmer.nb function from *lme4* package (Bates et al., 2015). We quantified differences between treatments in operational efficiency (wood volume per hour), wood properties, woodpecker activity, as well as alpha diversity of saproxylic beetles, fungi and bacteria with linear mixed-effects models (function lmer) from the package *lme4* (Bates et al., 2015). To meet normality assumptions, operational efficiency and woodpecker activity data were log-transformed and log diameter at breast height (DBH) was included as a covariate to control for surface-area effects. Site was included as a random effect in all mixed models to account for site-specific variations. Fixed treatment effects were assessed using Type III analysis of variance with Satterthwaite's approximation for denominator degrees of freedom for linear mixed models (package *lmerTest*; Kuznetsova et al., 2020) and likelihood ratio tests (χ^2) for generalized mixed models (package *lme4*; Bates et al., 2015). Finally, we used the *emmeans* package (Lenth et al., 2024) to calculate estimated marginal means and perform post hoc pairwise comparisons with Tukey's adjustment for family-wise error.

To evaluate diversity across spatial scales of our study region, we expanded our analysis from site-level alpha diversity to landscape-scale gamma diversity. This approach was chosen because site-level means can underestimate total community richness due to high spatial turnover and the presence of rare species that are only captured when pooling data across the landscape. Hence, we applied coverage-based extrapolation to analyse total estimated species richness (number of species/OTUs) for the different treatments across the landscape scale (gamma diversity), to account for sampling effort and species detection probabilities (Chao et al., 2014). The estimates and confidence intervals were based on bootstrapping ($n = 50$) and extrapolated to the minimum sample coverage at double the sample size (Table S3) with estimateD from the *iNext* package (Hsieh et al., 2022).

We used piecewise structural equation modelling from the package *piecewiseSEM* with the function psem (Lefcheck et al., 2024) to analyse direct and indirect effects among bark cover (representing treatment intensity, Figure S4), *I. typographus* abundance, woodpecker activity, saproxylic beetle richness, fungal and bacterial OTU richness and change in wood properties. The model consisted of a series of mixed-effects models with site as a random effect to account for spatial variations, such as differences in climate. (Table S6). Bark cover was modelled as influencing wood moisture, biotic communities and woodpecker activity through possible habitat modifications (Dossa et al., 2018; Ulyshen et al., 2016). Moisture change was included as a mediator affecting beetle richness, *I. typographus* density, woodpecker activity and microbial diversity (Hagge et al., 2024; Parisi et al., 2018). Both *I. typographus* density and overall beetle richness were hypothesized to influence the fungi richness through spore dispersal, habitat alteration and shared resource use (Ulyshen, 2018) and to serve as woodpecker prey. Beetle and fungal richness were assumed to affect bacterial richness through substrate modification and interactions. Changes in H, C and N were modelled as outcomes of moisture change and biodiversity measures, representing the contribution of biotic interactions to elemental decomposition processes and chemical transformation in deadwood.

We applied two-dimensional non-metric multidimensional scaling (NMDS) with the function metaMDS from *vegan* (Oksanen et al., 2022) based on Bray–Curtis dissimilarity matrices to investigate differences in saproxylic beetle, fungi and bacteria assemblages between treatments. Pairwise analysis of variance was performed with the function adonis2 from the package *vegan* (Oksanen et al., 2022). The resulting *p* values were adjusted for multiple testing with Bonferroni correction. With the function envifit from the *vegan* package (Oksanen et al., 2022), we tested all wood properties (Δ moisture content, H, C, N, net. calorific value), DBH and site-level temperature and precipitation against the NMDS ordinations of the different species groups.

3 | RESULTS

A total of 43,512 saproxylic beetles from 232 different species out of 37 families were collected in the emergence traps over the three sampling seasons. Three bark beetle species were the most abundant beetles: *I. typographus* (10,253 individuals), *Crypturgus subcribrosus* (8535) and *Crypturgus pusillus* (6757) (complete species list in Table S2). The metabarcoding of wood samples revealed a total of 9402 fungal and 20,171 bacterial OTUs.

3.1 | Bark beetle regulation efficacy

Compared to the untreated control, the three passes through the harvester aggregate significantly reduced the amount of emerging *I. typographus* by 76 ± 8% ($p = 0.005$, Figure 2a, Table S4). In contrast, the normal harvester treatment did not significantly reduce beetle emergence compared to the control ($p = 0.479$). Gouging the bark reduced the emergence of *I. typographus* by 87 ± 5% ($p < 0.001$) and the two treatments that completely debarked the logs led to a reduction of >97 ± 1% ($p < 0.001$; Figure 2a, Table S4).

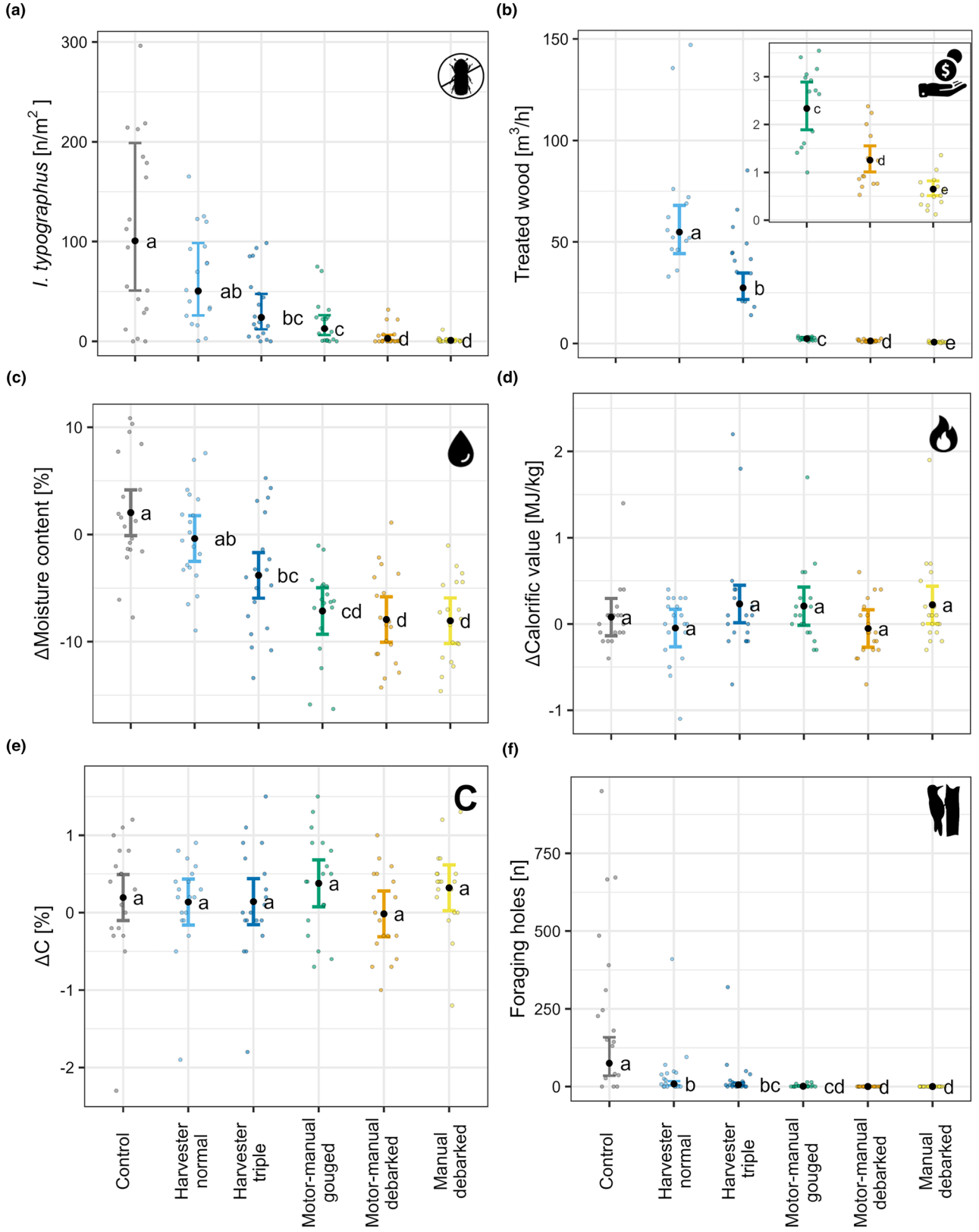

FIGURE 2 Model results for (a) *Ips typographus* regulation (19 sites), (b) operational efficiency (14 sites), (c) change in moisture content (19 sites), (d) change in net calorific value (19 sites), (e) change in carbon content (19 sites) and (f) woodpecker foraging holes (19 sites). Black dots indicate the estimated marginal means (EMMs) for the respective treatment based on mixed models. Error bars are the 95% Confidence Interval. Letters specify significant differences among treatments with Tukey's adjustments for multiple testing at a significance level of $p < 0.05$. Raw data are included as points coloured by treatment.

3.2 | Operational efficiency

For the comparison of the operational efficiency the treatment ($F_{4,53.7}=359.0$, $p<0.001$) and the control variable DBH ($F_{1,62.4}=34.7$, $p<0.001$) were both significant. Post hoc comparisons showed that the amount of wood treated per hour differed significantly among all treatments ($p<0.001$, Figure 2b, Table S4). The three passes through the harvester aggregate doubled the time needed to the normal harvester processing while it was still able to treat 10 times more wood in the same time as (motor-) manual treatments ($p<0.001$, Figure 2b, Table S4). Bark gouging, with a mean productivity of $2.3\pm0.25\,m^3$ per hour, was approximately twice as fast as complete debarking (motor-manual: $1.3\pm0.13\,m^3$ per hour; manual: $0.7\pm0.08\,m^3$ per hour; Figure 2b, Table S4).

3.3 | Wood properties

Treatment effect was significant for the change in log moisture content ($F_{5,89.2}=20.62$, $p<0.001$) and net calorific value ($F_{5,89.2}=359.0$, $p<0.049$) over 2 years. For the change in carbon ($F_{5,89.3}=1.07$, $p=0.38$), nitrogen ($F_{5,89.4}=0.65$, $p=0.66$) and hydrogen ($F_{5,89.4}=1.87$, $p=0.11$) content, the treatment effects were not significant. In the control logs, moisture content increased over the two-year sampling period, while most logs with bark treatments indicated a reduction. The change in moisture content in the harvester triple ($p<0.001$) and all motor-manual techniques ($p<0.001$) differed significantly from the control logs (Figure 2c, Table S4). Change in net calorific value, carbon, nitrogen and hydrogen content did not differ among treatments (Figure 2d,e, Table S4, Figure S5). The colonization intensity of blue-stain fungi (ophiostomatoids: *Ophiostomataceae* and *Ceratocystidaceae*) did not have a significant difference between treatments ($\chi^2=9.91$, df = 5, $p=0.078$; Figure S6).

3.4 | Woodpecker foraging activity

Bark treatment had a significant effect on the number of woodpecker foraging holes ($F_{5,91.3}=25.55$, $p<0.001$), whereas the covariate DBH was not a significant predictor in the model ($F_{1,88.6}=0.29$, $p=0.59$). The control logs had significantly more foraging holes than all other treatments ($p<0.001$), with observed foraging activity decreasing progressively with increasing treatment intensity and consequently bark cover loss.

3.5 | Diversity of saproxylic beetles, fungi and bacteria

On the landscape scale, the species richness (gamma diversity) of saproxylic beetles was only slightly reduced in the logs with normal harvester, motor-manual gouging and debarking, when compared to the control group (Figure 3a). Manual debarked and harvester triple treated logs had similar levels like the control. On site-level estimates (alpha diversity), the treatment effect was significant ($F_{5,89.1}=17.8$, $p<0.001$) and both complete debarking techniques indicated significantly lower beetle species richness ($p<0.001$, Figure 3b). For landscape-level fungi richness, we observed a decrease in the logs with partial bark manipulation, while the completely debarked treatment had similar estimates like the control (Figure 3c). Alpha diversity of fungi OTU richness was significantly influenced by treatment ($F_{5,89.3}=5.6$, $p<0.001$) and logs without bark had a higher observed OTU richness than the control ($p<0.001$, Figure 3d). The diversity of bacteria OTUs decreased only for gamma diversity in the gouged and completely debarked logs (Figure 3e). The treatment effect was not significant for bacterial alpha diversity ($F_{5,89.2}=0.85$, $p=0.52$) and no pairwise differences were detected between treatments.

The global goodness-of-fit test indicated that the structural equation model captured the observed structure of the data well ($p=0.309$, Fisher's *C*: 35.44, df = 32, AIC = 5727.93). The bark cover had a positive effect on the density of emerging *I. typographus* ($\beta=0.53$, $p<0.001$), woodpecker activity ($\beta=0.184$, $p<0.001$), saproxylic beetle species ($\beta=0.764$, $p<0.001$), as well as log moisture change ($\beta=0.630$, $p<0.001$). However, saproxylic beetle species richness decreased with higher moisture change ($\beta=-0.352$, $p<0.001$). Fungi OTUs significantly decreased when more beetle species were present ($\beta=-0.229$, $p=0.041$). Bacteria richness increased with fungi richness ($\beta=0.485$, $p<0.001$) and change in hydrogen content ($\beta=0.254$, $p=0.029$) was higher in logs with higher bacteria richness. Nitrogen content change was lower in logs with higher fungi richness ($\beta=0.241$, $p=0.045$), while carbon was not significantly influenced (Figure 4, Table S7).

3.6 | Assemblages of saproxylic beetles, fungi and bacteria

The saproxylic beetle assemblages differed significantly between logs with (motor-) manual debarking and control logs as well as those treated conventionally with the harvester. In contrast, all other bark treatments resulted in species assemblages similar to those of the control logs (Table S5). The differences among treatments were mainly associated with variation along the second NMDS axis, while the site-level temperature ($p=0.001$, $R^2=0.54$) and precipitation ($p=0.001$, $R^2=0.46$) vectors strongly correlated with the first NMDS axis (Figure 5a). Assemblages of fungi and bacteria diverged along the first NMDS axis, which was mainly associated with differences in moisture content change ($p=0.001$, Fungi: $R^2=0.42$; Bacteria: $R^2=0.48$) and DBH ($p=0.001$, Fungi: $R^2=0.18$; Bacteria: $R^2=0.17$) between treatments (Figure 5b,c). The second NMDS axis was correlated with site-level differences in precipitation ($p=0.001$, Fungi: $R^2=0.70$; Bacteria: $R^2=0.46$) and temperature ($p=0.001$, Fungi: $R^2=0.68$; Bacteria: $R^2=0.46$). Notably, bacterial assemblages did not differ significantly between the harvester triple and either the motor-manual debarked ($p=0.095$) or gouged assemblages ($p=0.095$), although differences were detected between the two motor-manual treatments (Figure 5, Table S5).

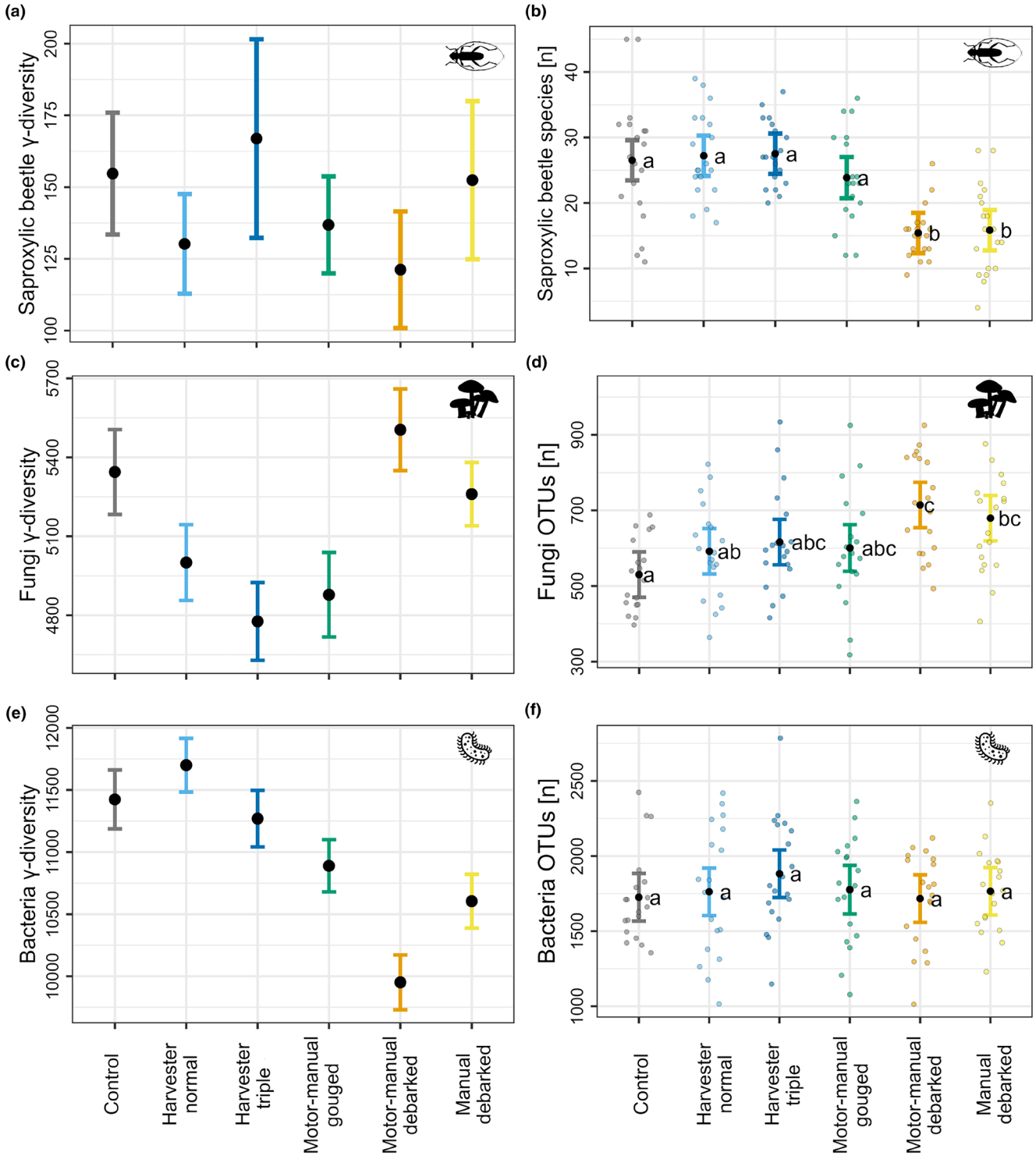

FIGURE 3 Treatment effect on (a, b) saproxylic beetle, (c, d) fungi and (e, f) bacteria OTU richness (number of species/OTUs). Results in the left panels are gamma diversity (black dots) based on coverage-based extrapolation of presence–absence data. Error bars indicate the lower and upper bound of the 95% confidence intervals based on bootstrapping ($n = 50$) and non-overlapping confidence intervals indicate significant differences between groups. The right panels show black dots for estimated marginal means of observed species and OTUs at site level (alpha diversity) for each treatment based on mixed models with 95% confidence interval. Letters specify significant differences between treatments with Tukey's adjustments for multiple testing at a significance level of $p < 0.05$. Raw data are included as points coloured by treatment.

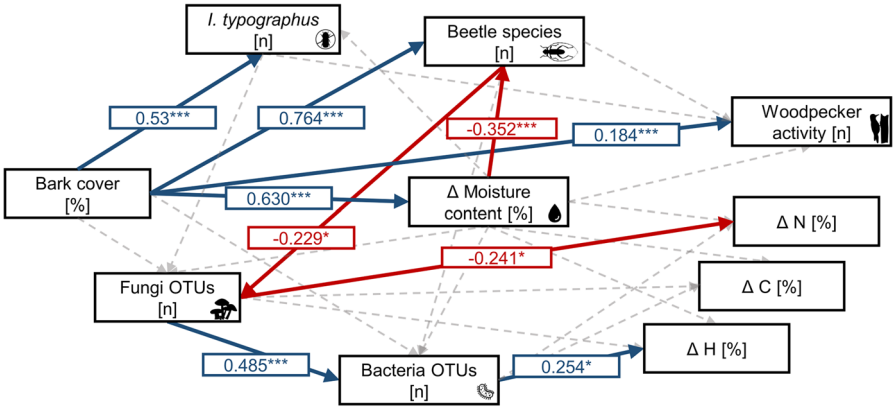

FIGURE 4 Structural equation model with bark cover (%), wood moisture, carbon, hydrogen, nitrogen change (%) over two years, *I. typographus* density, woodpecker activity, saproxylic beetle and fungal/bacterial richness (number of species/OTUs). Blue arrows indicate positive and red arrows negative relationships. Standardized path coefficients (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) are shown in boxes. Dashed lines denote tested but non-significant paths.

4 | DISCUSSION

Our results indicate that bark removal and manipulation represent effective and operationally feasible alternatives to salvage logging for regulating bark beetle emergence, although it involves important ecological trade-offs affecting saproxylic biodiversity and microbial community structure, while maintaining wood bioenergy potential. Supporting our first and second hypotheses (i, ii), we found that conventional harvester handling was not effectively reducing bark beetle emergence, while three passes through the harvester aggregate combined substantial emergence reduction with high operational efficiency (wood volume processed per hour). In line with our hypotheses, bark removal reduced saproxylic beetle richness, lowered woodpecker activity, increased fungal richness (iii) and influenced community assembly of saproxylic taxa (iv). These effects were identified in mixed-effects models that accounted for site-level variability, suggesting that the observed treatment effects are not driven by individual sites. Even though complete debarking was the most effective for bark beetle reduction, the negative effects on saproxylic biodiversity and woodpecker activity suggest this method is best reserved for logs intended for intermediate storage rather than dead wood retention to fulfil conservation goals. Furthermore, while we predicted a decrease in bacterial diversity (iii), alpha diversity remained stable across treatments, with differences only emerging at the landscape level (gamma diversity). Regarding wood properties (v), our findings confirmed a significant reduction in moisture content following debarking. However, contrary to expectations, no observable change occurred in the colonization intensity of blue-stain fungi. Finally, our results diverged from our fifth hypothesis (v): despite the microbial activity, the wood's net calorific value and elemental composition (H, C, N) remained stable over 2 years, reinforcing the feasibility of using logs for bioenergy, independent of bark treatment, after 2 years of on-site storage.

4.1 | Bark beetle regulation

Overall, mechanical bark treatments are an additional tool and can be integrated into the existing strategies to control bark beetle outbreaks at the landscape scale. (Motor-) manual debarking and bark gouging were effectively reducing the emerging *I. typographus* density by more than 88% but are, due to the low output per workhour, only suitable for treatment of small-scale or harvester-inaccessible terrain. Earlier studies have shown that bark gouging can be effective before bark beetle colonization and during the larval stage, although these studies were confined to small geographic regions (Hagge, Leibl, et al., 2019; Thorn et al., 2016; Zarges et al., 2023). By passing logs through the conventional harvester aggregate three times, enough bark was destroyed to achieve a reduction close to the 80% limit to likely prevent outbreaks (Fahse & Heurich, 2011). In general, it is approximately 10 times faster than bark gouging, but includes cut-to-length and debranching. Hourly rates for harvester-based operations are about four to five times higher than motor-manual felling (KWF, 2023). Bark treatments not only affected *I. typographus*, but also reduced populations of other bark beetle species, such as *Pityogenes chalcographus* (Table S2), which is generally less harmful in mature stands but can pose a threat to young spruce trees (Holuša & Fiala, 2024). A more specific solution is the use of harvester aggregates modified for debarking (debarking heads), which efficiently remove the complete bark and reduce bark beetle emergence (Zarges et al., 2024). The harvester triple treatment in our study is comparable in terms of operational efficiency, as the use of debarking heads typically requires three passes through the aggregate to achieve complete debarking (Delb et al., 2021; Heppelmann et al., 2019). In terms of operational efficiency, Heppelmann et al. (2019) reported that the processing time increases by 48%, whereas Mergl et al. (2021) state that 41.2 to 41.8% of the efficiency of a machine with the conventional head can be processed with the debarking head setup. Nevertheless, additional time for refitting and modifications, as well as investments in specialized components, need to be

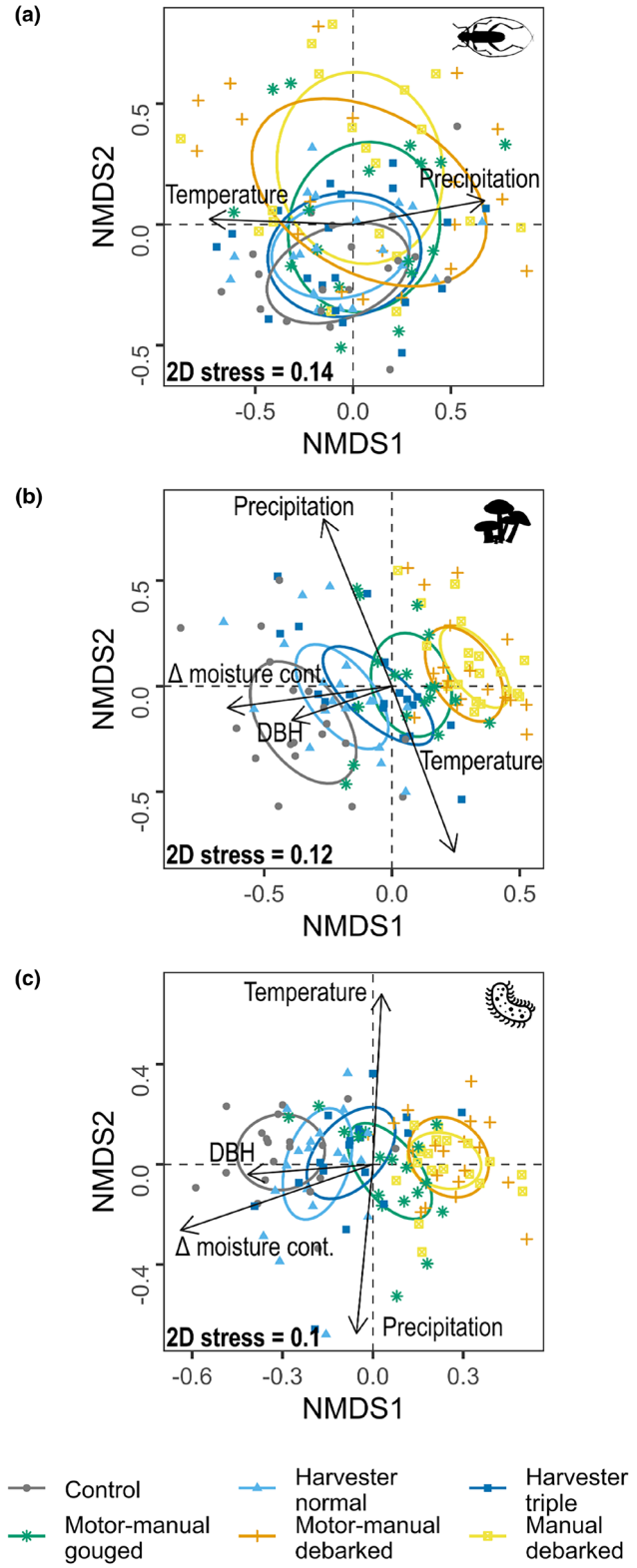

FIGURE 5 Two-dimensional non-metric multidimensional scaling (NMDS) based on presence–absence data Bray–Curtis dissimilarity matrix of (a) saproxylic beetle species, (b) fungi OTUs and (c) bacteria OTUs in *P. abies* logs with different treatment (colours and shapes). With only the significant environmental effects included as vectors.

considered. With respect to bark beetle regulation, biodiversity and wood properties, the observed effects for motor-manual debarking are likely similar to logs treated with the debarking head, since both treatments result in high bark cover reduction of approximately 90% (Delb et al., 2021; Zarges et al., 2024).

In general, on-site debarking has the advantages to maintain nutrient cycling (Vos et al., 2023) and reduce transport volume and weight (Heppelmann et al., 2019). Nevertheless, large fragments of removed bark must be handled carefully on-site, as bark beetles in the brown stage can use the substrate to complete their life cycle (Delb et al., 2021; Hoch et al., 2020). The continued emergence of *I. typographus* in the second year of our study indicates that infested logs with bark (control and harvester treatments) can remain a source of high population densities and thereby contribute over this period to the landscape outbreak risk (Figure S7). However, this effect appears to be shorter than what has been reported in previous studies, which reported periods of attractiveness of more than 2 years (Schroeder, 2010; Wermelinger et al., 2013). This discrepancy is likely due to differences in breeding substrate, as those studies were based on windthrown trees that often remain connected to the root system and therefore dry out more slowly. Consequently, our results suggest that the window for effective reactive management of cut logs is limited to approximately 1 year after felling, emphasizing the need for early intervention.

4.2 | Biodiversity

Bark treatments effectively reduce bark beetle emergence (see above), while allowing deadwood to be retained for the support of natural ecosystem dynamics and functions. Completely debarked logs showed a significant reduction in saproxylic beetle species richness at site level, while at the landscape-scale mean values were lower for treated logs but without significant difference. The reduction in beetle diversity at the site level with bark treatments may be attributed not only to the habitat loss for specialized species, but also the removal of the energy-rich bark. This is consistent with the species-energy hypothesis, which links higher species richness to greater energy availability (Wright, 1983). Bark—especially the phloem—provides an energy-rich substrate and habitat in the early stages of wood decomposition, particularly for saproxylic beetles (Kriegel et al., 2023). In general, many saproxylic species of early deadwood colonization are specialized on bark as a resource for nutrition and shelter (Ulyshen, 2018). To foster saproxylic biodiversity it is important to maintain diversity, continuity and quality of deadwood (Saine et al., 2024; Thorn, Seibold, et al., 2020). In the structural equation model, the bark cover (as treatment intensity) had a positive correlation with saproxylic beetle diversity and log moisture content. However, logs with a higher moisture content had lower beetle richness, which confirms the significance of dry microclimates for saproxylic beetle diversity (Hagge et al., 2024; Seibold et al., 2016). Woodpecker activity was significantly higher on control logs, indicating a negative impact on the food chain when

bark removal reduces deadwood habitat quality and, consequently, food availability (Aszalós et al., 2020). Overall, woodpecker activity was not influenced by *I. typographus* density, supporting an indirect relationship in which woodpeckers benefit primarily from increased deadwood volume rather than from bark beetle abundance (Basile et al., 2025). For beetle community assemblages, log-level parameters (moisture content, net. calorific value, H, C, N) were not significant. Completely debarked logs exhibited high dispersion, partially explained by site-level temperature and precipitation, but also with some unexplained variation. This pattern suggests that bark removal may weaken deterministic environmental filtering associated with colonization of specialized species. Consequently, the influence of stochastic colonization processes increases, leading to greater heterogeneity and lower specialization in saproxylic beetle assemblages in logs without bark.

For fungi and bacteria assemblages, the change in moisture content due to bark removal was the most prevalent driver, while the remaining variation can be explained primarily by site-level differences in temperature and precipitation. When extrapolated to the landscape-level diversity, the bacterial richness was highest in the control and harvester-treated logs, while in logs with (motor-) manual debarking, more fungi OTUs than in the other treated logs were found. This shift from bacteria to more fungi richness with the removal and manipulation of bark has already been observed in previous studies (Hagge, Bässler, et al., 2019), and our findings can confirm this pattern also under variable site conditions. Because the results are based on the presence/absence of OTUs, we cannot directly derive the rates for activity or decomposition. The change in hydrogen content was significantly influenced by the number of bacterial OTUs, suggesting that higher bacterial richness may slow hydrogen depletion during decay. Logs with greater fungal richness exhibited lower nitrogen concentrations, indicating that diverse fungal communities accelerate nitrogen immobilization. The positive relationship between fungal and bacterial richness reflects the provision of metabolites by fungi, which, in turn, facilitate bacterial diversity throughout the process of decomposition (Seibold et al., 2021; Ulyshen, 2018).

4.3 | Timber utilization

In case the wood is not intended for permanent retention for conservation, our results indicate that the wood retains properties that may allow for subsequent use after treatment and intermediate on-site storage. However, repeated handling with harvester aggregates is likely to cause damages to the wood fibre with the feed rollers and delimbing knives, which in turn lowers the yield of good quality timber (Nuutinen et al., 2010). Although intact bark is a barrier for fungi colonization in deadwood (Hagge, Bässler, et al., 2019), it also retains higher wood moisture content, which in turn can foster the growth of blue-stain fungi (Böhm et al., 2025; Wingfield et al., 2017) that can significantly reduce the marketable timber value (Barrette et al., 2015). *I. typographus* is a major vector commonly associated with blue-stain fungi (Linnakoski et al., 2016; Wingfield et al., 2017), for which we observed no significant differences among treatments. Although control logs tended to show a lower mean abundance and variability, this pattern was not statistically significant (Figure S6). Debarking also reduces the colonization of other saproxylic insect and fungi species that can cause economically relevant mechanical damage (e.g. wood-boring insects) and decay (e.g. brown rot) to the wood (Böhm et al., 2025). Hence, debarking combined with storage under dry conditions (e.g. sun exposed, no soil contact) can help to preserve economically important wood properties when disposal options within the supply chain are limited. In contrast to wet storage, where constant watering limits oxygen availability, dry storage needs no further investments and is not subjected to regulatory measures. It also creates unfavourable conditions for the growth of wood-staining and wood-decaying fungi, as moisture contents below the fibre saturation point (~30%) limit fungal decay activity (Brischke & Alfredsen, 2020). However, timely removal and appropriate storage of infested wood are critical, as delays increase fungal development and associated blue-staining and decay, thereby downgrading timber quality and reducing its market value (Böhm et al., 2023). After 2 years, the calorific value in our experimental logs did not decrease for all five mechanical bark treatments, indicating that their energy content was maintained during storage. Additionally, the debarked logs had a lower moisture content, therefore, reducing the need for pre-drying after storage in the forest and lowering transport costs. Even if the wood is extracted after intermediate on-site storage, insects with short development cycle can still reproduce and long-term studies on decomposing logs have shown a high number of species in the first 3 years (Lettenmaier et al., 2025). Populations of natural bark beetle antagonists like woodpeckers and predatory flies can also profit when logs remain at least for one season on site (Weslien et al., 2024).

5 | CONCLUSIONS

Disturbances can create opportunities for natural adaptation and provide a pulse of energy and resources to deadwood-dependent food webs. Our results demonstrate that mechanical bark treatments can effectively balance bark beetle regulation (pest control) efficacy with timber utilization, operational efficiency and biodiversity conservation. For management practice, harvester-based bark treatments with three passes through the aggregate are most suitable where large volumes of damaged or infested timber must be processed rapidly. Motor-manual bark gouging offers a low-cost, flexible and effective alternative for smaller volumes or in areas where harvester access is limited. Retaining bark and deadwood supports key conservation goals and forest functionality without substantially increasing the number of emerging bark beetles in susceptible stands. Consistent calorific value of treated wood over 2 years allows for its potential use as a regional renewable energy source.

Following effective bark treatments, two complementary management pathways can be implemented: permanent on-site retention to support biodiversity conservation, ecosystem functioning and deadwood-dependent communities; or temporary on-site

storage for up to 2 years to buffer operational and economic constraints during periods of unfavourable timber market conditions after large-scale disturbances.

AUTHOR CONTRIBUTIONS

Jonas Hagge and Simon Thorn designed and conceived the research. Sebastian Zarges set up the experiment, conducted the statistical analysis and wrote the first draft of the manuscript. Sebastian Zarges, Ole Henning and Peter Kriegel collected the data in the field. Sebastian Zarges and Ole Henning prepared the insect samples for identification. Peter Kriegel prepared the sequencing data for analysis. Jonas Hagge and Simon Thorn supervised and administrated the project. All authors contributed and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are openly available in the *Dryad Digital Repository*: https://doi.org/10.5061/dryad.k6djh9wns (Zarges et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Debarking device with the rotating cylinder at two positions equipped with the four modified knifes for bark gouging. Dimensions for (a) the adjustable depth for different bark thickness, (b) the distance between the tips of the v-shaped knives and (c) the width of treatment area are given.

Figure S2. Scatterplot comparing the 20 sites (black squares) with temperature and precipitation in 1000 random points across the distribution of *Picea abies* forests in German (grey points). Mean annual precipitation and temperature for the period 1990–2020. Data source: Deutscher Wetterdienst (DWD) Open Data Portal (https://opendata.dwd.de) and the German tree species map (Blickensdörfer et al., 2024).

Figure S3. Sampling design for each individual log with the 2 years of emergence traps and the four drilling locations for the thick, middle and thin stem section. Traps were shifted by 50 cm between years. For logs with a greater diameter than the length of the drill, sampling was done from both sides until the whole cross section was drilled. A 1 m distance to the section cuttings was maintained to avoid colonization effects through the open surface.

Figure S4. Boxplots with the bark cover in percentage of intact bark for each treatment directly after mechanic bark treatments. A transparent sheet with an area of 0.125 m^2 and 25 randomly distributed points was placed at the emergence trap and three drill locations of the first year (2022, Figure S3). For each point it was assessed if the bark beneath is intact, injured or missing.

Figure S5. Estimated marginal means for the difference between first measurement and after 2 years (Δ) of (a) Nitrogen and (c) Hydrogen content in the wood samples. Letters specify significant differences between treatments with Tukey adjustments for multiple testing at a significance level of $p < 0.05$. Error bars indicate 95% CI and coloured dots show the observed data for each site.

Figure S6. Number of reads for blue-stain fungi (ophiostomatoids: Ophiostomataceae and Ceratocystidaceae) after excluding OTUs detected in the initial drill samples to focus on post treatment colonization. Read counts were then pooled across the remaining three sampling periods for each site and treatment. Letters specify significant differences between treatments with Tukey adjustments for multiple testing at a significance level of $p < 0.05$. Error bars indicate 95% CI and coloured dots show the observed data for each site.

Figure S7. Emerging *Ips typographus* (individuals per m^2) from the experimental logs with different bark treatments for bark beetle reduction in the three sampling years (2022, 2023, 2024).

Table S1. Summary of mean diameter at breast height (DBH) and tree volume (± standard deviation) for each treatment and overall.

Table S2. Abundance of the 232 saproxylic beetle species from the 19 experimental logs in each treatment over the three-year sampling (2022–2024) period with stem emergence traps.

Table S3. Observed coverage for each of the treatments and extrapolated value for minimum of sample coverage within a treatment at double sample size for saproxylic beetles, fungi and bacteria.

Table S4. Estimated marginal means (EMM) with standard error, 95% confidence intervals (CI) as well as grouping letters specifying significant differences between treatments with Tukey adjustments for multiple testing at a significance level of $p < 0.05$ for number of emerging *I. typographus* per m^2, m^3 of wood that can be treated per workhour, change in moisture content, calorific value and carbon content inside the experimental logs over 2 years, together with model estimates for the observed number of woodpecker foraging holes, saproxylic beetle species, fungal and bacterial OTUs.

Table S5. Results from pairwise analysis of variance (adonis) of

beetle species assemblages between bark treatments. The analysis is based on Bray–Curtis dissimilarity matrix with abundance of saproxylic beetle species emerging from the experimental *Picea abies* logs within the forest stand. *p* values were adjusted with Bonferroni correction for multiple testing.

Table S6. Linear mixed models with the study sites as random effect which were combined for the piecewise structural equation modelling (SEM).

Table S7. Coefficients of the structural equation model (SEM). Shown are response and predictor variables, unstandardized estimates, standard errors, degrees of freedom (DF), test statistics (critical values), *p* values and standardized path coefficients. Significant paths ($p < 0.05$) are highlighted in the main text and figures.

Text S1. Methods Metabarcoding.

Text S2. Methods Wood properties.

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