Reconciling pest control and nature conservation in bark beetle management

Dissertation

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Submitted by

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"We must work. We must make money.
But more than that Bella, we must experience everything.
Not just the good, but degradation, horror, sadness.
This makes us whole Bella, makes us people of substance. Not flighty, untouched children.
Then we can know the world. And when we know the world, the world is ours."

— Madame Swiney, *Poor Things*

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Summary

Climate change is intensifying disturbance regimes in forest ecosystems by increasing the frequency, intensity, and severity of events such as droughts, storms, and insect outbreaks. These shifts alter fundamental environmental conditions, threatening ecosystem services and resilience. In Central Europe, this vulnerability is exacerbated by past forest management favoring structurally simplified, even-aged Norway spruce (*Picea abies)* stands, which have been severely affected in recent years by large-scale outbreaks of the European spruce bark beetle (*Ips typographus*), generating unprecedented volumes of damaged timber. Conventional disturbance management, such as salvage logging, is primarily driven by economic objectives, but is constrained by operational capacities as well as the risk of pest emergence and timber devaluation during on-site storage. Removing deadwood, however, can undermine biodiversity and ecosystem resilience, highlighting the need for alternative approaches that regulate bark beetles while maintaining ecological integrity and wood quality (Chapter 1).

This thesis evaluates in three studies mechanical bark treatments as an alternative approach, by integrating economic and ecological trade-offs related to pest control, operational feasibility, wood properties and effects on saproxylic biodiversity. In mountainous and inaccessible terrain manual debarking remains common and motor-manual bark gouging (partial bark removal in stripes) was identified as a more cost-effective and conservation-friendly alternative, with sufficient pest reduction, even at low accuracy (Chapter 2). For large wood volumes during landscape scale disturbances harvester-based bark treatments are an operationally scalable solution to treat suitable and bark beetle-infested logs. Debarking heads reduced *I. typographus* emergence while conserving non-target beetle richness, whereas conventional harvester processing alone was ineffective for pest control (Chapter 3). A three-year assessment across the range of *P. abies* forests in Germany provided generalizable results and demonstrated that three passes through the conventional harvester aggregate can efficiently suppress bark beetle emergence. Complete debarking reduced species richness of saproxylic beetles and bacteria as well as woodpecker foraging activity, while species richness of fungi increased and species assemblages differed from untreated controls in all three groups. Wood moisture content depended on bark

treatment intensity, while net calorific value was not affected, supporting a potential economic utilization for bioenergy (Chapter 4).

Synthesizing these findings provides a comprehensive framework ranging from motor-manual bark gouging for small-scale infestations and inaccessible sites to harvester-based solutions for landscape-scale disturbances. Bark treatments enhance forest management flexibility by enabling either intermediate on-site storage to buffer logistical bottlenecks, or permanent deadwood retention to promote biodiversity and ecological functioning. Preserving the biological legacies essential for forest resilience contributes to achieving conservation goals in protected areas, and facilitates integration of conservation strategies in managed forests (Chapter 5).

Overall, this thesis demonstrates that mechanical bark treatments offer a scientifically grounded and operationally feasible alternative to salvage logging for *I. typographus* regulation, reconciling forest protection with conservation goals and economic objectives under increasingly severe and uncertain disturbance regimes.

Zusammenfassung

Der Klimawandel verschärft die Störungsregime in Waldökosystemen, indem Frequenz und Stärke von Ereignissen wie Dürren, Stürmen und Insektenbefall zunehmen. Diese veränderten Umweltbedingungen beeinträchtigen die Widerstandsfähigkeit der Wälder und gefährden damit die Bereitstellung von Ökosystemleistungen. In Mitteleuropa wird diese Anfälligkeit durch die weitverbreiteten, strukturell vereinfachten und gleichaltrigen Fichtenbestände (*Picea abies*) begünstigt. In den letzten Jahren führte der Buchdrucker (*Ips typographus*) zu großflächigen Waldschäden und historisch hohen Mengen an Kalamitätsholz. Herkömmliche Waldschutzmaßnahmen, wie die Flächenräumung, sind in erster Linie wirtschaftlich motiviert, können aber durch eingeschränkte Transportkapazitäten nicht immer gewährleistet werden. Bei der Lagerung vor Ort besteht die Gefahr einer Buchdruckervermehrung und Wertminderung des Holzes. Das Entfernen von Totholz kann jedoch die Biodiversität und die Widerstandsfähigkeit des Ökosystems beeinträchtigen. Dies verdeutlicht die Notwendigkeit von Alternativen, die sowohl den Befall regulieren als auch die ökologische Integrität und Holzqualität erhalten (Kapitel 1).

Diese Arbeit untersucht in drei Studien mechanische Rindenbehandlungen als alternative Waldschutzmethoden und berücksichtigt dabei ökonomische und ökologische Zielkonflikte in Bezug auf Buchdruckerregulierung, betriebliche Durchführbarkeit, Holzeigenschaften sowie die xylobionte Biodiversität. Im alpinen und unzugänglichen Gelände ist das manuelle Entrinden nach wie vor üblich. Das motormanuelle streifenförmige Entrinden wurde als eine wirtschaftlichere und zugleich naturverträgliche Alternative identifiziert, die selbst bei geringer Genauigkeit eine ausreichende Buchdruckerregulierung gewährleistet (Kapitel 2). Bei großen Kalamitätsholzmengen auf Landschaftsebene bieten Rindenbehandlungen mit dem Harvester eine skalierbare Lösung zur Behandlung von bruttauglichen (z. B. nach Sturmwurf) und bereits befallenen Stämmen. Während speziell für die Entrindung umgerüstete Harvesteraggregate (Debarking Head) die Anzahl der Buchdrucker reduzierten und die Artenvielfalt von Nicht-Zielkäfern bewahrten, erwies sich die konventionelle Aufarbeitung mit dem Harvester als unwirksam für den Waldschutz (Kapitel 3). Im Rahmen einer dreijährigen Untersuchung im gesamten Verbreitungsgebiet der Fichte in Deutschland konnten verallgemeinerbare Ergebnisse gewonnen werden. Dabei zeigte sich, dass ein dreifacher Durchlauf durch das Harvesteraggregat die Buchdruckerdichte wirksam

reduziert. Bei vollständiger Entrindung nahmen die Artenvielfalt xylobionter Käfer und Bakterien sowie die Nahrungssuche von Spechten ab, während die Pilzdiversität zunahm und sich die Artenzusammensetzung in allen drei Gruppen von den unbehandelten Stämmen unterschied. Die Intensität der Rindenbehandlung verringerte die Holzfeuchte, beeinflusste jedoch nicht den Heizwert, was eine potenzielle wirtschaftliche Nutzung für Bioenergie nahelegt (Kapitel 4).

Auf Grundlage dieser Erkenntnisse werden Handlungsempfehlungen abgeleitet, die motormanuelles Rindenstreifen für kleine Befallsflächen oder schwer zugängliche Bestände sowie den Einsatz von Harvestern für großflächige Störungen umfassen. Rindenbehandlungen stellen eine flexible Waldschutzmaßnahme dar, da sie sowohl eine Zwischenlagerung im Bestand zur Überbrückung logistischer Engpässe als auch die dauerhafte Anreicherung von Totholz zur Förderung von Biodiversität und Waldfunktionen ermöglichen. Durch waldschutzkonforme Totholzanreicherung werden wichtige ökologische Strukturen bewahrt, Naturschutzziele in Schutzgebieten unterstützt und Naturschutzstrategien in bewirtschafteten Wäldern integriert, wodurch die Resilienz des Waldes gegenüber Störungen gestärkt wird (Kapitel 5).

Insgesamt zeigt diese Dissertation, dass mechanische Rindenbehandlungen eine wissenschaftlich fundierte und umsetzbare Alternative zur Flächenräumung für die Buchdruckerregulierung darstellen, indem sie Waldschutz, Naturschutzziele und ökonomische Zielsetzungen unter zunehmend intensiveren und unsicheren Störungsregimen in Einklang bringen.

Contributions to the research chapters

Chapter 2: Low accuracy bark gouging controls Ips typographus outbreaks while conserving non-target beetle diversity

(published in *Forest Ecology and Management*)

Sebastian Zarges[1,2], Simon Thorn[3,4], Heinz Bußler[5], Harald Siegler[6], Josef Wolf[7], Jonas Hagge[1,2]

Author contributions: JH and ST designed and conceived the research. JH, ST, HS and JW conducted the experiments. JH collected the samples and HB identified the beetle species. SZ conducted the literature research, statistical analysis and wrote the first draft of the manuscript. All authors contributed and approved to the final version of the manuscript.

Chapter 3: Debarking harvesters simultaneously combat the European spruce bark beetle (*Ips typographus*) and conserve non-target beetle diversity

(published in *Ecological Solutions and Evidence*)

Sebastian Zarges[1,2], Jan Wohlert[8], Johannes Kamp[9], Simon Thorn[3,4,10], Jörg Müller[11,12], Jonas Hagge[1,2]

Author contributions: JH and JM designed and conceived the research. SZ conducted the literature research, statistical analysis and wrote the first draft of the manuscript. JH collected the insect samples. JW processed the insect samples. All authors critically contributed by reviewing and editing the manuscript. JH supervised and administrated the project. All authors contributed and approved to the final version of the manuscript.

Chapter 4: Regulating bark beetles with mechanical bark treatments: Trade-offs among pest control, operational efficiency and biodiversity

(under revision in *Journal for Applied Ecology*)

Sebastian Zarges[1,2], Peter Kriegel[10], Ole Henning[1], Andreas Schuldt[2], Simon Thorn[3,4,10], Jonas Hagge[1,2]

Author contributions: JH and ST designed and conceived the research. SZ set up the experiment, conducted the statistical analysis and wrote the first draft of the manuscript. SZ, OH and PK collected the data in the field. SZ and OH prepared the insect samples for identification. PK prepared the sequencing data for analysis. JH and ST supervised and

administrated the project. All authors contributed and approved to the final version of the manuscript.

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Chapter 1: General Introduction

1.1 Temperate forests in the Anthropocene

Over the past centuries, temperate forest ecosystems have primarily been valued for their provision of natural resources, predominantly timber. Consequently, forest management was optimized for high and predictable timber yields, minimal management complexity, and relatively short rotation periods (Erdozain et al., 2024). This management paradigm led to the widespread establishment of even-aged monocultures of fast-growing tree species in temperate forests, particularly conifers like *Picea* and *Pinus* (Spiecker, 2003). As a result, most forests in Central Europe and North America today are strongly shaped by human land-use objectives rather than natural vegetation and ecosystem processes (FAO, 2020). This widespread transformation is part of a broader global trend in which land-use change and ecosystem homogenization have become major drivers of biodiversity loss. Forest ecosystems worldwide have experienced substantial declines in species richness and compositional changes as diverse natural forests are replaced by simplified and intensively managed systems, contributing to the ongoing global biodiversity crisis (Díaz et al., 2019; Watson et al., 2018).

In Central Europe, the natural broadleaved beech (*Fagus sylvatica* L.) forests in the lowlands were replaced with Norway spruce (*Picea abies* (L.) H. Karst*)* plantations, even though the native distribution range of *P. abies* is in the boreal and subalpine climatic zones (Caudullo et al., 2016). Particularly after the Second World War and the associated destruction and overexploitation of forests, large areas of the Central European lowlands were rapidly afforested with *P. abies*, resulting in human-made even-aged monocultures (Erdozain et al., 2024). These structurally simplified stands are characterized by reduced genetic and species diversity, uniform age and canopy structure, and shallow root systems. Collectively, such characteristics reduce their resistance to abiotic disturbances such as windthrow, drought, and snow breakage, as well as to biotic agents like pathogens and insects (Seidl et al., 2011). By now, these forest stands have accumulated high timber stocks in old age classes, compounding their vulnerability as stand-level susceptibility to both abiotic and biotic disturbances increases with tree age and low structural complexity (Seidl et al., 2011).

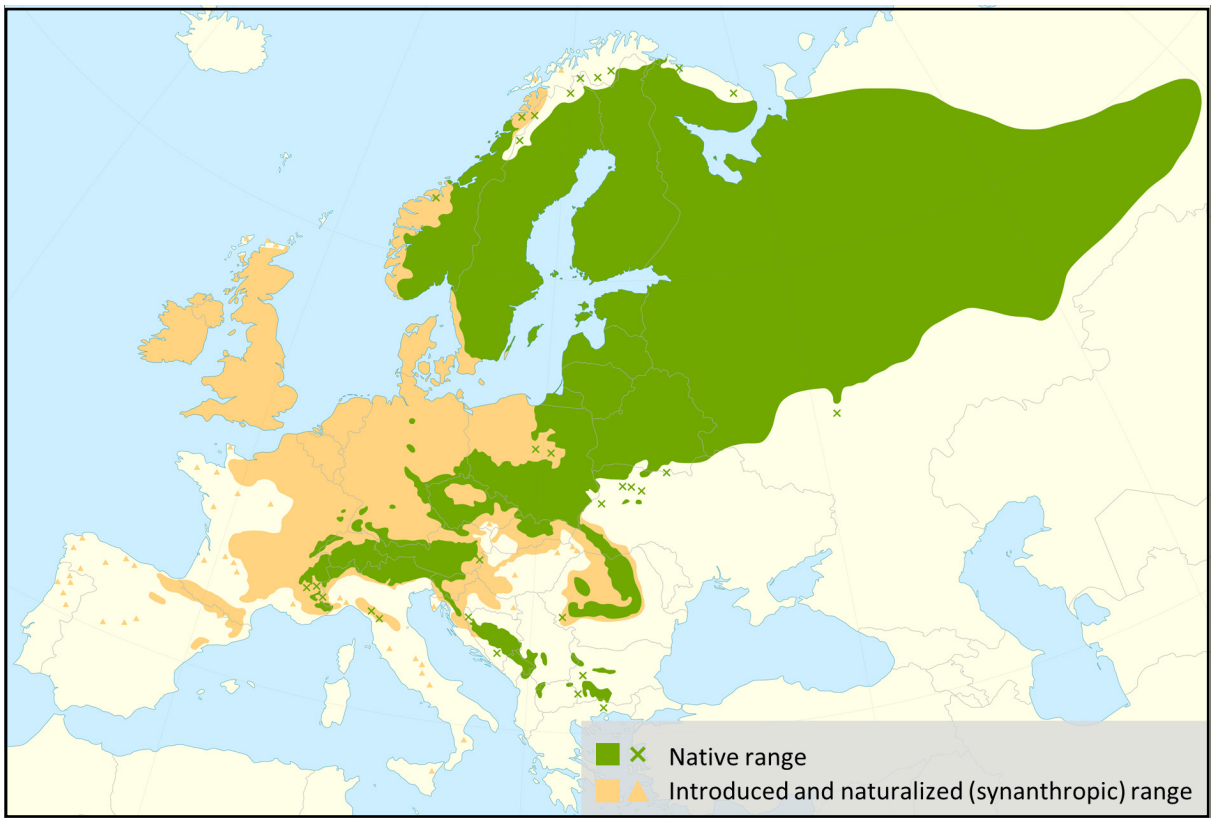

Figure 1.1: Native and introduced/naturalized distribution range of Norway Spruce (*Picea abies)* in Europe (Caudullo et al., 2017).

1.2 Forest disturbances in the Anthropocene

Within this context of highly susceptible forest landscapes, human-induced climate change is intensifying weather and climate extremes, such as heatwaves, droughts, and storms, leading to an amplification of the frequency, size, and severity of natural disturbance events (Knutzen et al., 2025; Seidl et al., 2017; Thonfeld et al., 2022). These changes threaten ecosystem stability by fundamentally altering abiotic and biotic site characteristics that shape ecosystems (Jentsch et al., 2022; Seidl et al., 2017). Disturbances were defined by Jentsch and White (2019) as pulse events with abrupt changes in one or more measurable system variables deviating from their average conditions. Such pulses may occur periodically or episodically, and vary in their predictability. The long-term patterns, interactions and statistical behavior of disturbances within a landscape are referred to as disturbance regimes (Jentsch et al., 2022; Jentsch & White, 2019). The capacity of an ecosystem to absorb disturbances without fundamentally altering its typical structures and processes is defined as ecological resilience (Seidl et al., 2022). This capacity is maintained when disturbances fall

within a safe operating space, meaning the system may be displaced but does not transition to an alternative stable state (Johnstone et al., 2016).

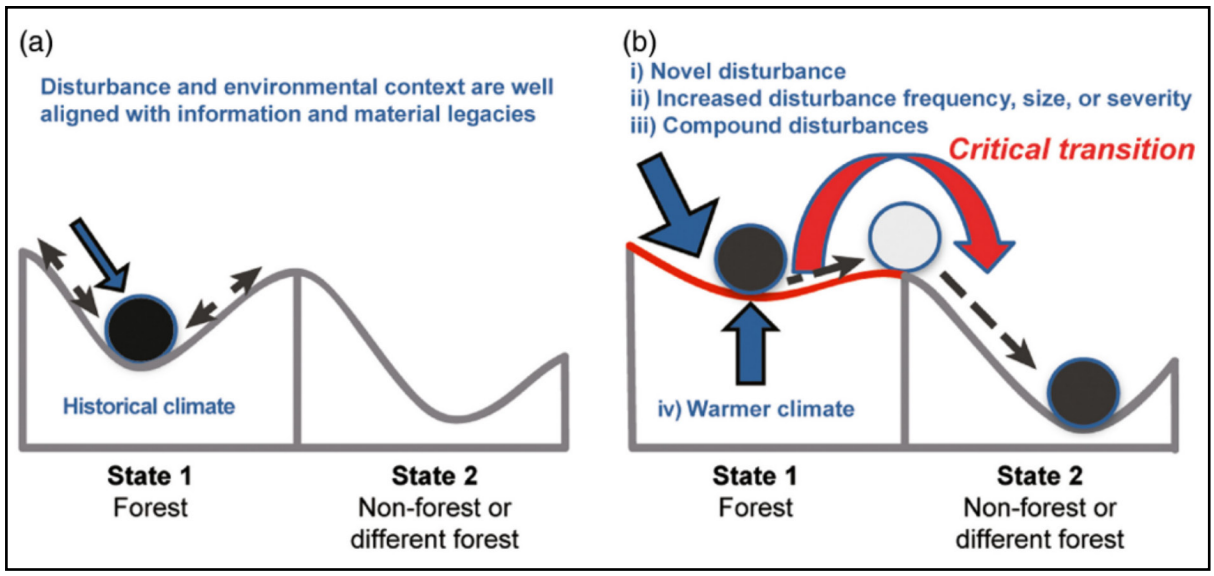

Figure 1.2: Conceptual stability landscape illustrating ecological resilience and critical transitions in forest ecosystems. (a) Under historical disturbance regimes, disturbance and environmental context remain well aligned with ecosystem legacies, and the forest ecosystem (ball) can move but stays within its basin of typical structure and function (State 1). (b) Novel disturbances, increased disturbance frequency, size or severity, compound events, and warmer climatic conditions can erode resilience, pushing the forest ecosystem toward a critical transition and into an alternative stable state (State 2: Non-forest or different forest type). Reproduced from Johnstone et al. (2016).

In recent decades, both frequency and magnitude of disturbances such as wildfires, windstorms, and insect outbreaks have increased and are predicted to intensify in forest ecosystems (Altman et al., 2024; Patacca et al., 2023; Seidl, Schelhaas, et al., 2014; Seidl et al., 2017). As climatic conditions and disturbance regimes increasingly deviate from historical norms, forest ecosystems may cross critical thresholds and shift into alternative stable states, including non-forest systems or novel forest types (Fig. 1.2b; Johnstone et al., 2016). Since trees have long life cycles, often exceeding 100 years, forest ecosystems are particularly vulnerable to the rapid pace of the ongoing climate change and the associated disturbance regimes (Lindner et al., 2010). This vulnerability is further amplified by the structural simplification due to past intensive management, as described in 1.1. A central mechanism underlying ecological resilience is the capacity of ecosystems to draw on the structural and biological legacies of past disturbances, such as deadwood, seed banks, and adapted species assemblages, to reorganize and recover after disturbance events (Johnstone

et al., 2016). Where disturbance regimes shift beyond the range to which species and communities are historically adapted, or where management repeatedly removes these legacies as a compounding disturbance, the ecological resilience becomes progressively depleted (Johnstone et al., 2016, Fig 1.2).

From an ecological perspective, natural disturbances are integral components of forest ecosystem dynamics, initiating processes of regeneration and reorganization (Franklin et al., 2002; Müller et al., 2008). By increasing light on the forest floor, enhancing the structural heterogeneity of stands, and contributing deadwood as resource and habitat for many species, disturbances can create favorable conditions for forest regeneration and biodiversity (Cours et al., 2023; Hilmers et al., 2018). This aligns with the intermediate disturbance hypothesis (Connell, 1979; Jentsch et al., 2022), which predicts that species diversity is highest at intermediate levels of disturbance frequency and intensity. In this case, neither competitive exclusion under stable conditions nor the elimination of less resilient species under severe disturbance dominates community assembly. Early successional stages and open areas following disturbance typically support high faunal and floral diversity, yet such conditions are relatively rare and often avoided in managed forests (Hilmers et al., 2018; Swanson et al., 2011).

1.3 Post-disturbance management and ecological trade-offs

When forest ecosystems cross ecological thresholds, this can impair their capacity to provide ecosystem services essential to human well-being, including timber production, biodiversity conservation, and climate change regulation through carbon storage (Forzieri et al., 2022; Seidl et al., 2017). Climate change and the associated challenges have driven a shift toward a more holistic understanding of forest ecosystems, with additional services such as carbon sequestration and biodiversity increasingly recognized and incorporated into policies and management strategies (Díaz et al., 2018). Nevertheless, after disturbance events and tree-dieback, intensive management interventions are often applied to recover economic value and reduce perceived subsequent risks (Leverkus et al., 2018; Lindenmayer et al., 2012). Severe human interference with resource legacies (e.g. deadwood, seed banks, microhabitats) can reduce niche availability for biodiversity and may thereby undermine ecological resilience (Folke et al., 2004; Lindenmayer et al., 2012; Messier et al., 2019). With the ongoing biodiversity crisis and international efforts to halt species loss, such as the Global Biodiversity Framework (CBD, 2022), natural resources need to be managed in an

adaptive way guided by ecological processes and functions, to maintain resilient ecosystems that reliably support human well-being (Boran & Pettorelli, 2024; Folke et al., 2004). Hence, post-disturbance and pest control management must account for ecosystem functionality to avoid exacerbating stress or creating additional anthropogenic disturbances (Lindenmayer et al., 2017; Messier et al., 2019).

This tension between economic recovery and ecological functionality is well illustrated by management reactions to control mass reproduction of forest pest insects. For example, outbreaks of *Lymantria dispar* (L.) in broadleaved forests across Europe and North America have repeatedly triggered large-scale aerial insecticide applications (Boukouvala et al., 2022; Tobin et al., 2012). Although these treatments can effectively reduce defoliation, broad-spectrum insecticides may generate unintended cascading effects across trophic levels. In particular, the suppression of natural enemy populations including parasitoid wasps, predatory beetles, and insectivorous birds can disrupt the natural control mechanisms that would otherwise regulate future outbreak dynamics (Wan et al., 2025; Wolz et al., 2024). At an even larger scale, outbreaks of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) across western North America have affected tens of millions of hectares of boreal and montane forest since the 1990s. These outbreaks are compelling evidence of how the shifting disturbance regimes, combined with even-aged forest landscapes, can overwhelm both forest resilience and conventional management responses (Kurz et al., 2008; Raffa et al., 2008). In both cases, reactive management struggled to keep pace with outbreak dynamics, and pest control interventions that focus on individual disturbance agents often overlook broader ecological interactions, with potential consequences for long-term ecosystem functioning.

In Central European forests, windstorms represent the most important abiotic disturbance agent in terms of affected timber volume (Seidl et al., 2017). Major storm events such as Vivian (1990), Lothar (1999), and Kyrill (2007) generated large volumes of wind-felled timber across Central Europe (Patacca et al., 2023; Sanginés de Cárcer et al., 2021). Beyond their direct effects, windstorms act as critical predisposing events because the abundance of damaged and felled trees creates ideal breeding conditions for bark beetles, generating a disturbance interaction in which the biotic agent amplifies and spatially extends the impact of the initial abiotic event (Seidl et al., 2016). This coupling is particularly pronounced in the structurally simplified, even-aged *P. abies* monoculture plantations in Central Europe, which are highly susceptible to storm (Schelhaas et al., 2003) and drought stress (Netherer

et al., 2015). Under these compounding vulnerabilities, outbreaks of the European spruce bark beetle *Ips typographus* (L.), an otherwise secondary pest, have become the dominant biotic driver of large-scale forest dieback in Central Europe.

1.4 *Ips typographus* outbreaks in European *Picea abies* forests

In recent years, *I. typographus* outbreaks have caused substantial economic losses and ecosystem changes across Central Europe, with tens of millions of cubic meters of standing timber lost annually (Hlásny et al., 2021; Mohr et al., 2025; Patacca et al., 2023). At the outbreak peak in 2020, up to 75% of the total wood harvest in Germany was classified as unplanned (Fig. 1.3; Statistisches Bundesamt, 2025b). Although the share of unplanned harvest declined by 2024, 15.6 million m^3 of coniferous timber was still harvested due to insect infestation (predominantly *I. typographus* in *P. abies*) in Germany, corresponding to approximately 57% of the total unplanned harvest volume (Statistisches Bundesamt, 2025a). These overall high shares, even after the peak, provide clear evidence that disturbances can significantly impact wood harvest and, consequently, alter existing management plans and targets.

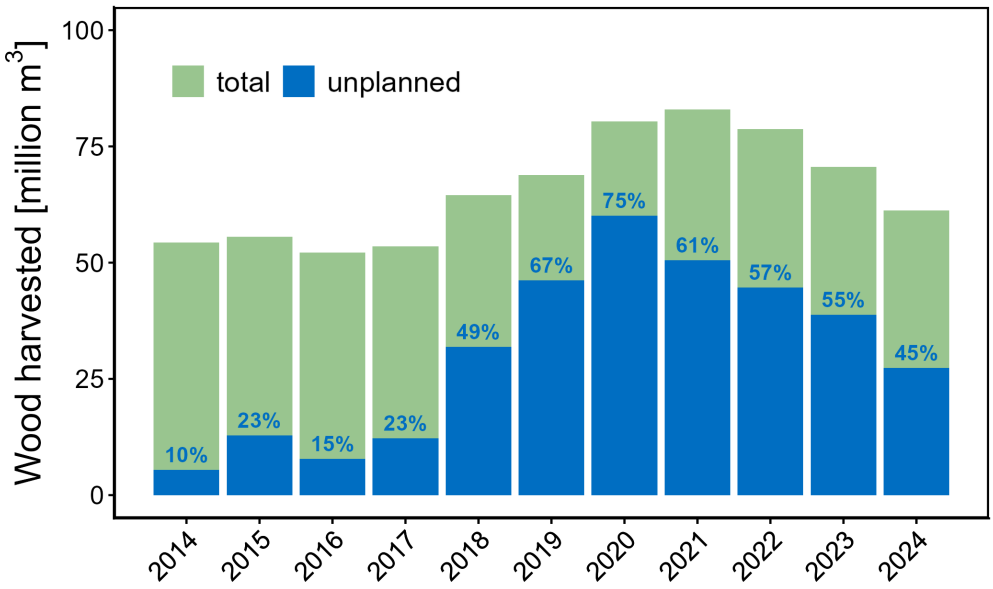

Figure 1.3: Harvested wood in Germany with shares of unplanned harvest due to disturbances 2014–2024; Data source: Statistisches Bundesamt (2025b).

One of the most economically important and widespread tree species in Central Europe is *P. abies*, with the genus representing approximately one quarter of the growing stock in the

region (Caudullo et al., 2016; Köhl et al., 2020; Schelhaas et al., 2018). Recent diebacks and ongoing efforts to transform forests toward mixed stands have reduced its relative share, yet *P. abies* is expected to remain an important tree species due to its high historical prevalence, large natural range, strong regeneration potential, and economic advantages (Caudullo et al., 2016; Macek et al., 2017). Outbreaks of *I. typographus* are naturally recurring events in Central Europe, with historical records documenting repeated mass outbreaks since the mid-17th century (Hoch et al., 2020; Schelhaas et al., 2003), yet the magnitude of the most recent diebacks is unprecedented (Hlásny et al., 2021). Additionally, climate change is amplifying outbreak dynamics not only in planted forests but increasingly also within the natural distribution range of *P. abies* (Jakoby et al., 2019; Jian et al., 2025; Marini et al., 2017).

I. typographus is a 4–5.5 mm long bark beetle (Coleoptera: Curculionidae, Scolytinae) that completes its life cycle beneath the bark of *P. abies*. In Central Europe, the species typically produces one to two generations per year under normal conditions (Hoch et al., 2020; Wermelinger, 2004). In spring, when temperatures exceed approximately 16°C, the first swarming flight is initiated. Following successful host localization and colonization, each male establishes a mating chamber in the phloem, attracting one to three females. Each female then excavates a maternal gallery 6–12 cm in length, running parallel to the stem axis, and deposits up to 80 eggs along the gallery walls (Wermelinger, 2004). Larvae feed in the phloem layer perpendicular to the maternal gallery, disrupting carbohydrate transport from the leaves to the roots, which leads to fine root mortality and, ultimately, tree death (Hoch et al., 2020). Experimental studies have shown that the life cycle of *I. typographus* takes six to ten weeks, depending on weather conditions, with a temperature optimum around 30 °C (Frühbrodt et al., 2023; Hofmann et al., 2024; Wermelinger & Seifert, 1998). Sun-exposed logs and trees warm up faster and have higher bark temperatures, therefore, bark beetles also develop more rapidly under these conditions (Baier et al., 2007). After pupation, the brown and soft teneral beetles conduct maturation feeding and, depending on thermal conditions, either proceed with a second reproductive flight or enter diapause in the soil or litter layer (Wermelinger, 2004). Additionally, *I. typographus* is associated with a variety of fungi, which are introduced into the host during beetle colonization and may impair tree defenses and accelerate host mortality (Zhao et al., 2019). Blue-stain fungi in particular, for which *I. typographus* is a major vector (Linnakoski et al., 2016), can be

introduced into the wood and cause sapwood discolorations, downgrading timber quality (Böhm et al., 2023).

Under endemic conditions, bark beetle populations are constrained by the limited availability of suitable host material (storm- or snow-felled logs, or physiologically weakened trees) and are primarily regulated by pathogens and natural enemies, including parasitoids, predatory beetles, and woodpeckers (Biedermann et al., 2019; Wermelinger, 2004). Undamaged *P. abies* trees can resist beetle colonization through resin flow, which can physically expel attacking beetles, seal the entrance wound, and protect the tree from other biotic agents, especially fungi (Netherer et al., 2015). The transition from endemic to epidemic population dynamics occurs when bark beetle population density exceeds the defensive capacity of the host population. When large volumes of suitable host material become available, *I. typographus* can rapidly build up population densities sufficient to overcome the defenses of otherwise undamaged trees through mass attack (Biedermann et al., 2019; Hoch et al., 2020; Seidl et al., 2016). Once population densities are sufficiently high, a positive feedback loop is initiated in which beetle-killed trees further fuel population growth and spatial spread. Epidemic outbreaks are therefore typically started by extreme weather events at landscape scales, particularly windstorms and drought, that generate large quantities of stressed or dead host material while simultaneously weakening adjacent forest stands (Seidl et al., 2016).

On the landscape level, climate change is fundamentally altering the ecological relationship between *I. typographus* and *P. abies* (Biedermann et al., 2019). Since insect activity is temperature-dependent, rising temperatures accelerate beetle development and increase the likelihood that a second and third reproductive generation will successfully complete within a single season, thereby effectively amplifying population growth rates (Baier et al., 2007; Jakoby et al., 2019; Wermelinger & Seifert, 1998). Rising temperatures in early spring trigger earlier swarming flights, effectively extending the outbreak season (Hofmann et al., 2025; Potterf et al., 2025). Simultaneously, the physiological resistance mechanisms of trees are further undermined by climate change-induced extreme and persistent soil moisture deficits, as observed during the hot summer droughts between 2018 and 2020 (Knutzen et al., 2025; Schuldt et al., 2020; Thonfeld et al., 2022). Under these drought conditions, resin flow declines, facilitating bark beetle colonization (Netherer et al., 2015, 2019). This combination of high reproductive rates, physiologically weakened host trees, and increasing disturbances that generate large pulses of damaged wood fundamentally shifts the balance of the interaction in favor of the beetle (Biedermann et al., 2019; Singh et al., 2024). At the

landscape scale, extensive areas of mature, even-aged stands provide continuous host availability, facilitating rapid spatial spread of outbreaks and creating levels of susceptibility that increasingly exceed the capacity of conventional forest protection measures (Hlásny et al., 2021; Seidl et al., 2016, Fig. 1.4).

1.5 Forest protection strategies during *Ips typographus* outbreaks

Forest protection is a vital economic and ecological safeguard, aiming to prevent or mitigate damage from biotic and abiotic disturbances. Large-scale tree mortality caused by bark beetle outbreaks can substantially alter provisioning services such as timber production, regulating services including carbon sequestration and water regulation, and supporting services such as habitat provision and soil protection (Chen et al., 2025; Raffa et al., 2008; Seidl et al., 2016; Stritih et al., 2021). In alpine regions, the loss of forest cover and structural integrity from bark beetle outbreaks can significantly reduce the protective function of forests, increasing risks to infrastructure and settlements from avalanches, rockfall, landslides, and soil erosion (Brang et al., 2006; Moos et al., 2018). Consequently, the sustainable provision of ecosystem services and the continued maintenance of forest resilience are central objectives of forest protection, underlining the necessity for reactive pest management activities within forest resource management (Boyd et al., 2013).

While long-term silvicultural strategies focus on reducing host tree shares by restructuring forest stands from monocultures to mixed-species forests to enhance stand stability and resilience, reactive bark beetle regulation remains essential during active outbreaks or periods of high availability of suitable breeding substrate (de Groot et al., 2019; Hoch et al., 2020). In these situations, the primary goal of forest protection interventions is to suppress beetle populations and reduce the likelihood of a transition from endemic to epidemic population levels (see 1.4), thereby avoiding premature dieback and unplanned harvests. Salvage logging (removal of suitable host material with focus on economic recovery) and sanitation felling (removal of freshly infested trees with focus on pest reduction) operations are the most common management responses to regulate bark beetle density on a landscape and stand scale, respectively (Leverkus et al., 2021; Stadelmann et al., 2013). Beyond removal of suitable host material for bark beetles, salvage logging serves as a critical mechanism for recovery of capital and investments, by extracting wood before degradation and decomposition (Leverkus et al., 2021; Müller et al., 2019). Additional motivations for salvage logging activities are the preparation of sites for regeneration and planting, reduction

of fuel loads to prevent forest fires, and ensuring safe accessibility for machinery and forest users (Leverkus et al., 2020; Lindenmayer & Noss, 2006; Müller et al., 2019).

A prerequisite for successful *I. typographus* regulation is the implementation of efficient detection and monitoring systems to localize and quantify infested material or logs suitable for reproduction (Hoch et al., 2020; Kautz et al., 2023; Stadelmann et al., 2013). Monitoring and forecasting of population densities as well as beetle phenology (the timing of life cycle stages), using pheromone traps, geographic information systems, and weather data, provide the spatial and temporal information necessary for planning reactive pest control measures (Baier et al., 2007; Potterf et al., 2025). To be effective, all logs with signs of colonization (brown bore dust) or suitable host material which can be used for reproduction have to be treated or removed outside of the dispersal range (minimum of 500 m) from forest stands with host trees before beetles can emerge (Kautz et al., 2011; Wermelinger, 2004). Once the swarming and reproductive cycle has started in spring (see 1.4), forest protection measures are required to be conducted within approximately six to ten weeks before the next generation emerges, depending on weather conditions (Hoch et al., 2020). Mis-timed or incomplete operations may not only fail to reduce population densities but can also unintentionally provide additional breeding substrates or attract beetles to newly created forest edges (Kautz et al., 2013; Stadelmann et al., 2013). Delayed removal (after emergence or during winter) may reduce long-term control effectiveness and can disproportionately impact natural population control agents, such as predatory flies (Weslien et al., 2024) and woodpeckers (Basile et al., 2022). The application of insecticides for pest control is highly regulated, has negative effects on non-target organisms (Wan et al., 2025), and can only be applied as a measure of last-resort in accordance with the integrated pest management principles (Leroy, 2024).

1.6 Bark beetles as ecosystem engineers

In contrast to reactive forest protection management, the principle of protecting natural processes in unmanaged conservation forests (e.g. national parks) prioritizes natural ecosystem dynamics without human intervention (Müller et al., 2019). In this case, *I. typographus* is considered an ecosystem engineer and “keystone” species rather than a pest species (Biedermann et al., 2019; Müller et al., 2008). Tree dieback creates a pulse in deadwood, increases light availability on the forest floor, and promotes greater structural and compositional heterogeneity within forest stands (Müller et al., 2008), which serve as critical

biological legacies and can enhance long-term ecological resilience (Beudert et al., 2015; Sommerfeld et al., 2021; Viljur et al., 2022). These natural habitats support a wide array of specialized and often endangered species (Busse et al., 2022; Müller et al., 2010). Evidence from bark beetle outbreaks indicates an increase in species numbers of bees, wasps, lichens, hoverflies, cicadas, vascular plants, spiders, and particularly saproxylic beetles, while wood-inhabiting fungi declined (Beudert et al., 2015).

Therefore, to support biodiversity, non-intervention sites that retain deadwood should also be promoted outside of protected, inaccessible, or protective forests. More heterogeneous forest landscapes can support high species diversity, thereby enhancing their adaptive potential and securing continuous provision of forest goods and services in the face of ongoing global change (Kulakowski et al., 2017; Lindenmayer et al., 2017; Seidl et al., 2018). Particularly in protected areas, conflicts between the goal of protecting natural processes without human interventions and the necessity of preventing beetle "spillover" into neighboring commercial forests are predominant (Müller & Imhof, 2019). Given that approximately 40% of Europe's protected areas fall within the natural distribution range of *P. abies* (Hagge, Leibl, et al., 2019), there is an urgent demand to apply alternative pest control methods that facilitate the retention of biological legacies on-site while effectively disrupting the beetle's reproductive cycle. In management zones of protected areas, pest control is required to also meet the objectives of biodiversity conservation, environmental education, and recreation (www.iucn.org, Schiermeier, 2017), all of which can be negatively affected by salvage logging (Lindenmayer et al., 2017; Thorn et al., 2018).

Nevertheless, the dieback of large forest areas can create a conflict with the local population and particularly forest enterprises close to protected areas perceive unmanaged areas as the source of uncontrolled bark beetle outbreaks (Müller, 2011; Müller & Imhof, 2019). To reconcile conservation goals with the protection of timber production in adjacent forests, conflicts are addressed with the establishment of buffer zones. These zones typically extend approximately 500 m into the protected area, where intensive monitoring and reactive bark treatments are prioritized to prevent spillover from core zones to commercial forests. In the strictly protected areas, a non-intervention or "benign neglect" strategy ensures natural processes and ecosystem development (Müller et al., 2010). Within management buffer zones, however, salvage logging following windthrow or during bark beetle outbreaks is a common strategy, despite its potential conflict with the preservation of biological legacies

that are essential for ecosystem functioning (Cours et al., 2023; Lindenmayer et al., 2017; Müller et al., 2019; Schiermeier, 2017).

1.7 Economic and ecological trade-offs from salvage logging

From an economic perspective, large-scale outbreaks often lead to a local surplus of timber, causing market prices to collapse and an increase in timber export (Camia et al., 2021; Jandl, 2020; Toth et al., 2020). Part of this surplus is increasingly diverted to bioenergy production, as wood and logging residues gain importance in the context of rising energy prices and the transition toward renewable resources (Barrette et al., 2015; Camia et al., 2021).

Operationally, salvage and sanitation logging are cost- and labor-intensive, may be constrained by difficult terrain or adverse weather, and often require logistical planning to prioritize stands and schedule interventions efficiently (Leverkus et al., 2021). Large-scale pest outbreaks intensify operational challenges for forest owners and managers, requiring substantial investments in timber transport, storage infrastructure, and labor (Hlásny et al., 2021). Consequently, the volume of attacked and windthrown trees that need to be removed during disturbances at landscape-scale can exceed locally available capacities for transport and storage (Hallas et al., 2024; Hlásny et al., 2021). In steep terrain, where cable yarding or helicopter extraction are often the only mechanized harvesting options, operational costs can approach or exceed timber revenues, limiting the economic feasibility of salvage logging in many mountain forests (Spinelli et al., 2015; Stoilov et al., 2021).

To prevent outbreak spread, simulation experiments indicate that 80% of beetles must be eliminated (Fahse & Heurich, 2011) or, alternatively, 95% of suitable host material must be removed from the forest stand (Dobor et al., 2020). However, the real-world efficacy of these measures appears to be variable. For instance, empirical evidence from Switzerland linked the large-scale removal of damaged timber to lower infestation levels in following years (Stadelmann et al., 2013), yet similar efforts in the Western Carpathians indicated only limited impacts on the regulation of beetle populations (Vanická et al., 2020). When wood cannot be moved within the limited timeframes, it requires intermediate storage, which introduces new risks. Long-term storage can lead to a significant decline in timber value due to discoloration caused by blue-stain fungi or decomposition by microorganisms (Barrette et al., 2015; Böhm et al., 2023). While storage methods such as water sprinkling or foil

wrapping can preserve wood quality and inhibit beetle emergence, they are technically demanding and costly (Beiglböck et al., 2024; Costa & Ibanez, 2005; Hoch et al., 2021).

Ecologically, salvage logging has detrimental effects on forest ecosystems, beginning with intensive use of heavy machinery which often leads to soil compaction and increased erosion risk (Cambi et al., 2015). The removal of large volumes of wood negatively impacts biodiversity (Georgiev et al., 2020; Thorn et al., 2018; Thorn, Chao, et al., 2020) and can compromise forest resilience against future disturbances (Leverkus et al., 2021). Since approximately one quarter of all temperate forest species depend at least for a part of their life cycle on dead or decaying wood (saproxylic) as a resource or habitat (Stokland et al., 2012), this specialized biodiversity is negatively affected by salvage logging (Thorn et al., 2018). Insects, specifically beetles (Coleoptera), and microorganisms (fungi and bacteria) constitute the majority of saproxylic biodiversity (Stokland et al., 2012). These organisms serve as essential agents of ecosystem functioning, acting as drivers of wood decomposition and thereby maintaining nutrient, carbon, and water cycles (Seibold et al., 2021; Stokland et al., 2012; Ulyshen, 2018). The intensive management of forest resources has led to a decrease in arthropod richness over the last decade (Seibold et al., 2019), with unmanaged areas identified as saproxylic biodiversity hot spots (Paillet et al., 2010).

On a functional level, deadwood plays an important role in forest ecosystems as a long-term reservoir in nutrient, carbon, and water cycles, stabilizing the forest microclimate and maintaining site productivity (Harmon, 2021; Herrmann & Bauhus, 2018). Soil properties and biogeochemical functioning can remain altered for years after salvage logging, with significant changes in soil fungal communities and decomposition processes that are linked to organic matter dynamics and nutrient availability (Mayer et al., 2022). In steep terrain, deadwood fulfils important protective functions by increasing surface roughness and thereby reducing risk of avalanches (Caduff et al., 2022; Wohlgemuth et al., 2017) and rockfall (Ringenbach et al., 2022). Furthermore, forest regeneration can also profit from deadwood as substrate (Steinebrunner et al., 2025; Zielonka, 2006) and physical barrier against ungulate browsing (Hagge, Müller, et al., 2019). To resolve these ecological trade-offs from salvage logging, methods are required that allow for the retention of wood within the forest, to preserve ecosystem functionality and biodiversity, without risking further pest outbreaks.

1.8 Bark treatments for bark beetle regulation

A strategic solution to avoid the removal of *P. abies* wood from the forest stand and overcome transport constraints, can be the mechanical treatment of the bark to reduce or eliminate *I. typographus'* reproductive habitat. For effective on-site regulation, the bark and underlying phloem must be physically removed or manipulated to render the logs unsuitable for reproduction. By utilizing these methods, forest managers can inhibit both the colonization of fresh substrate (preventive) and the emergence of new generations from already infested logs (therapeutic) (Hagge, Leibl, et al., 2019; Thorn et al., 2016). Once logs are colonized, the pest regulation efficacy of bark treatments is highly time-sensitive and their success depends on the development stage in the bark beetle's life cycle. Therapeutic bark treatments must be conducted in the larval stage, which ends five to seven weeks after first signs of colonization (Fig. 1.4). Beyond this period, teneral beetles may complete their life cycle in large bark pieces which remain on the log or in the forest (Delb et al., 2021). If teneral beetles are present, current management guidelines recommend burning or chipping residues from bark treatments, to ensure successful regulation (Kautz et al., 2021; Wermelinger, 2004).

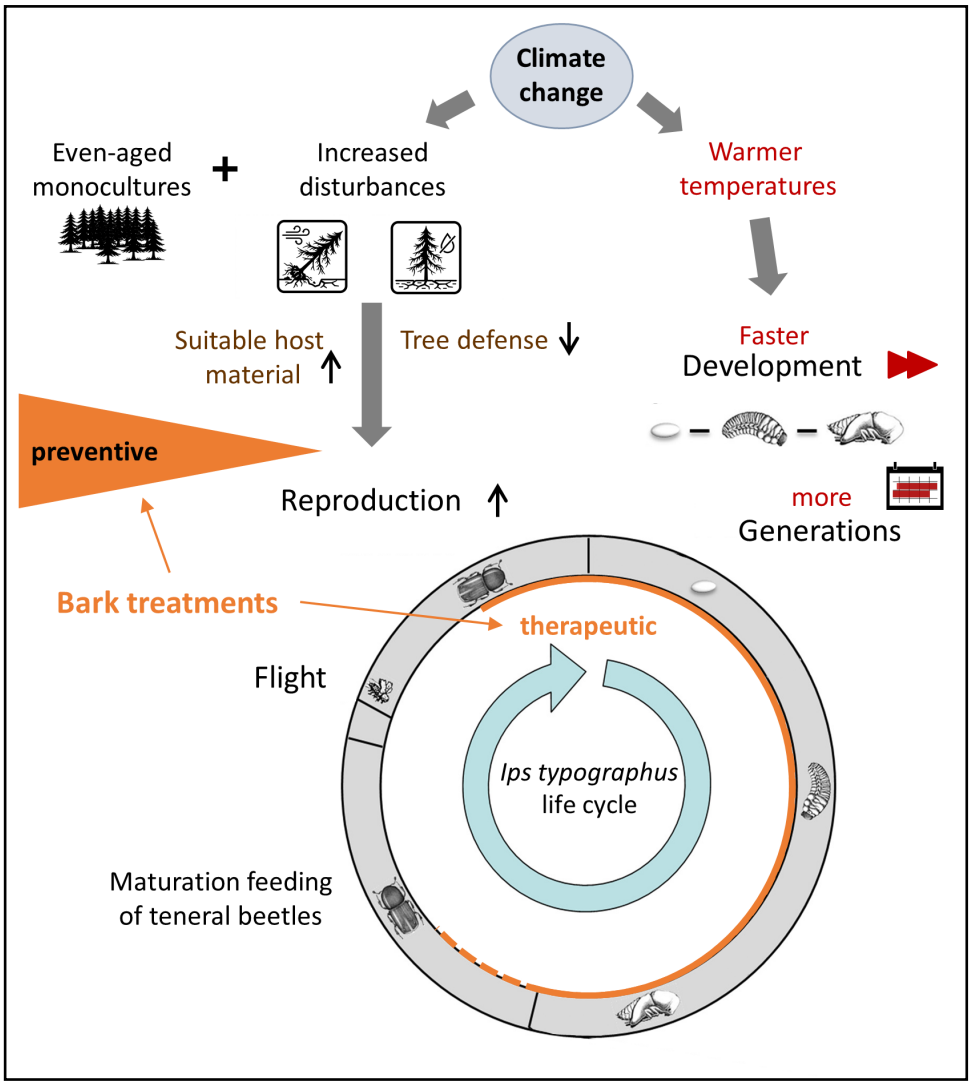

Figure 1.4: Conceptual overview of how climate change and forest structure influence Ips typographus reproduction and the timing of preventive and therapeutic bark treatments. Life cycle adapted from (Jakoby et al., 2019).

In regions where access for large machinery is restricted—such as protected areas, wetlands, or steep terrain—manual debarking with a debarking spud is an established and effective treatment. In the alpine region of the Bavarian state forests alone, approximately 25,000 m³ of timber is manually debarked annually (BaySf, 2022). Chainsaw-mounted attachments (motor-manual) with rotating flat knives for complete debarking have been developed as more efficient motor-manual alternatives (Hagge, Leibl, et al., 2019; Thorn et al., 2016). Milling the bark off with the chainsaw attachments not only removes the breeding habitat, but can also kill teneral beetles mechanically and directly chips the bark into small pieces, unsuitable for maturation feeding.

Further innovation led to an updated knife configuration that gouges regular stripes parallel to the stem axis with a distance of approximately 2 cm into the bark, leaving 30% of the bark intact (Hagge, Leibl, et al., 2019; Thorn et al., 2016). This so-called bark gouging or bark scratching has less resistance than complete debarking during processing due to the smaller area of bark removal. Controlled experiments indicate a higher cost-effectiveness than complete debarking due to faster treatment times and lower fuel consumption (Bachinger et al., 2024; Hagge, Leibl, et al., 2019). The remaining phloem does not provide sufficient space for the extension of larval galleries during the development of *I. typographus* and the regular cuts lead to a fast desiccation pf the breeding habitat. By retaining portions of the bark intact, essential microhabitats and structural complexity of deadwood can be preserved for saproxylic species and higher trophic levels, such as woodpeckers. Regional pilot studies have shown that complete debarking negatively affects saproxylic organisms as well as woodpecker activity (Hagge, Leibl, et al., 2019; Thorn et al., 2016).

Overall, bark and the underlying phloem in particular contribute as an important source of nutrients and carbohydrates to the early saproxylic colonization processes, with many species directly dependent on it for habitat, foraging, and shelter (Dossa et al., 2018; Ulyshen, 2018). Intact bark also serves as a protective layer against fungi colonization and maintains the environmental conditions within deadwood (Dossa et al., 2018). Hagge, Bässler, et al. (2019) found an increase of wood fungi with the (partial) removal of bark, while bacterial richness decreased. The presence of bark can thus shape the assemblage process and define which saproxylic species are present and may fundamentally alter the decomposition trajectory of deadwood and the associated saproxylic organisms.

1.9 Knowledge gaps

Despite growing interest in bark treatments as an alternative to salvage logging, several critical gaps currently limit their transition into standard forestry practice. While bark gouging has been shown to outperform chainsaw-based debarking devices in terms of economic efficiency (Bachinger et al., 2024; Hagge, Leibl, et al., 2019; Thorn et al., 2016), a direct comparison with manual debarking, which is the established and most widely applied method in steep and inaccessible terrain, has not been conducted. A direct comparison is therefore essential for evidence-based management recommendations, particularly for mountain forests, where machinery access is limited and deadwood retention provides important protective functions (see 1.7). Furthermore, bark gouging accuracy can be variable under field conditions, as personal handling experience, terrain, and time pressure all influence the consistency of phloem disruption, and thus breeding substrate destruction. It therefore remains unclear how much accuracy is required to achieve sufficient pest control efficacy, and how bark removal intensity affects saproxylic beetle diversity.

In times of landscape-scale disturbances with large volumes of damaged and/or infested wood, (motor-)manual labor is insufficient to ensure treatment within the necessary time frames. Additionally, forest workers can be exposed to multiple hazards (Sullman & Kirk, 2001). Harvester-based bark treatments may be an economically scalable alternative to guarantee fast reaction times for large volumes of damaged and/or infested wood. Specialized harvester aggregates for debarking (debarking heads) with modified feed rollers rotate the logs during processing and multiple passes through the aggregate can remove more than 90% of the bark (Delb et al., 2021; Heppelmann, Labelle, Wittkopf, et al., 2019; Mergl et al., 2021). The pest control efficacy has been tested in a pilot study by Delb et al. (2021), indicating sufficient reduction. As a currently more widely available alternative, conventional harvester aggregates have also demonstrated promising pest control efficacy when logs were passed multiple times through the aggregate (Delb et al., 2021). In case the wood is considered for on-site retention (e.g. buffer zone management of protected areas), studies assessing the impact on non-target beetle diversity and assemblages are still lacking for the ecological assessment of harvester-based bark treatments.

Existing studies on bark treatments have been conducted predominantly in the Bavarian Forest region and not longer than two years, limiting the generalizability of their findings across the diverse site conditions of Central European *P. abies* forests and the temporal

dynamics of saproxylic biodiversity colonization. Developing scientifically sound recommendations for bark treatment applications requires simultaneous consideration of both economic and ecological factors, yet such integrated assessments across large geographic ranges are still lacking. Furthermore, the direct and indirect pathways through which bark removal cascades across multiple trophic levels, from wood moisture and saproxylic beetles to woodpeckers, microbial communities, and wood properties, have not been disentangled, leaving the mechanistic understanding of treatment effects on deadwood ecology incomplete.

When logs are stored on-site, the wood decomposition processes are of high economic relevance for forest managers and owners, since they directly affect potential use scenarios (e.g. bioenergy), while blue-stain fungi colonization leads to aesthetic alterations of the wood and hence reduces timber value (Böhm et al., 2023). However, the effects of bark treatments on potential changes in moisture content, elemental composition, calorific value, and blue-stain fungi during on-site storage remain poorly understood, highlighting the need for studies to assess post-treatment timber use potential.

1.10 Main objectives

The main objective of this thesis is to advance the understanding of mechanical bark treatments for bark beetle regulation by evaluating their practical applicability from both economic and ecological perspectives. The changing disturbance regimes with their subsequent operational and economic constraints drive the need for the implementation of novel tools for reactive disturbance management. Scientific evidence is still lacking for bark treatments across larger scales and for long term effects on biodiversity and wood value. Across three research chapters, pest control efficacy, operational feasibility, biodiversity impacts, and wood properties were assessed to provide a robust scientific basis for integrating bark treatments into forest protection and conservation strategies. With effective and efficient bark treatments, wood can be retained on-site and reliance on salvage logging and its associated ecological and economic trade-offs can be reduced.

Each of the three research chapters addresses one of the following main research questions:

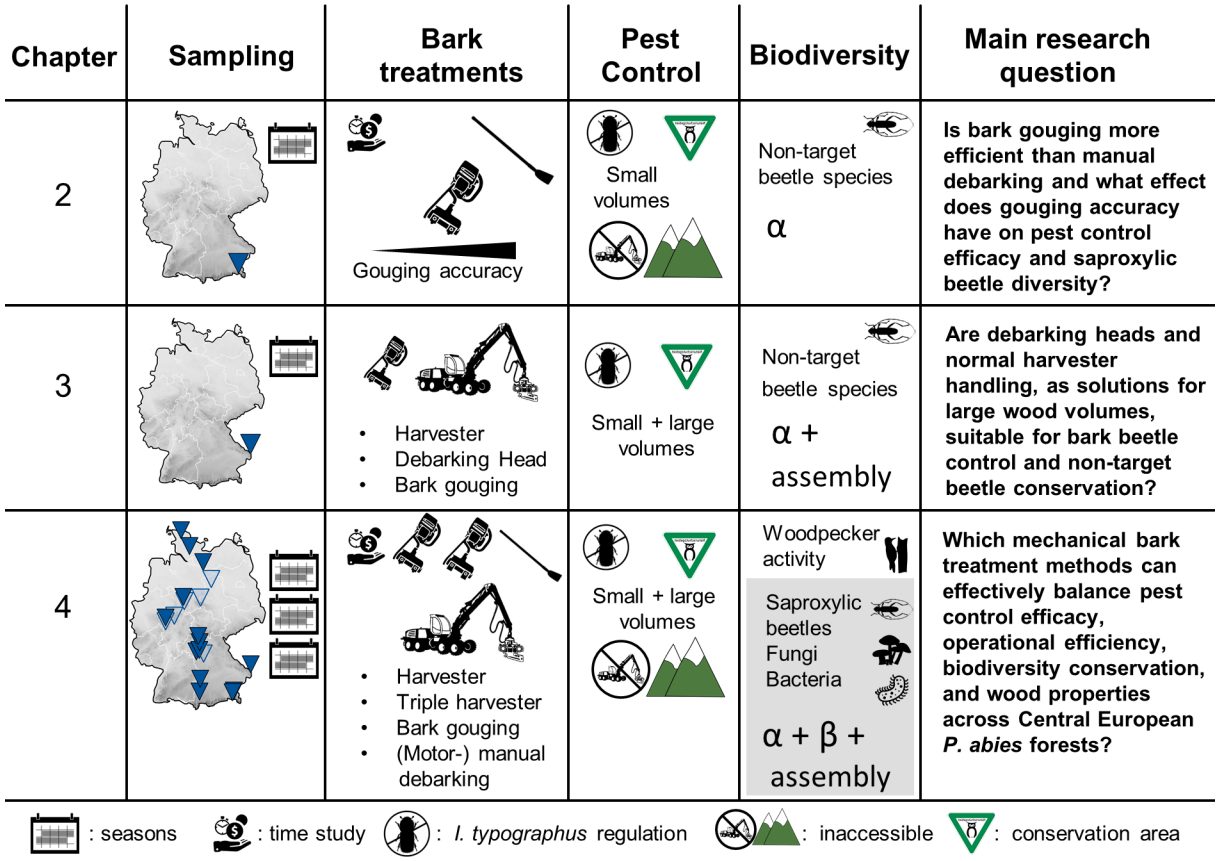

Figure 1.5: Graphical overview on the sampling design, tested bark treatments, pest control with operational feasibility, assessed biodiversity parameters and main research question for each of the three research chapters.

Chapter 2 assessed the practicality and efficacy of bark treatments in mountainous regions, where the removal or treatment of damaged wood with heavy machinery is often not possible or not economically viable. It aimed to compare manual debarking and bark gouging in a time study to evaluate operational efficiency in steep terrain, and to quantify the effects of variable gouging accuracy on pest control efficacy and non-target saproxylic beetle diversity (Fig. 1.5).

Chapter 3 investigated the feasibility of harvester-based bark treatments for processing large wood volumes that motor-manual methods cannot address at the landscape scale. Conducted in the management zone of the Bavarian Forest National Park, the study compared normal harvester processing, a specialized debarking head aggregate, and motor-manual bark gouging in terms of pest control efficacy and their effects on non-target beetle diversity and assemblages (Fig. 1.5).

Chapter 4 built upon these findings by applying an experimental design with 20 sites distributed across the German forest landscape to derive generalizable conclusions for Central European *P. abies* forests. The study aimed to evaluate all readily available mechanical bark treatment methods, including multiple passes of logs through a conventional harvester aggregate as the scalable alternative to specialized debarking heads. Over the three-year study period, it assessed pest control efficacy and operational efficiency alongside ecological impacts on saproxylic beetles, fungi, and bacteria, specifically their alpha and gamma diversity and assemblages, as well as on woodpeckers. In addition, changes in moisture content, elemental composition, net calorific value, and blue stain fungi abundance were evaluated to determine post treatment timber utilization potential. By linking pest control, biodiversity, and wood properties, the study provided a multifaceted assessment of bark treatments as scalable solutions for intermediate on-site wood storage during logistical bottlenecks, as well as for deadwood retention to support conservation goals (Fig. 1.5).

Chapter 2: Low accuracy bark gouging controls *Ips typographus* outbreaks while conserving non-target beetle diversity

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Abstract

Natural disturbances and subsequent outbreaks of forest insects led to unprecedented amounts of damaged timber. In Eurasia, the European Spruce Bark Beetle (*Ips typographus*) breeding in Norway spruce (*Picea abies*) is creating the main share of infested trees in recent years. As alternative to salvage logging, different technics of mechanical and manual methods of bark removal for pest control are frequently applied in areas with conservation status or in protective forests that mitigate or prevent the impact of a natural hazard. To test the field applicability of bark removal technics, we compare work productivity mirroring economic costs between the widely used manual debarking and the new technique of bark gouging. Additionally, we evaluate how pest control and non-target biodiversity are affected from bark gouging if the phloem is cut with decreasing accuracy mirroring practical application by forest enterprises. Based on data of an experimental design we show, that bark gouging is twice as fast as manual debarking. From complete debarked *P. abies* logs no *I. typographus* emerged (pest control efficiency of 100%) but diversity of other emerging beetle species is reduced near zero. If bark gouging is conducted with high accuracy (phloem sufficiently cut in more than half of stripes) pest control efficiency is 99.9% and for low accuracy (below 50%) pest control efficiency is still 95.7%. Non-target beetle diversity increases with reduced accuracy. Bark gouging combines sufficed pest control with biodiversity conservation at lower work productivity than manual debarking and can thus be recommended for protected areas and protective forests, in particular.

2.1 Introduction

Severe natural disturbances are an integral part of many forest ecosystems around the globe and can appear as 'stand-replacing' events that remove all or most of the forest canopy (Svoboda et al., 2012). Coniferous forests are naturally prone to an increasing amount and frequency of large-scale stand-replacing disturbances, such as high-severity wildfires, windstorms, and insect outbreaks (Kurz et al., 2008; Seidl, Schelhaas, et al., 2014). The amount of timber volume affected by natural disturbances has increased over the last decades on a global (Kurz et al., 2008; Seidl, Schelhaas, et al., 2014). The largest portion is generated by small to medium-size forest disturbance due to bark beetles and/or windstorms, resulting in small to medium-sized canopy gaps (Čada et al., 2016). Nevertheless, disturbances by bark beetles can also impact forests up to the landscape level (Vega & Hofstetter, 2015). In some European countries, unprecedented amounts of timber from disturbances have been recorded recently with up to 50% of the total annual harvest (Hlásny et al., 2019). The mostly homogenous forest stands of Norway spruce (*Picea abies* (L.) Karst.) are predisposed and affected with utmost severity (Kausrud et al., 2012), while the estimated cumulative damage is predicted to further increase in the near future (Seidl, Schelhaas, et al., 2014). Facilitated by preceding droughts and windstorms (Marini et al., 2017), outbreaks of the European Spruce Bark Beetle (*Ips typographus* (Linnaeus, 1758)) led to a strong rise in canopy die-offs in recent years (Patacca et al., 2023; Senf et al., 2018). The main drivers are an increasing growing stock of coniferous trees coupled with the impact of global climate change (Biedermann et al., 2019; Schelhaas et al., 2003; Seidl et al., 2011, 2016). Since *P. abies* is one of the most important tree species for commercial timber production, outbreaks of *I. typographus* are associated to large financial losses (Hlásny et al., 2021). As a consequence, forest management has developed a search-and-destroy strategy with the aim to reduce populations of insect pests by different methods, including prescribed burning, sanitation logging, salvage logging, cut-and-leave tactics, and poisoned trap trees (Fettig et al., 2022). Salvage logging is mainly applied in commercial forests but also in protected areas to safeguard nearby timber production (Lindenmayer et al., 2017; Müller et al., 2019). Timely intervention is the most important factor to control and decrease *I. typographus* populations (Wermelinger, 2004). Yet, in times of large quantities of timber volume affected, this is difficult to achieve due to limited availability of machinery and workers. Strategies of removing *I. typographus* affected trees outside the forest have shown to be only efficient

when > 95% of disturbed trees are detected and removed, which do match realistic values of effectiveness (Dobor et al., 2020) but rarely practicality when confronted with intensifying disturbance regimes.

In times of *I. typographus* affected timber volumes on a landscape scale, financial losses from the retention of logs in the forest are not obligatory. Economical profits can be low or even negative due to excess supply on the timber market. In special cases, i.e. inaccessible mountain forests, harvesting costs are exceptionally high. On the contrary, decoupling pest control from timber market, and thus no need of timely transport of infected logs, is an option for more effective and economic pest control on-site. Furthermore, maintaining the tree trunk biomass in the forest promotes nutrition supply and water retention, reduces browsing pressure of deer on regeneration (Hagge, Müller, et al., 2019), provides substrate for recruitment (Zielonka, 2006) and supports multiple aspects of forest biodiversity (Thorn et al., 2018). Conversely, with salvage logging after disturbances, saproxylic biodiversity (Cours et al., 2023; Georgiev et al., 2020; Müller et al., 2010; Thorn, Chao, et al., 2020; Uhl et al., 2023) as well as ecosystem resilience (Leverkus et al., 2021) are compromised. Thus, on-site bark beetle control measures, which maintain the tree biomass in the forest stand and decrease the population of insect pests are increasingly promoted to combine multiple purposes of forest use (Hagge, Leibl, et al., 2019). In case biomass retention is intended, the complete (manual) debarking of (i.e. wind-felled) *P. abies* logs is the conventional and widely used method for reduction of bark beetle populations and breeding material (Hlásny et al., 2021; Wermelinger, 2004). As an alternative, scratching the bark has the advantage to combine efficient pest control with preserving most of the non-target biodiversity (Thorn et al., 2016). Bark scratching by chainsaw or scratching devices has been replaced by the debarking device with modified knives, which gouge parallel stripes into the bark (hereafter referred to as gouging; see Fig. 2.1a and Fig. A2.1). The technique of bark gouging relies on the mechanism that the bark layer, including the phloem, is mechanical manipulated in a way that the bark is not a feasible habitat for the phloem-feeding bark beetle I. typographus. Habitat functions for other (saproxylic) species are retained, since only approximately 30% of the bark is removed. Bark gouging can be applied not only as a preventative method, i.e. before bark beetles colonize a storm-felled tree, but also to decrease the population densities of bark beetles in already infested trees (therapeutic) (Hagge, Leibl, et al., 2019). Economic costs in regard to work productivity have only been compared between chainsaw

attachments for debarking and gouging, with the result of 28% lower costs for the gouging device (Hagge, Leibl, et al., 2019; Thorn et al., 2016). However, a comparison with manual debarking is particularly relevant for implementation in mountain forests.

Yet, two open questions remain, which so far omitted the upscaling of bark gouging to larger spatial scales. First, how efficient is the treatment of bark gouging compared to manual debarking in reducing densities of *I. typographus* from an economic point of view? Manual debarking is a labor-intensive, but very effective, technique for the regulation of bark beetles. Due to its practicality in steep terrain, it is widely applied as the primary method for reducing bark beetles in the remaining breeding material found in mountain areas. Here, the retention of dead wood reduces the risk of avalanches (Caduff et al., 2022; Wohlgemuth et al., 2017) and rock fall (Ringenbach et al., 2022) in forests with protective functions to mitigate or prevent natural hazards (Brang et al., 2006; Moos et al., 2018; Perzl et al., 2022). Thus, bark gouging could be an alternative to manual debarking in mountain forests, offering higher work productivity, while effectively regulating bark beetle populations.

Second, how effective is bark gouging for pest control if the phloem is not sufficiently cut? This is an urgent question because current technical solutions of bark gouging highly depend on personal handling and thus lead to differences in accuracy of phloem disruption, which could result in reduced pest control. Finally, the effects on non-target biodiversity need to be considered as well in the comparison and are an indication for nature conservation value, in case the wood biomass remains in the forest.

2.2 Methods

2.2.1 Study area and bark treatments

The study was conducted close to Ruhpolding in the German Alps (47.658 N, 12.540 E) in a forest stand with protective function against gravitational natural hazards. For each of the two research questions a separate set of *P. abies* logs was subjected to the mechanical and manual bark treatments for bark beetle regulation. For the mechanical treatment a debarking device attached on a conventional chainsaw was used with the modified gouging knifes "Streifenmesser Nationalpark Bayrischer Wald" (EDER Maschinenbau GmbH, Wolfenbüttel, Lower Saxony, Germany). The four knifes are mounted parallel in pairs and have a V-shape to gouge the bark every 16 mm with a width of 14 mm (Fig. 2.1a, Fig. S2.1). A gouging depth of 14-16 mm is reliable for most trees, while for logs with a thick bark the depth can be adjusted to up to 20 mm to ensure disruption of phloem. Previous studies have already compared the debarking and gouging device for chainsaw attachment in regards to work productivity (economic costs) and pest control efficiency (Hagge, Leibl, et al., 2019). Here, we focus on the comparison between mechanical gouging and manual debarking. Manual debarking removes the bark of the logs completely using a debarking spud and is still very common in alpine regions (Fig. 2.1a).

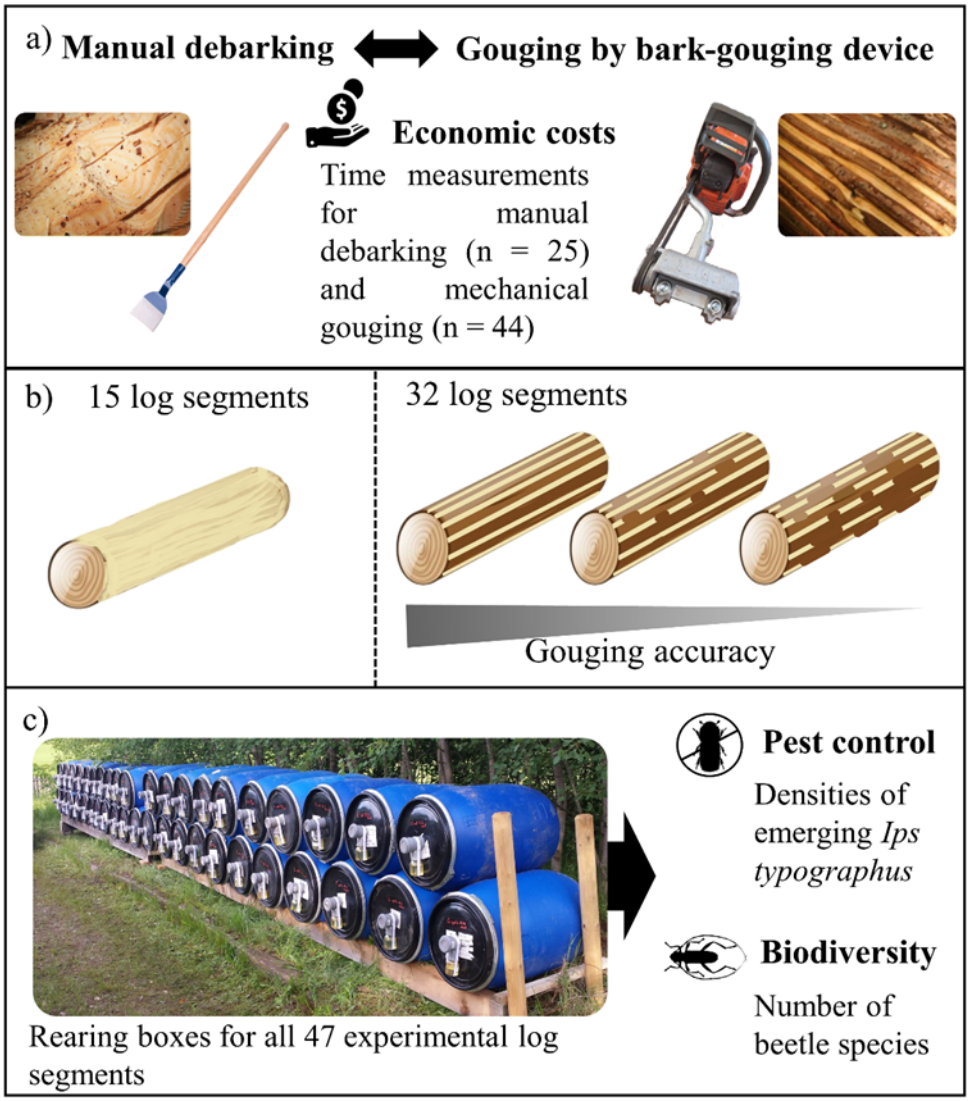

Figure 2.1: Experimental design: Comparison of manual debarking with mechanical bark gouging and the effect of gouging accuracy. a) A debarking spud and a modified debarking device mounted on a chainsaw were compared in time completing the treatment (n = 69 *Picea abies* logs) as a measure of work productivity and surrogate of economic costs. b) A second set of logs were manually debarked and gouged after *Ips typographus* colonization. 47 Segments with a length of 70 cm were included for the study and for the gouged segments proportion of incomplete gouging stripes was assessed as a measure of accuracy. c) After the treatment, segments were put into rearing boxes for 2 years to collect densities of emerging I. typographus as a proxy for pest control and number of collected beetle species as a representation of biodiversity.

2.2.2 Work productivity mirroring economic costs

To evaluate the work productivity, we recorded the time needed to complete the two bark treatments on felled spruce trees following standard procedure. For the time study the bark

of *P. abies* logs was manually removed with a debarking spud (n = 25; 0.47 m3 ± 0.28 SD; diameter at breast height (DBH): 17.6 cm ± 4.1) and gouged with the modified debarking device (n = 44; 0.59 m^3 ± 0.35; DBH: 19.4 cm ± 5.1; Fig. 2.1a) by four professional forest workers. Time measurements started with cutting off the root plate and ended when bark treatments were completed for the entire logs. In the subsequent analysis, we used the time needed to complete bark treatment standardized by tree volume (m^3 per hour) as our response variable (work productivity) and surrogate of economic costs (Thorn et al., 2016). To test for differences between the two bark treatments we used a linear mixed model with Gaussian normal distribution and reduced maximum likelihood (REML) provided in the function *lmer* from the lme4 package (Bates et al., 2015). We treated the four different forest workers as random term to account for differences in skill and experience.

2.2.3 Pest control and biodiversity

For the evaluation of pest control and biodiversity a separate set of 47 *P. abies* logs were experimentally exposed to I. typographus colonization during spring and summer 2019 with swarming periods in late April, early June and late July. After successful colonization, the logs were manually debarked (n = 15; diameter: 25.3 cm ± 2.2) and mechanically gouged (n = 32; diameter: 27.6 cm ± 2.5) in June, August and September 2019 in accordance to the three swarming periods. Logs were cut into 70 cm segments, and segments with varying levels of gouging accuracy were selected from the gouged logs to represent a gradient. Subsequently, we assessed the proportion of gouging stripes that did not have a complete disruption of phloem over the full segment length of 70 cm, relative to all stripes. In the analysis of pest control and biodiversity, the proportion of incomplete stripes was used as a measure of accuracy and as a proxy for bark cover, i.e. the proportion of undisturbed bark beetle breeding habitat (Fig. 2.1b). The log segments were put into rearing boxes to collect all emerging beetles over a two-year period (Fig. 2.1c). This method of in situ rearing of experimental log segments is representative for pest control and the species densities of beetles emerging in the field (Hagge, Leibl, et al., 2019). The number of emerging I. typographus, standardized by the bark surface area of the respective log segment (individuals per m^2), was used as proxy for pest control. Because 37.5 % of the observations recorded zero *I. typographus* instances in the pest control data, we applied a zero-inflated model with Poisson error distribution (function *zeroinfl* from the package pscl (Jackman et al., 2023)). Additionally, we tested the effect of gouging accuracy on the abundance of non-target

beetles (25% observations with zero) based on the same model. F-statistic and p-values for the zero inflation models were calculated with the function *Anova* from the package car (Fox et al., 2023). The number of emerging beetle species is representing the effect on biodiversity. We used a linear regression model to test the effect of gouging accuracy on biodiversity in the 32 log segments. The number of beetle species per segment as the dependent variable was log-transformed to meet model assumptions of residual normality. To control for the differences in surface area of the logs it was included as predictor variable in the biodiversity model. Percentage of failed gouges as a measure of accuracy was used as predictor variable in all models. Additionally, we analyzed the differences in community assemblages in relation to gouging accuracy using non-metric multidimensional scaling (NMDS) based on bray Curtis dissimilarity matrix (functions *metaNMDS* and *envfit* from the package vegan (Oksanen et al., 2022)). All data analyses were performed with R version 4.1.2 (R Core Team, 2022).

We collected natural emergence densities of *I. typographus* provided by eight experimental studies (Table A2.3) to calculate pest control efficiency of our results. We only included the values based on cut or wind felled *P. abies* trees without pest control measures applied. From the given quantities, based on bark samples or emergence traps, we calculated or extracted the mean and standard error of beetles emerging per surface area. To represent logs with high and low accuracy we divided our results into below and above 50% gouging accuracy in the comparison.

2.3 Results

2.3.1 Work productivity mirroring economic costs

With a mean of 3.2 m^3 of spruce timber processed per hour bark gouging was twice as fast as manual debarking with 1.6 m^3 per hour ($F_{1, 67} = 36.07$, $p < 0.001$, Fig. 2.2). Conditional and marginal r^2 are equal ($r_c^2 = r_m^2 = 0.35$) and the intraclass correlation coefficient (ICC) cannot be calculated. Hence, the variance in work productivity between forest workers has no effect on the overall variance in the data (see Table A2.1).

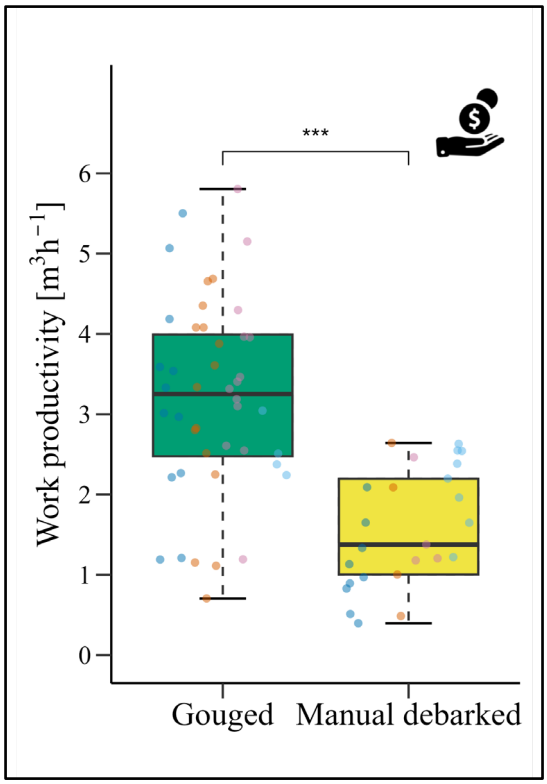

Figure 2.2: Comparison of work productivity mirroring economic costs for gouged and manual debarked logs measured as the processed timber volume per hour. Boxes represent the interquartile range with median value indicated by bold line and whiskers at quartile ±1.5 * interquartile range. Points represent single measurements for mechanical gouging (n = 44) and manual debarking (n = 25) with different colors for each of the four forest workers. The three asterisks indicating significant ($p < 0.001$) differences according to the linear mixed model.

2.3.2 Pest control and biodiversity

In total, we sampled 360 beetles belonging to 32 species reared from the 47 experimental log segments over the two-year period. The most abundant species were I. typographus (204

individuals) and *Serropalpus barbatus* (60 individuals). However, no *I. typographus* and only three individuals of *Glischrochilus quadripunctatus* emerged from only one of the 15 completely debarked log segments (see Table A2).

The density of emerged I. typographus ($p = 0.001$, $F_{1, 28} = 15.04$; Table A2.3), the number of beetle species ($p = 0.046$, $F_{2, 29} = 2.43$, Fig. 3), and the abundance of non-target beetles ($p = 0.223$, $F_{1, 28} = 5.85$, Table A2.4, Fig. A2.2) per segment significantly increased with an increasing portion of incomplete gouges (Fig. 2.3, Table A2.2). In the biodiversity model 8% of the variance in the data (r^2) can be explained by the proportion of incomplete stripes.

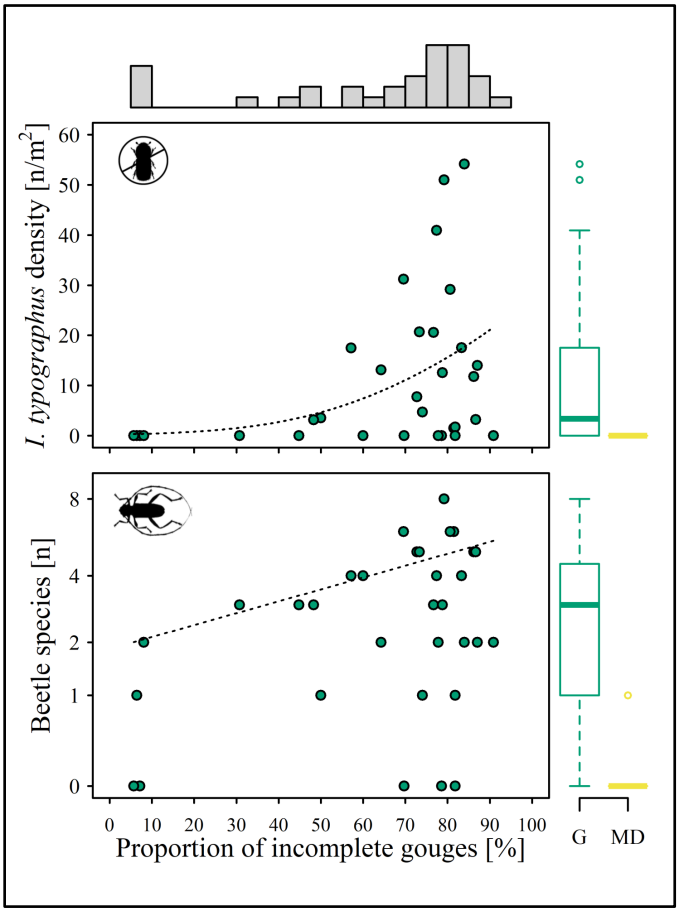

Figure 2.3: Effect of gouging accuracy on pest control and beetle species: Density of *Ips typographus* per m2 of bark surface and number of beetle species emerging from gouged *Picea abies* log segments in response to gouging accuracy. The histogram above indicates the frequency distribution of the 32 gouged log segments to proportion of incomplete stripes. The dashed lines correspond to the model fits. Boxplots on the right show the distribution of the two dependent variables for gouged (G) and the 15 manually debarked (MD) segments. Note the log-scale for the y-axis in the biodiversity model.

Compared to the mean number of I. typographus per square meter (800 beetles per m²) derived from 8 studies (see Table A5) pest control efficiency is at 99.9% for logs with more than 50% continuous gouging stripes (1 ± 0.5 (SE) per m², n = 8) and 98.1% for logs with an accuracy of less than 50% (15 ± 3.3 (SE) per m², n = 24). Even when related to the lowest population density, which was recorded for univoltine populations at high altitude in the Alps (352 per m²; Wermelinger et al., 2013), the efficiency for the low accuracy gouging is at 95.7% (see Fig. 4).

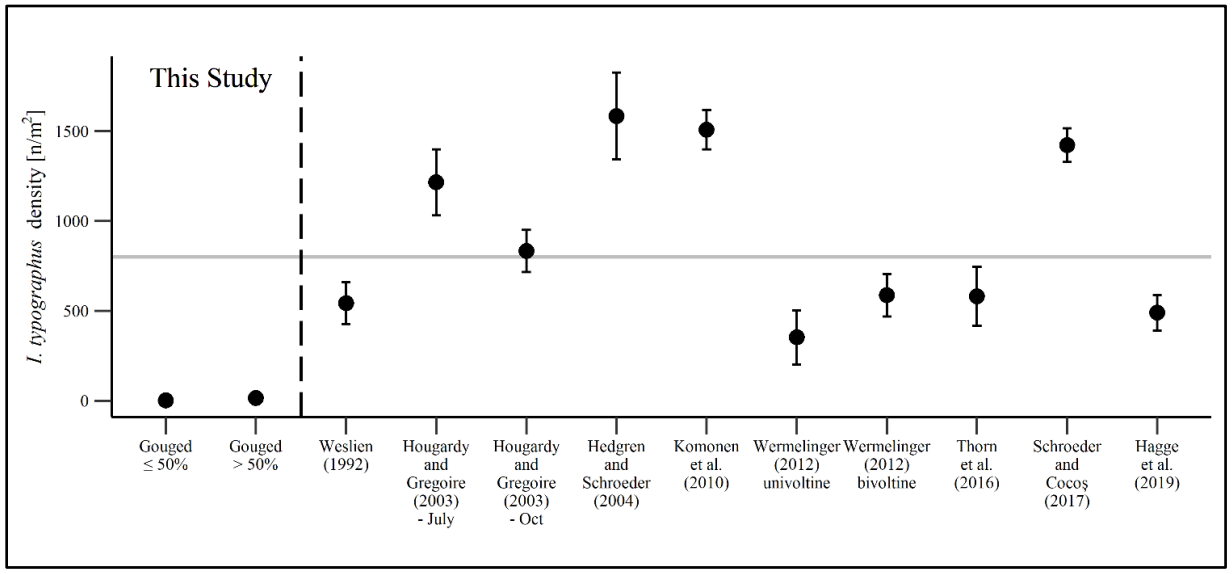

Figure 2.4: Density of Ips typographus per m² of bark surface. Points indicate the mean and bars the respective standard error (SE). Data from this study (left side) the results of the gouged log segments are separated for logs with greater than or equal to 50% continuous gouges (n = 8) and less than 50% accuracy (n = 24). For logs without pest control treatment, we show data extracted from Weslien, (1992), Hougardy and Gregoire (2003), Hedgren and Schroeder (2004), Komonen et al. (2011), (Wermelinger et al., 2012), Thorn et al. (2016), Schroeder and Cocoş, 2018, Hagge, Leibl, et al. (2019) for comparison. The grey horizontal line is indicating the mean value of 800 beetles per m² (see Table A2.5 for more information on the respective studies).

2.4 Discussion

While disturbances in European *P. abies* forests are on the rise, there is also an increasing need for the preservation of biodiversity through means such as retention forestry. Thus, we endorse bark gouging as an economic and conservation friendly pest control intervention to combine the regulation of *I. typographus* populations with the retention of dead wood biomass, particularly in inaccessible terrain or at small scales. Bark gouging has an economic advantage to manual debarking, since double the amount of *P. abies* logs can be treated to control *I. typographus* populations (Fig. 2.2). When compared to natural emergence densities, the pest control efficiency of bark gouging is even with a low accuracy (less than 50% of gouging stripes continuously cut) very high (Fig. 2.4). This will allow forest workers to work also under challenging conditions and process a higher amount of breeding material. The number of beetle species is reduced when the gouging stripes are more consistently removed and less bark remains intact (Fig. 2.3), confirming bark gouging as the conservation friendly alternative to complete (manual) debarking.

2.4.1 Bark gouging cost half of manual debarking

We highly recommend the conversion of pest management of *I. typographus* from manual debarking with spud to machinery bark gouging. To prevent outbreaks also without necessity of removal, with bark gouging breeding material can be made unsuitable more efficiently. Solely for forests in the alpine region this accounts for annually 25.000 m^3 of manually debarked timber in the administration of the Bavarian state forests (BaySf, 2022). Here, approximately 7800 workhours can be saved every year with bark gouging. Together with the concomitant benefits of bark gouging in protected areas and in forest mires (Hagge, Leibl, et al., 2019; Thorn et al., 2016), the economic benefits of bark gouging compared to manual debarking is relevant for a wider range of applications. In general, acquisition and maintenance cost are higher for the bark gouging device. Nevertheless, labor costs take up the main share for (motor) manual work assignments in forestry. Initial and regular expenses for the gouging device will recoup quickly due to the higher output per work hour. While accurate delimbing is essential for manual debarking, with the bark gouging device small remnants of branches can also be milled away mechanically. Otherwise, the debarking spud is light and flexible which is particularly beneficial in challenging or steep terrain and could oppose the economic advantage of the gouging device in for example mountain forests.

Productivity with the motor- manual devices is likely lower in rugged terrain, since forest workers need to find a secure stand before performing the work and have to carry more weight. However, the overall physical demand on forest workers is higher when the debarking is done manually. If the wood is not fresh the strength needed to separate the bark from the wood is increasing (Duchesne & Nylinder, 1996), which in the case of the bark gouging device is carried out motorized. The time study of this experiment was based on logs with relatively small diameters and hence thin bark that can be removed with less effort than from trees with larger diameters. Consequently, the economic advantage of the bark gouging device is likely to increase with larger diameters. Yet, work conditions like different work experience, challenging terrain and contract work can lead to a decrease in gouging accuracy with this relatively new device. When less focus is placed on the accuracy, the amount of wood that can be treated should increase, thereby reducing economic costs even further. Nonetheless, with enough bark intact to support high densities of bark beetles emerging, pest control efficiency could be reduced.

2.4.2 Bark gouging controls *Ips typographus* outbreaks also with low accuracy

We demonstrate with our results that even when the phloem is not cut on the full length and gouging stripes are not continuous *I. typographus* populations can be reduced sufficiently. When compared to natural emergence densities, we were able to determine that the number of emerging I. typographus is reduced by at least 95.7% even with a gouging accuracy below 50% (Fig. 2.3). With salvage logging after i.e. wind disturbance, *I. typographus* populations are reduced by about 90% when compared to unlogged areas (Thorn et al., 2014). Consequently, beetles can still emerge in high numbers from the logging residues, i.e. remaining stumps and crowns. Since pest control efficiency is also sufficient with low accuracy and more wood can be processed than with manual debarking, with gouging additional capacities can be expected to increase focus on the treatment of residues. The logs with gouged bark can then remain in the forest without threatening nearby commercial *P. abies* forests. Therefore, we can recommend bark gouging under field conditions where accuracies can be expected to variegate. We also suggest that the continuity of phloem disruption is not the most important factor for successful pest control, but rather the amount of potential breeding material treated.

Bark gouging destroys the majority of the existing beetle larvae and galleries mechanically. The remaining bark stripes dry out quickly and are thus unsuitable as food source for

surviving larvae or further colonization (Hagge, Leibl, et al., 2019). If bigger pieces of infested bark remain sufficiently intact (i.e. gouging with low accuracy) the ability to expand remaining breeding galleries is limited. Subsequently, this leads to a high colonization density and competition for the leftover sugar reserves in the phloem before it dries out. With increasing colonization density, the impact of pathogens intensifies (Wegensteiner & Weiser, 1996), while the size and fitness of the offspring can also be negatively affected from the intraspecific competition for the limited foraging resources (Anderbrant et al., 1985; Salle et al., 2005). Consequently, with the reduction of breeding area not only the number of emerging beetles is reduced, but also their fitness and ability to spread might be compromised. Henceforward, research also needs to study the possible impairment of relevant traits in bark beetle populations emerging from trees with partly removed bark.

Besides, we confirmed the applicability of the traditional method of manual debarking with a pest control efficiency of 100% for *I. typographus* in *P. abies* logs. Nonetheless, it is important to consider, that early intervention (maximum five weeks after colonization) is imperative for this method to assure desiccation of larvae. In case the larval stage is already surpassed the fully developed beetles can finish their lifecycle also in the detached bark pieces. Thus, guidelines recommend to burn, chip, cover, or remove the residues (Kautz et al., 2021) or use the debarking device, which is milling the bark in small pieces and mechanically decimates also fully developed beetles. In the case of late intervention, we can therefore advise to preferably use bark gouging over manual debarking. Given that bark gouging is based on the debarking device, yet with less area of contact, bark beetle populations can be reduced correspondingly, but to a lower extent.

2.4.3 Bark gouging for biodiversity and dead wood retention

Our results for the impact on the non-target beetle species diversity indicate that increasing gouging accuracy and consequently a decrease of intact bark has a compromising effect on the number of species. Dead wood from bark beetle outbreaks is an important resource for many species and a crucial element for forest biodiversity and nature conservation (Müller et al., 2010). To reduce the impact of pest control on natural processes and to maximize habitat functionality it is vital to only apply the minimum required intensity of intervention. Manual debarking, in contrast, is removing the bark very accurately and, accordingly, only one beetle species emerged from the completely debarked segments (Fig. 2.2, Table A2.2). Even when the bark was gouged with high precision and less than 50% of the gouging stripes

were interrupted, on average two beetle species emerged from the experimental log segments. The abundance of non-target beetles increased with the proportion of incomplete gauges (Fig. A2). However, gouging accuracy had no significant effect on community composition of beetles ($r^2 = 0.07$, $p = 0.499$, Fig. A3).

Especially in early decay stages the bark is an important source for nutrients supporting a wide variety of specialized saproxylic species (Parisi et al., 2018; Ulyshen, 2018). Due to the phloem, the tissue to transport photosynthetic products in life trees, carbon and nutrient concentration are higher in the bark than xylem (Martin et al., 2015). Following the species energy theory (Wright, 1983), this means that the increased nutritional capacity can support a wider range of species when bark remains on the log. Additionally, as a protective outer layer the bark regulates the moisture content as well as the decomposition of the underlying biomass. Thus, it acts as an environmental filter in the early stages of species assembly in decaying wood (Dossa et al., 2018; Zuo et al., 2016) which in turn affects the later community composition and decomposition rates. Therefore, we are further endorsing the importance of bark as a structural component of dead wood supporting biodiversity in forests. Previous studies already indicated that bark gouging maintains natural levels of biodiversity in dead wood, while the complete removal of bark is significantly reducing it (Hagge, Leibl, et al., 2019; Thorn et al., 2016). This reduction in beetle biodiversity, abundance and structural integrity of the dead wood can also negatively influence higher trophic levels like i.e. foraging woodpeckers (Thorn et al., 2016).

However, first and foremost, it is imperative to retain and accumulate dead wood biomass in protected as well as commercial forests (Müller & Bütler, 2010). On the one hand, insect outbreaks and the resulting dieback are inherent parts in coniferous forest dynamics (Franklin et al., 2002). On the other hand, salvage logging after wind disturbance or bark beetle infestations is even in protected areas a common management response (Lindenmayer et al., 2017; Müller et al., 2019). Here, the effectiveness of pest control interventions is currently debated due to the concurrent reduction in natural control agents (i.e. pathogens and predators), which usually limit pest outbreaks (Vanická et al., 2020). In fact, due to salvage logging after disturbances important forest functions as well as services can be degraded (Leverkus et al., 2020; Lindenmayer & Noss, 2006; Mayer et al., 2022). To uphold specified species diversity in disturbed forests it is beneficial to sustain unlogged areas with dead wood biomass (Thorn, Chao, et al., 2020). Saproxylic diversity does not depend solely

on the availability of dead wood, but also its dimensions, exposition and quality (Müller et al., 2015; Seibold et al., 2015; Thorn, Seibold, et al., 2020). In accordance to our results, the quality of the wood for beetle biodiversity is increasing the more bark remains intact. Thus, with bark gouging important structural components of dead wood can be uphold after pest control. The integration into pest control operations will support biodiversity conservation efforts, without subsequent risks for timber production.

2.4.4 Management recommendations

This is particularly applicable for the 39% of European protected areas which are overlapping with the range of Norway spruce (Hagge, Leibl, et al., 2019) and hence susceptible to natural disturbances, such as bark beetle outbreaks following windstorms (Thorn et al., 2016). These areas include national parks, where a potential pest management must fulfil the additional requirements of biodiversity protection, environmental education, and recreation (IUCN primary objective of a national park; www.iucn.org). Consequently, bark beetle control measures which are poorly perceived by national park visitors may potentially lower the recreational value of the respective protected area (Berto, 2005). However, pest control interventions within protected areas are a common response to mitigate their spread and protect economic interests (Hlásny et al., 2021; Lindenmayer et al., 2017; Müller et al., 2019). To avoid large scale salvage logging in protected areas with all its negative effects we endorse to also integrate bark gouging as well as motor-manual debarking to slow down the spread and establish pest free buffer zones. In commercial forests, bark gouging and motor-manual debarking can particularly provide advantages in small-scale disturbances where transport and harvesting cost exceed profits from timber sales. In mountain forests, where accessibility for machinery is not given or very costly, pest control treatments based on manpower are often the only economic option. Thus, manual debarking is, based on authors experience working in alpine forestry, still the most prominent treatment for bark beetle regulation. The retention of dead wood provides valuable protection for infrastructure and people (Caduff et al., 2022; Ringenbach et al., 2022). The Bavarian state forestry already endorses mechanical bark gouging as a forest protection measure not only due to the economic, but also ecological, advantages. Logs designated for biomass retention are recommended to be gouged instead of debarked for preventative as well as early therapeutic treatment (BaySf, 2022). When compared to the currently available alternatives manual debarking and motor-manual debarking, 100% or 28% more wood can

be treated with the bark gouging device in the same time, respectively. Completely mechanized methods (i.e. modified heads of harvesters for debarking) for the treatment of breeding material are a possible forest protection measures for large scales (Heppelmann, Labelle, Wittkopf, et al., 2019; Mergl et al., 2021). Nevertheless, pest control efficiency has only been investigated at small scales (Delb et al., 2021) and needs yet to be confirmed.

2.5 Conclusions

We highlight bark gouging as comprehensive bark beetle management option for biomass retention, especially in areas set aside for biodiversity conservation, recreation and protection. Also, with a low accuracy, gouging of the bark has comparable—and thus sufficient—pest control efficiency to salvage logging or debarking. With the current increase in climate change impacts, one of the main concerns for forest management is the integration of unpredictable disturbance regimes. We endorse the practicality and effectiveness of bark gouging as a conservation friendly method for bark beetle regulation. Particularly, in mountain forests, protected areas and small-scale bark beetle infestations this economic forest protection intervention enables foresters to retain dead wood after disturbances. This is imperative to sustain protective functions, natural regeneration and biodiversity, as well as other ecosystem services.

Appendix

Acknowledgments

We are grateful for the support from the Forestry Enterprise of Ruhpolding in particular Ludwig Huber, Dejan Kolesar and Richard Partholl for providing experimental resources and for conducting the bark treatments for the time study and the experimental logs. We would also like to thank the Bavarian Forest National Park for providing the facilities of emergence barrels.

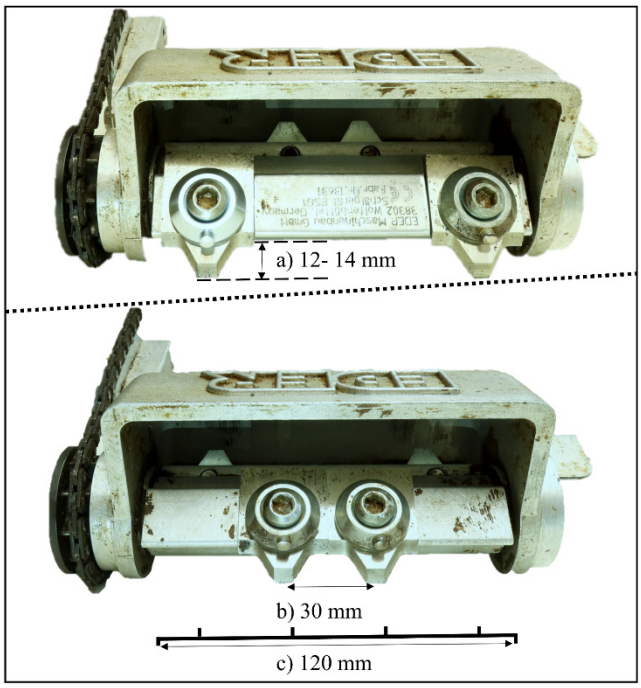

Figure A2.1: Debarking device with the rotating cylinder at two positions and the modified knifes for bark gouging. Dimensions for a) the adjustable depth for different bark thickness, b) the distance between the tips of the v-shaped knives and c) the width of treatment area are given.

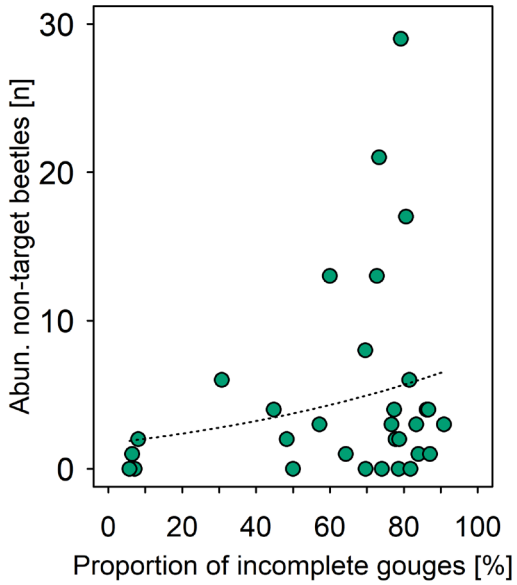

Figure A2.2: Abundance of non-target beetle species emerging from gouged Picea abies log segments in response to proportion of incomplete stripes. The dashed line indicates the fit of the zero-inflation model.

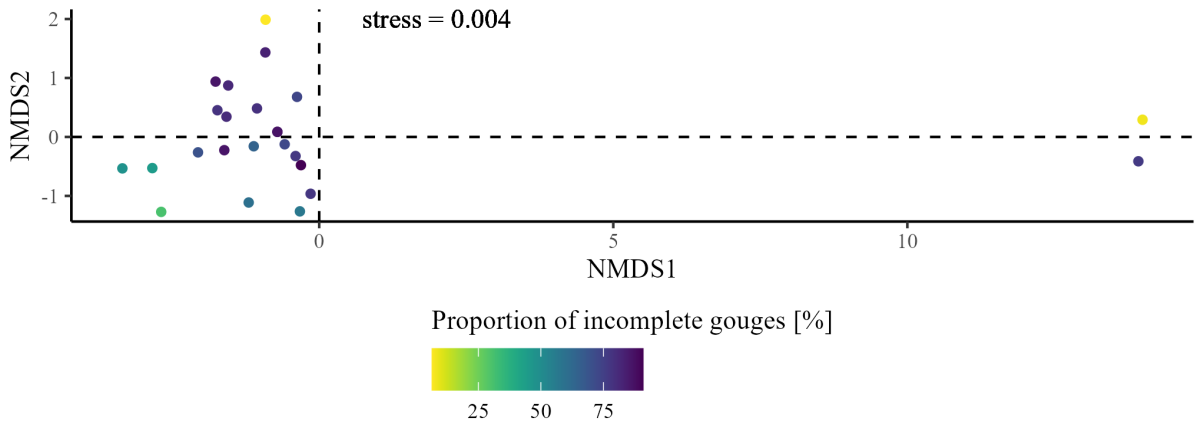

Figure A2.3: Non-metric multidimensional scaling based on Bray-Curtis dissimilarity matrix of non-target beetle species emerging from spruce logs with different gouging accuracy (proportion of incomplete gouges).

Table A2.1: Result table of the linear mixed model with Gaussian distribution for the comparison of work productivity (hours needed for treating one m^3 of spruce wood) between manual debarked and machine gouged logs.

Predictors	**Estimates**	**CI**	***p***
(Intercept)	3.19	2.87 – 3.51	**<0.001**
treat [Manual debarked]	-1.61	-2.15 – -1.08	**<0.001**
Random Effects			
σ^2	1.15		
$\tau_{00\ Name}$	0		
N_{Name}	4		
Observations	69		
Marginal r^2 / Conditional r^2	0.347 / NA		
ICC	NA		

Table A2.2: Beetle species list with total number of emerged individuals from the experimental logs in the rearing barrels for gauged (n = 32) and manual debarked (n = 15) *P. abies* log segments. Species are sorted according to the FHL code and bark beetle species are highlighted bold.

Family	Genus	Species	Author, year	Gouged	Manual debarked
Staphylinidae	*Phloeonomus*	*pusillus*	Gravenhorst, 1806	6	0
Staphylinidae	*Phloeostiba*	*lapponica*	Zetterstedt, 1838	1	0
Staphylinidae	*Placusa*	*depressa*	Mäklin, 1845	1	0
Staphylinidae	*Placusa*	*incompleta*	Sjöberg, 1934	1	0
Staphylinidae	*Homalota*	*plana*	Gyllenhal, 1810	1	0
Staphylinidae	*Anomognathus*	*cuspidatus*	Erichson, 1839	1	0
Staphylinidae	*Leptusa*	*pulchella*	Mannerheim, 1830	2	0
Eucnemidae	*Hylis*	*olexai*	Palm, 1955	1	0
Nitidulidae	*Epuraea*	*marseuli*	Reitter, 1873	1	0
Nitidulidae	*Epuraea*	*pygmaea*	Gyllenhal, 1808	5	0
Nitidulidae	*Glischrochilus*	*quadripunctatus*	Linné, 1758	2	3
Monotomidae	*Rhizophagus*	*dispar*	(Paykull, 1800	2	0
Monotomidae	*Rhizophagus*	*bipustulatus*	Fabricius, 1792	2	0
Cryptophagidae	*Atomaria*	*pulchra*	Erichson, 1846	1	0
Laemophloeidae	*Leptophloeus*	*alternans*	Erichson, 1846	2	0
Mycetophagidae	*Litargus*	*connexus*	Geoffroy, 1785	13	0
Corylophidae	*Arthrolips*	*obscura*	C. R. Sahlberg, 1833	1	0
Corylophidae	*Orthoperus*	*atomus*	Gyllenhal, 1808	1	0
Corylophidae	*Orthoperus*	*corticalis*	L. Redtenbacher, 1845	3	0
Ptinidae	*Microbregma*	*emarginatum*	Duftschmid, 1825	1	0
Scraptiidae	*Anaspis*	*rufilabris*	Gyllenhal, 1827	1	0
Aderidae	*Euglenes*	*oculatus*	Paykull, 1798	1	0
Melandryidae	*Serropalpus*	*barbatus*	Schaller, 1783	60	0
Cerambycidae	*Monochamus*	*sartor*	Fabricius, 1787	4	0
Curculionidae	***Phloeotribus***	***spinulosus***	Rey, 1883	1	0
Curculionidae	***Hylurgops***	***palliatus***	Gyllenhal, 1813	1	0
Family	**Genus**	**Species**	**Author, year**	**Gouged**	**Manual debarked**
Curculionidae	***Crypturgus***	***subcribrosus***	Eggers, 1933	1	0

Curculionidae	***Crypturgus***	***hispidulus***	C. G. Thomson, 1870	1	0
Curculionidae	***Crypturgus***	***pusillus***	Gyllenhal, 1813	12	0
Curculionidae	***Dryocoetes***	***autographus***	Ratzeburg, 1837	16	0
Curculionidae	***Pityogenes***	***chalcographus***	Linné, 1760	7	0
Curculionidae	***Ips***	***typographus***	Linné, 1758	204	0

Table A2.3: Result table of the zero-inflation model with Poisson distribution and binomial link function for emergence density of *Ips typographus* in relation to the proportion of incomplete stripes.

Count model coefficients (Poisson with log link):				
Predictors	**Estimate**	**Std. Error**	**z value**	***p***
(Intercept)	1.296	0.422	3.073	**0.002**
% incomplete gouging stripes	0.021	0.005	3.878	**< 0.000**
Zero-inflation model coefficients (binomial with logit link):				
(Intercept)	2.860	1.515	1.888	0.059
% incomplete gouging stripes	-0.053	0.022	-2.418	**0.015**
Log-likelihood: -178.5 on 4 Df				

Table A2.4: Result table of the zero-inflation model with Poisson distribution and binomial link function for abundance of non-target beetles in relation to the proportion of incomplete stripes.

Count model coefficients (Poisson with log link):				
Predictors	**Estimate**	**Std. Error**	**z value**	***p***
(Intercept)	1.018	0.273	3.735	**< 0.000**
% incomplete gouging stripes	0.0212	0.004	6.133	**< 0.000**
Zero-inflation model coefficients (binomial with logit link):				
(Intercept)	-0.420	1.112	-0.375	0.708
% incomplete gouging stripes	-0.022	0.018	-1.234	0.217
Log-likelihood: -125.3 on 4 Df				

Table A2.5: Studies with their mean and Standard error (SE) for the emergence density of *Ips typographus* from *Picea abies* trees (n) with location and applied methodologies.

Study	**Mean**	**SE**	**n**	**Methods**
Weslien (1992)	543	116.8	6	central Sweden, from 2 trees, 70 cm bolts, pheromone baited colonization, 8 weeks exposed and then put into emergence trap

Hougardy (2003) - July	1215	184.0	10	France, year: 2000, windblown trees, 54 * 1 dm2 bark disks per tree
Hougardy (2003) - Oct	833	116.7	10	France, year: 2000, windblown trees, 54 * 1 dm2 bark disks per tree
Hedgren and Schroeder (2004)	1584	242	21	southern Sweden, 6 sites, felled trees, 45 cm bolts in emergence traps
Komonen et al. (2010)	1508	108.5	118	southern Sweden, wind felled trees, 100 m line transects (n = 21), 15 * 45 cm bark sample at intersection, every third sample (n = 118) number of exit holes was counted
Wermelinger (2012) - univoltine	352.6	151.0	10	Switzerland, 950-1030 m a.s.l., summer flight, emergence traps on 10 trees (lying and standing) over 3 years
Wermelinger (2012) - bivoltine	586.4	117.5	10	Switzerland, 545 m a.s.l., summer flight, emergence traps on 10 trees (lying and standing) over 3 years
Thorn et al. (2016)	581.1	163.8	12	Germany, Bavarian Forest National Park. uprooted tree, stem emergence trap
Schroeder et al. (2017)	1422	94.0	67	northern Sweden, storm felled tree, 15*45cm bark samples, exit holes and live beetles
Hagge et al. (2019)	490.3	98.9	12	Germany, Bavarian Forest National Park, felled trees, stem emergence trap and 70 cm bolts in rearing barrels

Chapter 3: Debarking harvesters simultaneously combat the European spruce bark beetle (*Ips typographus*) and conserve non-target beetle diversity

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Abstract

1. In the face of climate change, the European Spruce Bark Beetle (*Ips typographus*) breeding predominantly in Norway spruce (*Picea abies*) led to exceptional amounts of damaged timber in European forests. Up to now, if pest control is applied, damaged or weakened *P. abies* trees are either extracted by salvage logging or, when quantities are low, made unsuitable for breeding by manual debarking techniques. Both pest control interventions are costly, are often limited by the short timeframe of effectiveness and come with negative impacts on the non-target biodiversity.

2. As alternatives for timely removal, a debarking head for harvesters for large scale disturbances and a bark gouging device for motor-manual treatment have been developed in recent years to make breeding material unsuitable for bark beetles and reduce existing larvae.

3. Based on data from an experimental design with infested Norway spruce logs, we show that the harvester debarking head and the motor-manual bark gouging regulate *I. typographus* populations efficiently, whereas a conventional harvester did not reduce the emerging bark beetles. Species assemblages of non-target beetles living in the infested Norway spruce logs were altered from the natural species assemblages in control logs by processing logs with the debarking head or the bark gouging device but not by the conventional harvester. None of the bark treatments reduced non-target beetle species richness in this experiment.

4. Practical implication: We endorse the debarking head and bark gouging as alternatives to salvage logging and manual debarking. This uncouples pest control from in-time

dependencies on the availability of transport capacities. The debarking head and bark gouging open up the opportunity to retain dead wood biomass in the forest, supporting ecological benefits and conservation goals. Particularly for protected areas these two new management options better balance requirements of pest control and biodiversity conservation.

3.1 Introduction

Norway Spruce (*Picea abies* (L.) H. Karst.) is still the most economically important and abundant tree species in Europe (Schelhaas et al., 2018). *Picea abies* plantations for timber production are widely distributed in Europe, extending outside of their natural range (Hagge, Leibl, et al., 2019). Facilitated by preceding windstorms (Seidl & Rammer, 2017) and droughts (Marini et al., 2017)the European bark beetle (*Ips typographus* (Linnaeus, 1758)) is the major pest insect in Europe's forests, causing more than 50% of the annual *P. abies* timber harvest for some countries in recent years (Hlásny et al., 2019; Patacca et al., 2023).Windstorms are currently the most important disturbance agent in European forests (Seidl et al., 2017), with a projected climate change induced increase (Seidl, Schelhaas, et al., 2014). The abundance of damaged timber, serving as breeding substrate, in combination with favorable weather conditions for reproduction, promotes rapid population build-ups of *I. typographus*, enabling it to overcome natural defense mechanisms even of healthy spruce trees ((Biedermann et al., 2019; Netherer et al., 2019). Consequently, the disturbance regime of bark beetle outbreaks is amplified by the interaction with climatic extremes (Seidl & Rammer, 2017).

Insect outbreaks and the resulting canopy dieback are inherent elements of *P. abies* forest dynamics (Franklin et al., 2002) and play a key role for natural regeneration and biodiversity (Müller et al., 2008). Many species profit from the increased light availability, interior edges and the resource pulse of deadwood after disturbance (Beudert et al., 2015; Busse et al., 2022; Hilmers et al., 2018; Lehnert et al., 2013). The remaining dead biomass can increase ecosystem resilience by maintaining nutrient, water and carbon cycles (Leverkus et al., 2020). Windstorms and bark beetle outbreaks contribute to the transition of conventionally managed spruce forests to more heterogeneous, near-natural forests (Thorn et al., 2017).

Particularly in recent years, *I. typographus* outbreaks have caused large financial losses (Hlásny et al., 2021). The most common measure to halt eruptions of *I. typographus* after

windstorms or infestation of weakened trees, is the timely removal of suitable breeding material away from potential host trees within the first five weeks of infestation (Hoch et al., 2020; Schroeder & Lindelow, 2002; Wermelinger, 2004). This prevention measure of pest control seems only successful when 80-95% of (infected) trees and logs are detected and removed before beetles emerge (Dobor et al., 2020; Fahse & Heurich, 2011). However, when trees are affected at a landscape scale, capacities for wood transport often become limited and the retention of logs in the forest can minimize harvest costs and offset low timber prices (Toth et al., 2020). To counteract temporal bottlenecks in work capacity and to buffer price fluctuations, a temporary storage of infested timber in forests is an often-applied strategy. Nevertheless, it has to be secured that no *I. typographus* emerge from this intermediate storage of timber. The application of pesticides, plastic foil for wrapping or wet storage are effective measures, yet are accompanied with high additional costs and likely negative concomitant effects on the environment (Hlásny et al., 2019).

Integrated pest control methods that enable natural dynamics by retention of tree biomass after disturbances are especially needed for about 40% of Europe's protected areas within in the natural range of *P. abies* (Hagge, Leibl, et al., 2019). Particularly in national parks the pest management must fulfill the requirements of biodiversity conservation, environmental education, and recreation (IUCN primary objective of a national park; www.iucn.org, (Schiermeier, 2017). Owners of forests for timber production bordering protected areas identified these areas as a risk for their management goals and as the source of uncontrolled *I. typographus* outbreaks (Müller & Imhof, 2019). This conflict led to designated buffer zones with pest control interventions around strictly protected areas, where a "benign neglect strategy" is often applied for bark beetle outbreaks to allow for natural dynamics (Hlásny et al., 2021; Müller et al., 2010). To mitigate interactions and safeguard nearby timber production, salvage logging after wind disturbance or bark beetle infestations is a common management response in these buffer zones and sometimes also in the entire areas of protected areas (Lindenmayer et al., 2017; Müller et al., 2019; Schiermeier, 2017).

However, removing biomass is in strict contrast to the concept of conservation areas with natural ecosystem dynamics and without or minimal human interventions. Salvage logging is accompanied by a reduction in saproxylic biodiversity (Georgiev et al., 2020; Müller et al., 2010; Thorn, Chao, et al., 2020) and can decrease ecosystem resilience (Leverkus et al., 2021). Hence, on-site bark beetle control measures, which maintain the tree biomass in the

forest stand and regulate insect pest populations, are increasingly promoted to combine multiple purposes of forest use (Hagge, Leibl, et al., 2019). Recently, new technical solutions have been developed for the treatment of bark beetle breeding material at different scales and conditions.

For successful pest regulation, the bark, as breeding habitat of *I. typographus*, is either removed completely or manipulated in a way that renders the logs unsuitable for reproduction (preventative). In case the logs are already colonized by *I. typographus*, bark treatments need to ensure that no individuals are able emerge from the logs (therapeutic). The optimal time for mechanical treatment of infested logs is during the larval stage (first five weeks), since fully developed beetles can complete their life cycle also in the detached bark (Delb et al., 2021). In case teneral beetles are already present, guidelines recommend to burn, chip, cover, or remove bark residues from the forest ((Kautz et al., 2021; Wermelinger, 2004). In forestry, various techniques of bark manipulation to combat *I. typographus* are practiced. In forests with protective functions, terrain inaccessible by machinery, wetlands and conservation areas, logs are traditionally debarked manually with a debarking spud (flat knife attached on wooden stick; see Chapter 2). For mechanized debarking an attachment for conventional chainsaws with rotating knives has been developed. This device has undergone further development, resulting in a motor-manual bark gouging device that removes approximately 30% of the bark and phloem in regular stripes. This pest control method is more cost-effective than complete debarking and reduces *I. typographus* populations on logged wood greatly (Hagge, Leibl, et al., 2019; Thorn et al., 2016). The rotating knives are milling of the bark in small pieces, which likely also decimates fully developed beetles. Bark gouging is conservation-friendly, as the remaining bark preserves essential habitat functions for other (saproxylic) species (Hagge, Leibl, et al., 2019; Thorn et al., 2016).

Yet, regulating populations of eruptive pests with techniques based on (motor-) manual labor is neither cost effective nor fast enough, when large amounts of breeding substrate need to be processed. In salvage logging operations, conventional harvesters are commonly used to process (infested) *P. abies* logs. The pressure from the feed rollers and delimbing knives results in partial perforation, bruising and removal of the bark. In theory, this already reduces the potential for bark beetle reproduction by destroying existing beetles and larvae and an increasing desiccation of the phloem. However, preliminary studies suggest that damage to

the bark and larvae from salvage logging by conventional harvesters is insufficient to protect remaining trees from eruptive population densities of *I. typographus* (Delb et al., 2021). A fully mechanized solution to remove the bark from large quantities of (infested) logs is the modification of the conventional harvester aggregate for debarking (hereafter referred as debarking head) (Heppelmann, Labelle, Wittkopf, et al., 2019). The feed rollers are replaced with debarking rollers that force the log to rotate. By passing over three times, the delimbing knives remove the bark on the entire surface. Best results of debarking can be expected during the summer months when sap flow is high (Heppelmann, Labelle, Wittkopf, et al., 2019). Up to now, the impact of debarking heads on saproxylic organisms has not been studied, while empirical studies examining the pest control effectiveness are limited to preliminary results (Delb et al., 2021).

In this study we examine the effects of the harvester debarking head on the reproduction of bark beetles and biodiversity of non-target beetle species. In a field experiment, we surveyed logs treated with the harvester debarking head, the conventional harvester head and the motor-manual bark gouging device, and an untreated control group, for *I. typographus* infestation and the biodiversity of emerging beetles. We hypothesize that the extensive bark removal produced by the debarking head decreases the number of emerging *I. typographus* more than all other techniques, but also reduces the number of non-target beetle species and alters their assemblages.

3.2 Materials and Methods

3.2.1 Study area and bark treatments

The study was conducted in the buffer zone of the Bavarian Forest National Park, where active bark beetle interventions are implemented (N 49° 5' 13" E 13° 14' 0"). Forest stands in this area are dominated by *P. abies* and have experienced extensive *I. typographus* outbreaks in the past (Müller et al., 2010). Sixteen *P. abies* trees of similar size, age and with signs of early colonization (white larval stage without teneral beetles) by *I. typographus* were felled in June 2020. All trees met the criteria for removal of the regulations for the buffer zone management and were randomly assigned in groups of four trees to each of the treatments, to account for potential differences in colonization densities between trees. The control trees were felled without any further bark manipulation (Fig. 3.1). After felling, delimbing, and cutting into sections, the second group was treated with the bark gouging device attached on a conventional chainsaw ("Streifenmesser Nationalpark Bayerischer Wald", EDER Maschinenbau GmbH, Wolfenbüttel, Lower Saxony, Germany). The four modified knifes are mounted parallel in pairs and have a V-shape to gouge the bark every 16 mm with a width of 14 mm (Fig. S1). Another group of four trees was felled and processed with a harvester fitted with a conventional aggregate, representing the effect to logs from salvage logging and extraction operations. The last group was debarked using a John Deere 1270 G 8-wheel harvester in combination with a H 480 C debarking head, refitted with 4 debarking rolls and a Eucalyptus measuring wheel (Fig. S2). The bark was completely removed by passing over the logs multiple times (Fig. 3.1).

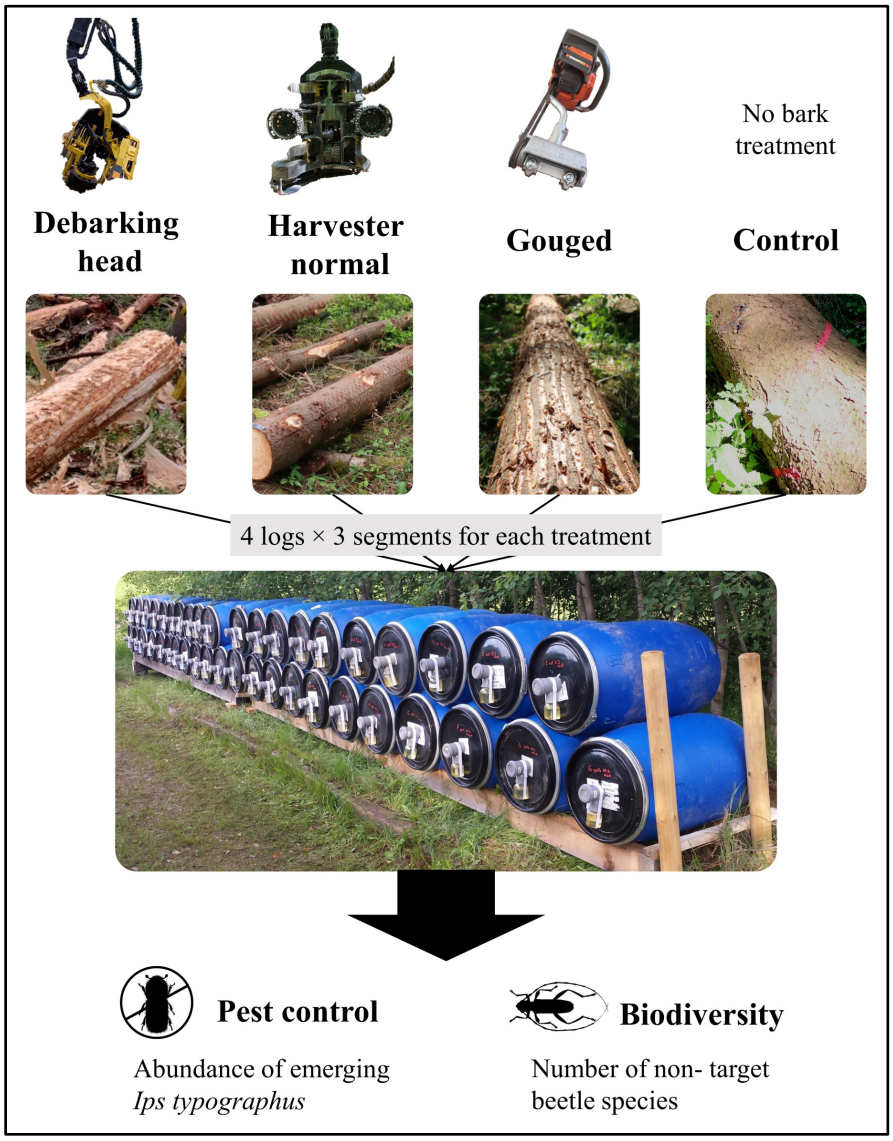

Figure 3.1: Experimental design with the machinery for the treatments and pictures of the condition of the bark on the logs after processing. From each of the four logs per treatment three 70 cm segments were cut out at random locations (n=12) and placed in rearing barrels to assess the abundances of emerging *I. typographus* for pest control efficiency and number of non-target beetle species as a measure of biodiversity.

3.2.3 Sampling

From each log, three segments, measuring 70 cm, were cut out at random locations to account for differences of colonization densities within the logs. Then, the 48 segments (12 per treatment) were placed in rearing barrels to collect abundances of all emerging arthropods from June until October 2020. All beetle species were separated from other arthropods and identified to species level by taxonomic expert Andreas Weigel. The abundance of emerging *I. typographus* was used to assess the pest control efficiency of the bark treatments. The species richness (number of species) and assemblage of non-target beetle species represent the impact of the different treatments on beetle biodiversity with the exclusion of the focal pest species *I. typographu*s.

3.2.3 Data analysis

All statistical analyses were performed in R 4.2.2 (R Core Team, 2022). To adjust for overdispersion in the count data, we used Quasi-Poisson linear models (function *glm)* to test for the effects of the four different bark manipulation treatments on the abundance of *I. typographus* and the number of non-target beetle species. We used multiple comparison tests using the function *glht* in R-package multcomp (Hothorn et al., 2023). Tukey contrasts were specified in the *glht* objects using the *mcp* function. To control for multiple testing in the comparison between treatments we utilized the function *cftest* from the package multcomp (Hothorn et al., 2023) with single-step adjusted p-values. Furthermore, the beetle assemblages were visualized and tested for differences between the treatments by means of non-metric multidimensional scaling (NMDS) using the function *metaMDS* from the R-package vegan (Oksanen et al., 2022). Species with only one or two observations (28 out of 62 non-target species) were removed due to their little contribution to the differences in assemblages in comparison to the more common species. Pairwise analysis of variance based on the Bray-Curtis dissimilarity community matrix were applied by the function *adonis* provided in vegan (Oksanen et al., 2022). P-values were adjusted for multiple testing with *Bonferroni* correction. Additionally, the individual percentage of contribution to the Bray-Curtis dissimilarity for each species was calculated to identify the key species in each community assemblage per treatment using the function *simper* in R-package vegan (Oksanen et al., 2022).

3.3 Results

In total we obtained 13,488 Coleoptera specimens of 63 species (Table A3.1). The four most abundant beetle species accounted for 91% of the individuals. *Dalotia coriaria* (Kraatz, 1856), a generalist predatory rove beetle, was the most abundant species accounting for 32% (n = 4,362) of all sampled beetles, followed by three bark beetle species, *Pityogenes chalcographus* (Linnaeus, 1760) with 21% (n = 2,770), *Ips typographus* with 20% (n = 2,729), and *Crypturgus cinereus* (Herbst, 1794) with 18% (n = 2,440).

3.3.1 Pest control of bark beetles

Both the harvester debarking head and the bark gouging reduced the emerging population of *I. typographus* significantly (Fig. 3.2, Table A3.2). When compared to the control logs (50.5 beetles), only 7.9% (median of 4 beetles) emerged from the logs processed with the debarking head and 3% (1.5 beetles) emerged from logs with gouged bark. Processing the infested logs with a conventional harvester aggregate had no significant effect on the population of *I. typographus* compared to untreated control logs.

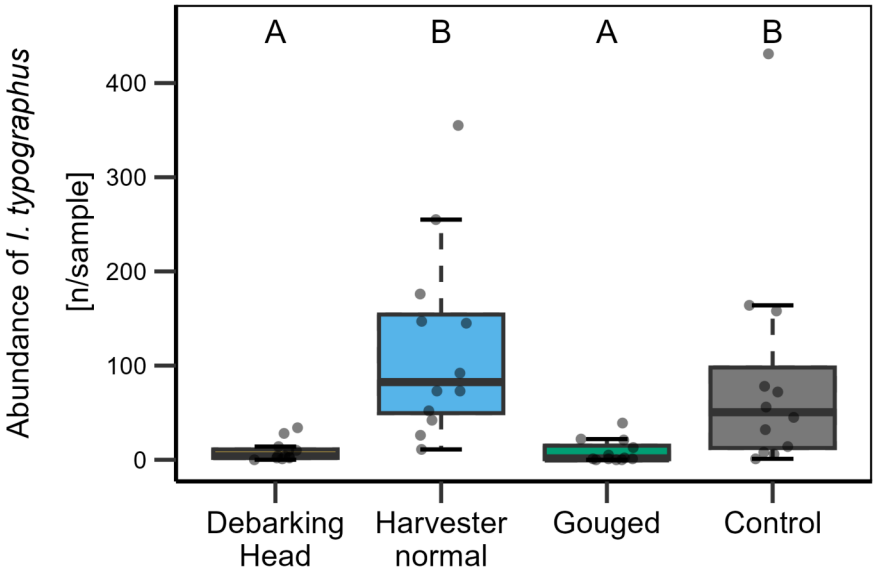

Figure 3.2: Abundance of *Ips typographus* sampled from the four different bark treatments. Points (n = 12) specify the 70 cm segments from *P. abies* logs. Different letters above indicate significant difference between treatments based on the Quasi-Poisson GLMs.

3.3.2 Species richness and assemblage composition of non-target beetles

None of the four treatments had a significant effect on the number of non-target beetle species (see Fig. 3.3, Table A3.2).

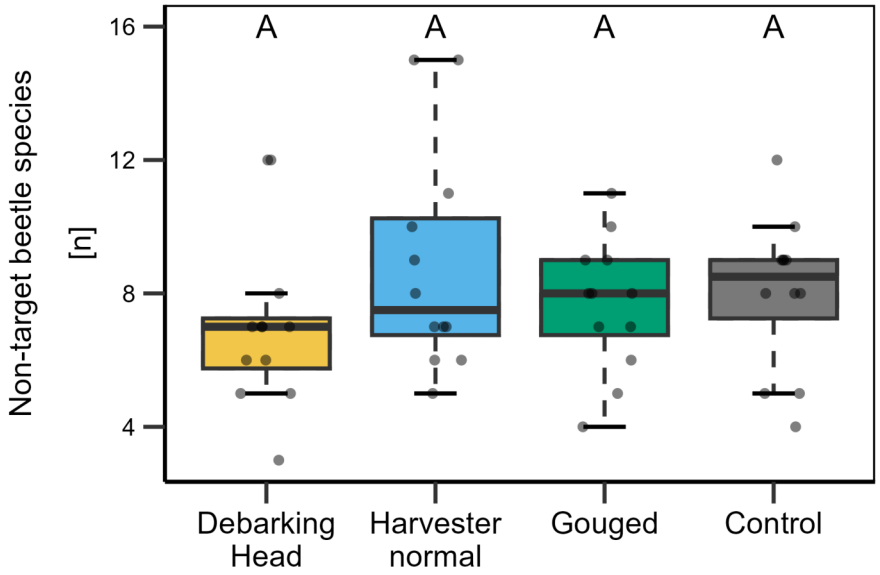

Figure 3.3 Species richness (number of species) of emerged non-target beetles per sample. Points (n=12) indicate the 70 cm segments from *P. abies* logs with four different bark treatments. Letters above indicate significant difference between treatments based on the Quasi-Poisson linear models.

Assemblage composition (NMDS 2D stress = 0.09) of logs treated with the regular harvester did not differ from control logs (P=0.13). However, for all other combinations, assemblage composition of non-target beetles between treatments were different from each other (P<0.05, see Fig. 3.4, Table 3.2). Dissimilarities in assemblages of beetle species between debarking head and control were mostly characterized by *Crypturgus cinereus* (5%), *Placusa depressa* (5%) and *Dalotia coriaria* (4%).While between debarking head and harvester normal *Crypturgus cinereus* (6%), *Crypturgus pusillus* (5%) and *Placusa depressa* (4%) were prevailing, between debarking head and bark gouging *Crypturgus pusillus* (7%), *Crypturgus cinereus* (5%) and *Placusa tachyporoides* (4%) contributed predominantly to differences in assemblages. Dissimilarities in beetle species assemblages between bark gouging and harvester normal were characterized by *Placusa depressa* (5%), *Pityogenes chalcographus* (4%), *Placusa tachyporoides* (3%). *Placusa depressa* (7%), *Dalotia coriaria* (4%), *Crypturgus pusillus* (4%) contributed most to the differences between bark gouging

and control. For differences between control and harvester normal *Pityogenes chalcographus* (4%), *Dalotia coriaria* (4%) and *Crypturgus pusillus* (3%) (Table A3.3).

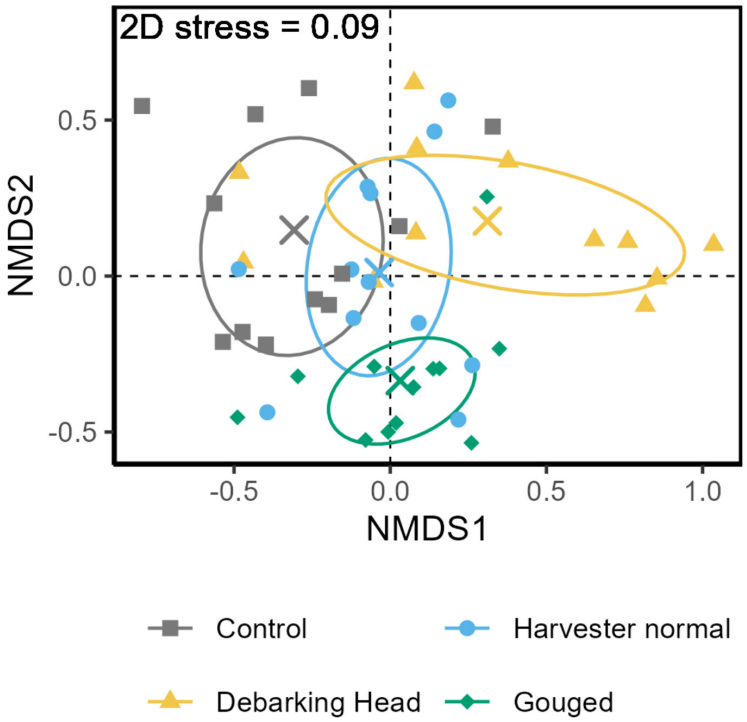

Figure 3.4: Non-metric multidimensional scaling based on presence-absence data Bray-Curtis dissimilarity matrix of non-target beetle species with more than two observations (34 species) in spruce logs treated with harvester debarking head (yellow squares), harvester normal (blue triangles), bark gouging (green crosses) and control (grey circles). For each treatment centroids are marked with 'X' and ellipses show the spread of 50% in the data.

Table 3.2: Results from pairwise analysis of variance (*adonis*) of beetle species assemblages between bark treatments. The analysis is based on Bray-Curtis dissimilarity matrix with presence and absence of non-target beetle species with more than two observations (34 species) emerging from 70 cm *P. abies* log segments. P-values were adjusted with *Bonferroni* correction for multiple testing.

Comparison	***F* value**	**R^2**	**adj. *P*-value**
All treatments	4.13	0.22	**0.007**
Control - Harvester normal	2.63	0.11	0.105
Control - Debarking head	4.71	0.18	**0.014**
Control - Gouging	5.86	0.21	**0.007**
Debarking head - Harvester normal	3.34	0.13	**0.021**
Debarking head - Gouging	4.3	0.16	**0.014**
Harvester normal - Gouging	4.22	0.16	**0.007**

3.3 Discussion

With a current increase in disturbance of European Norway spruce forests there is an urgent need for new management prospects, particular for a conservation-friendly regulation of pests in protected areas. Our results suggest that harvesters equipped with debarking heads could be a promising option for early therapeutic treatment of *I. typographus* populations before fully developed beetles are present. This approach allows for temporary storage of bark beetle breeding material within the forest or for permanent deadwood enrichment to support biodiversity conservation.

Handling bark beetle infested *P. abies* logs with a conventional harvester aggregate had no significant effect on the reduction of *I. typographus.* For the treatment of breeding material at small scales or in terrain inaccessible for machinery we endorse bark gouging as the economic and conservation friendly pest control method. None of the tested treatments had a significant effect on the species richness of non-target beetles. Assemblages of beetle species differed significantly between all treatments, except for the comparison between control and harvester normal logs, demonstrating the importance of bark for the colonization processes of wood inhabiting beetles.

3.3.1 Using debarking heads for efficient pest control after large scale disturbances

After storm damage and bark beetle infestation, timely intervention is the highest priority for successful pest regulation (Kautz et al., 2021; Wermelinger, 2004), while forest workers face numerous safety risks (Sanginés de Cárcer et al., 2021). Consequently, motor-manual work is discouraged since fully mechanized methods provide a safety advantage with the enclosed cabin. With the debarking head attached to the harvester, only one machine operator is needed to process large amounts of breeding material. Our finding, that with a conventional harvester aggregate bark beetle populations in infested *P. abies* trees, cannot be reduced sufficiently, is in contrast to previous studies showing that normal handling already had pest control effect in the larval stage (Delb et al., 2021). Delb et al., 2021 indicated that higher population reduction can be obtained when the logs were processed a second time through the conventional aggregate (similar to the debarking head, just without the modified feed rollers). In the same study, the debarking head was very effective in reducing pest populations at the larval stage. However, in case teneral beetles are already present, the removed bark pieces can be large enough for the beetles to finish their lifecycle and emerge from the residues, stressing the importance of intervention during the larval stage (Delb et al., 2021; Kautz et al., 2021).

Thus, removing the bark before or within a maximum of five weeks after colonization allows for timber storage near potential host trees, without risking a mass outbreak. Decoupling transport and sale of timber from large scale disturbances reduces dependencies on the availability of machinery as well as low market prices for raw timber. The cost of modifying conventional harvester aggregates for debarking can be achieved with less than €10,000, while the running costs per machine hour increase on average by 10% (Heppelmann, Labelle, Wittkopf, et al., 2019). Processing time per log increases, due to the need to pull the logs multiple times through the aggregate. The amount a conventional harvester usually processes is halved when logs are completely debarked with the debarking head (Heppelmann, Labelle, Wittkopf, et al., 2019; Mergl et al., 2021). A reduction in transport costs can be expected, as debarked logs are lighter and dry out faster (Heppelmann, Labelle, & Wittkopf, 2019). Even though the intense processing may increase damage to the wood by the delimbing knives, the usable quantity and value are not decreasing considerably (Labelle et al., 2019). While with the debarking head approximately 11 m^3 per hour

(Heppelmann, Labelle, Wittkopf, et al., 2019) are debranched, debarked and cut to length, with the bark gouging device only about 3 m^3 per hour after previous debranching (Hagge, Leibl, et al., 2019; Thorn et al., 2016) can be made unsuitable for bark beetle breeding. Thus, when compared to motor-manual bark gouging harvesters with debarking heads are feasible for timely interventions for bark beetle management also on larger scales.

In-stand debarking retains important nutrients in the forest that benefit nutrient cycling and stand productivity (Vos et al., 2023; Yan et al., 2017). When used for biomass as thermal energy, debarked logs have less ash and fine dust emissions than logs with bark (Werkelin et al., 2005). Conversely, many sawmills rely on the bark as a fuel to generate energy in their power plants. In case the debarked logs remain (for intermediate storage) in the forest stand, the bacterial richness of decomposer communities decreases, which in turn benefits wood decaying fungi species potentially devaluing the timber (Hagge, Bässler, et al., 2019).

3.3.2 Debarking head as possible solution to promote biodiversity

Deadwood from bark beetle infestations plays a significant role as a resource for various species and is essential for maintaining forest biodiversity and supporting nature conservation efforts (Müller et al., 2010; Viljur et al., 2022). Due to the fact that debarking heads can effectively reduce breeding habitat and emerging bark beetles, it is the sustainable alternative to salvage logging for phytosanitation at large scales. Profound interventions (like clearing of large areas) for the control of forest pests can lower the recreational value of protected areas due to its poor perception by national park visitors (Berto, 2005). Additionally, salvage logging shifts natural regeneration to a dominance of pioneer species, since the top soil is disturbed and the coarse woody debris (CWD) as regeneration niche of *P. abies* is removed (Fischer et al., 2002). Our results demonstrate that the number of emerging non-target beetle species was not reduced by debarking or gouging over the first year. However, in previous multiyear research, completely debarked logs contained fewer saproxylic species, which can affect higher trophic levels like woodpeckers (Hagge, Leibl, et al., 2019; Thorn et al., 2016). The fact that we found no reduction in beetle species, is likely connected to the absence of beetles with a longer development. Yet, the assemblages of beetle species between treatments is characterized by different species than in untreated logs. For crooked, very large or small diameter logs debarking percentages by the debarking head can be expected to be lower (Heppelmann, Labelle, Wittkopf, et al., 2019) which likely leads to a higher habitat heterogeneity affecting the species assemblages. For conservation

goals it is beneficial to sustain unlogged areas with dead wood biomass to uphold specified species diversity in disturbed forests (Thorn, Chao, et al., 2020). However, when it comes to supporting saproxylic biodiversity, it's crucial to provide a variety of CWD differing in size, exposition, and quality, rather than focusing solely on quantity (Müller et al., 2015; Seibold et al., 2015; Thorn, Chao, et al., 2020). Therefore, if extra focus is put on the habitat heterogeneity of retained CWD, ensuring a mix between standing and lying as well as shade and sun exposed locations, some of the wood can also be sold to offset operational costs.

3.3.3 Bark treatments for pest control shape assemblage of beetle species

Even though the species richness (number of species) was not reduced, the beetle species assemblages in the logs with (partly) removed bark differed from the logs with no or low (Harvester normal) impact on the bark layer. This shift needs to be disentangled in more detailed follow up research, to verify the additional benefit for biodiversity from debarked wood and which habitat characteristics influence the assembly processes. Bark is an important structural and nutritious component of dead wood. Especially during the initial colonization, numerous species specialize in utilizing phloem and bark as resources, habitats, or shelters (Parisi et al., 2018; Ulyshen, 2018).

The shifts we found in abundances of certain species between treated and control logs may be attributed to changes in habitat availability, nutrition supply, and competitive interactions with other species. For example, the generalized predatory rove beetle *Dolotia coriaria* showed higher total abundance in treated logs likely benefiting from reduced competition. *Monotoma longicollis* and *Cartodere nodifer* as two abundant facultative saproxylic species (Graf et al., 2022) showed higher total abundances in treated logs, which might be attributed to their connection to decaying plant matter or molds for their nutrient uptake. Molds growing on the wood surface and decomposing bark remnants might be more abundant and accessible in logs with manipulated bark. *Nudobius lentus* and *Placusa depressa* are predatory on bark beetles and use the galleries as their habitat (Möller, 2009) and both indicated highest total abundance in the control logs without bark treatment and high bark beetle abundance. *Cartodere constricta* is another saproxylic species feeding on fungi under the bark (Möller, 2009) with higher total abundance in the control logs (see Table A3.1).

Species assemblages in the later stages of decaying CWD are characterized by the preceding processes and assemblages. Thus, the primary structural integrity of dead wood after

treatment for bark beetle reduction is creating the legacy of saproxylic colonization. Intact bark also serves as barrier for wood decaying fungi and maintains constant conditions (i.e. humidity) for the succession of saproxylic beetle species (Hagge, Bässler, et al., 2019). With the multivariate analysis of the species data, we provide evidence that the assemblage of beetle species in the early colonization process is characterized by the intensity of bark removal. Biodiversity oriented management of disturbances and CWD will increase the resilience of forests in the face of the ongoing global environmental crises (Müller et al., 2023). Hence, the debarking head can be recommended to process large quantities of (infested) breeding material, without threatening the goals of biodiversity conservation.

3.4 Conclusions for practical implementations

We present a conservation-friendly method to safeguard timber production forests from bark beetle outbreaks after disturbances like windstorms. Wood treated during the larval stage or before infestation with the harvester debarking head or the bark gouging device can remain for intermediate storage or CWD retention within the forest stands. Harvesters equipped with debarking heads are a compromise between nature conservation and more economic "forest protection" goals. Due to the capacity of treating large amounts of wood, they are particularly well-suited for managing disturbances at large scales and can prevent dependencies on transport or fluctuating market prices for commercial forestry. In protected areas, the use of debarking heads for pest control should be considered as an alternative to salvage logging, to maintain ecosystem integrity. For the treatment of logs at small scales, bark gouging is the most conservation friendly bark beetle control method. In both cases, the wood can be retained within the stand to maintain natural processes in the re-growing forests. Despite an impact on species assemblage, the species richness of non-target beetles remains unaffected with the (partial) removal of bark. These alternative pest control methods are suitable for promoting biodiversity without the more detrimental effects to ecosystem functioning associated with salvage logging.

Apendix

Acknowledgments

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Data availability statement

Data supporting the findings of this research article are available at the DRYAD public repository with the following DOI: https://doi.org/10.5061/dryad.4f4qrfjmr

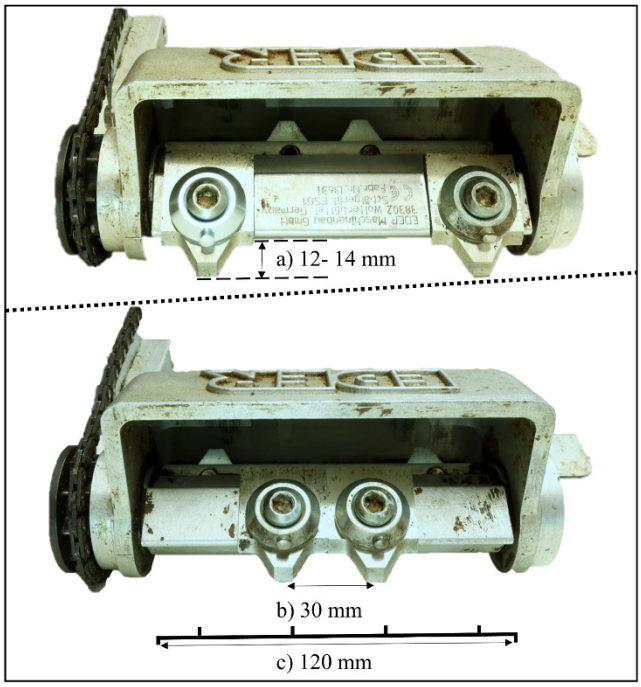

Figure A3.1: Debarking device with the rotating cylinder at two positions equipped with the four modified knifes for bark gouging. Dimensions for a) the adjustable depth for different bark thickness, b) the distance between the tips of the v-shaped knives and c) the width of treatment area are given.

Figure A3.2: a) Harvester John Deere 1270 G fitted with a b) harvesting aggregate H 480 C modified for debarking (debarking head) and the resulting debarked logs. c) Standing snags can also be debarked for phytosanitation with the debarking head to regulate *Ips typographus* populations and retain a variety in dead wood to support biodiversity.

Table A3.1: List of beetle species sorted according to FHL-Code with number of emerged individuals from the experimental logs for harvester debarking head, harvester normal, gauged and control. Abundances are based on 70 cm *P. abies* log segments (n = 12 per treatment) after 4 months in rearing barrels.

Family	Genus	Species	Author, year	Debarking Head	Harvester normal	Gouged	Control	Total
Hydraenidae	*Limnebius*	*truncatellus*	Thunberg, 1794	0	1	0	0	**1**
Histeridae	*Plegaderus*	*vulneratus*	Panzer, 1797	0	0	0	2	**2**
Leiodidae	*Agathidium*	*seminulum*	Linné, 1758	1	0	0	0	**1**
Ptiliidae	*Pteryx*	*suturalis*	Heer, 1841	1	0	0	0	**1**
Ptiliidae	*Acrotrichis*	*intermedia*	Gillmeister, 1845	0	1	0	0	**1**
Staphylinidae	*Megarthrus*	*depressus*	Paykull, 1789	2	0	0	0	**2**
Staphylinidae	*Omalium*	*caesum*	Gravenhorst, 1806	1	0	0	0	**1**
Staphylinidae	*Phloeonomus*	*pusillus*	Gravenhorst, 1806	1	3	1	2	**7**
Staphylinidae	*Nudobius*	*lentus*	Gravenhorst, 1806	1	1	6	50	**58**
Staphylinidae	*Xantholinus*	*laevigatus*	Jacobsen, 1849	0	0	4	1	**5**
Staphylinidae	*Quedius*	*cruentus*	A. G. Olivier, 1795	1	0	0	0	**1**
Staphylinidae	*Cypha*	*longicornis*	Paykull, 1800	0	2	0	0	**2**
Staphylinidae	*Gyrophaena*	*bihamata*	C. G. Thomson, 1867	0	0	1	0	**1**
Staphylinidae	*Gyrophaena*	*boleti*	Linné, 1758	0	1	1	0	**2**
Staphylinidae	*Placusa*	*depressa*	Mäklin, 1845	56	60	3	94	**213**
Staphylinidae	*Placusa*	*tachyporoides*	Waltl, 1838)	2	1	7	0	**10**
Staphylinidae	*Homalota*	*plana*	Gyllenhal, 1810	2	4	1	3	**10**
Staphylinidae	*Myrmecocephalus*	*concinnus*	Erichson, 1839	6	5	0	2	**13**
Staphylinidae	*Atheta*	*vaga*	Heer, 1839	4	7	0	3	**14**
Staphylinidae	*Atheta*	*harwoodi*	B.S. Williams, 1930	0	0	0	2	**2**
Staphylinidae	*Atheta*	*picipes*	C. G. Thomson, 1856	0	5	0	4	**9**
Staphylinidae	*Dalotia*	*coriaria*	Kraatz, 1856	683	1737	1827	115	**4362**
Staphylinidae	*Phloeopora*	*corticalis*	Gravenhorst, 1802	2	0	0	0	**2**
Staphylinidae	*Aleochara*	*sparsa*	Heer, 1839	0	2	0	2	**4**

Family	Genus	Species	Author, year	Debarking Head	Harvester normal	Gouged	Control	Total
Staphylinidae	*Euplectus*	*infirmus*	Raffray, 1910	0	0	0	1	**1**
Cleridae	*Thanasimus*	*femoralis*	Zetterstedt, 1828	0	0	0	1	**1**
Elateridae	*Agriotes*	*sputator*	Linné, 1758	0	1	1	0	**2**
Clambidae	*Clambus*	*simsoni*	Blackburn, 1902	3	1	1	0	**5**
Cerylonidae	*Cerylon*	*histeroides*	Fabricius, 1792	0	1	0	0	**1**
Nitidulidae	*Epuraea*	*pallescens*	Stephens, 1835	2	0	7	2	**11**
Nitidulidae	*Epuraea*	*thoracica*	Tournier, 1872	1	3	0	0	**4**
Nitidulidae	*Epuraea*	*marseuli*	Reitter, 1873	1	3	0	2	**6**
Nitidulidae	*Epuraea*	*biguttata*	Thunberg, 1784	3	2	2	1	**8**
Nitidulidae	*Epuraea*	*variegata*	Herbst, 1793	0	0	2	3	**5**
Nitidulidae	*Epuraea*	*muehli*	Reitter, 1908	0	8	2	3	**13**
Monotomidae	*Monotoma*	*picipes*	Herbst, 1793	0	1	1	0	**2**
Monotomidae	*Monotoma*	*longicollis*	Gyllenhal, V SZ	169	212	155	30	**566**
Monotomidae	*Rhizophagus*	*depressus*	Fabricius, 1792	1	0	0	1	**2**
Silvanidae	*Psammoecus*	*bipunctatus*	Fabricius, 1792	2	0	1	0	**3**
Cryptophagidae	*Cryptophagus*	*intermedius*	Bruce, 1934	0	0	6	1	**7**
Cryptophagidae	*Cryptophagus*	*dentatus*	Herbst, 1793	7	4	9	1	**21**
Cryptophagidae	*Atomaria*	*fuscata*	Schönherr, 1808	1	0	0	0	**1**
Cryptophagidae	*Atomaria*	*lewisi*	Reitter, 1877	0	0	1	0	**1**
Cryptophagidae	*Atomaria*	*rubella*	Heer, 1841	0	0	0	1	**1**
Laemophloeidae	*Cryptolestes*	*ferrugineus*	Stephens, 1831	0	0	3	0	**3**
Latridiidae	*Cartodere*	*constricta*	Gyllenhal, 1827	3	2	3	17	**25**
Latridiidae	*Cartodere*	*nodifer*	Westwood, 1839	32	22	0	2	**56**
Latridiidae	*Corticarina*	*similata*	Gyllenhal, 1827	0	0	0	5	**5**
Latridiidae	*Corticarina*	*minuta*	Fabricius, 1792	0	0	0	1	**1**
Latridiidae	*Cortinicara*	*gibbosa*	Herbst, 1793	2	0	0	0	**2**
Mycetophagidae	*Litargus*	*connexus*	Geoffroy, 1785	0	1	1	0	**2**
Corylophidae	*Sericoderus*	*lateralis*	Gyllenhal, 1827	0	3	1	4	**8**
Corylophidae	*Orthoperus*	*corticalis*	L. Redtenbacher, 1845	4	1	0	0	**5**

Family	**Genus**	**Species**	**Author, year**	**Debarking Head**	**Harvester normal**	**Gouged**	**Control**	**Total**
Endomychidae	*Symbiotes*	*gibberosus*	P. H. Lucas, 1846	2	0	0	0	**2**
Aderidae	*Euglenes*	*oculatus*	Paykull, 1798	4	2	2	1	**9**
Curculionidae	*Hylurgops*	*palliatus*	Gyllenhal, 1813	1	0	0	0	**1**
Curculionidae	*Polygraphus*	*poligraphus*	Linné, 1758	0	4	0	0	**4**
Curculionidae	*Crypturgus*	*cinereus*	Herbst, 1794	27	723	357	1275	**2382**
Curculionidae	*Crypturgus*	*pusillus*	Gyllenhal, 1813	2	19	22	15	**58**
Curculionidae	*Dryocoetes*	*autographus*	Ratzeburg, 1837	0	1	0	0	**1**
Curculionidae	*Pityogenes*	*chalcographus*	Linné, 1760	122	485	271	1892	**2770**
Curculionidae	*Ips*	*typographus*	Linné, 1758	112	1447	105	1065	**2729**
Curculionidae	*Trypodendron*	*lineatum*	A. G. Olivier, 1795	40	0	0	0	**40**

Table A3.2: Results of multiple comparisons of the differences in abundance of emerged *Ips typographus,* and number of non-target beetle species between treatments, based on results of the quasi-Poisson models. P-values were adjusted with single-step method.

Contrast	Estimate	std. error	z-value	adj. P-value
Ips typographus				
Control – Debarking Head	**2.252**	**0.834**	**2.700**	**0.031**
Harvester normal – Debarking Head	**2.559**	**0.824**	**3.106**	**0.009**
Gouged – Debarking Head	-0.065	1.141	-0.057	0.999
Harvester normal – Control	0.307	0.339	0.904	0.785
Gouged – Control	**-2.317**	**0.859**	**-2.697**	**0.031**
Gouged – Harvester normal	**-2.623**	**0.849**	**-3.090**	**0.009**
Species richness of non-target beetles				
Control – Debarking Head	0.087	0.151	0.577	0.939
Harvester normal – Debarking Head	0.261	0.145	1.804	0.271
Gouged – Debarking Head	0.051	0.152	0.333	0.987
Harvester normal – Control	0.174	0.141	1.233	0.606
Gouged – Control	-0.036	0.149	-0.244	0.995
Gouged – Harvester normal	-0. 211	0.143	-1.475	0.452

Table A3.3: Results of the simper analysis for the contribution of the top 3 species to the differences in beetle species assemblages between the four treatments.

Comparison	Species	Average	SD	cumsum	*P*-value
Debarking Head - Control					
	Crypturgus cinereus	0.052	0.039	0.085	0.001
	Placusa depressa	0.046	0.042	0.162	0.009
	Dalotia coriaria	0.040	0.042	0.228	0.024
Debarking Head - Harvester normal					
	Crypturgus cinereus	0.057	0.036	0.097	0.001
	Crypturgus pusillus	0.049	0.039	0.180	0.009
	Placusa depressa	0.041	0.040	0.250	0.1
Debarking Head - Gouged					
	Crypturgus pusillus	0.068	0.032	0.117	0.001
	Crypturgus cinereus	0.049	0.040	0.201	0.002
	Placusa tachyporoides	0.037	0.039	0.266	0.002
Harvester normal - Control					
	Pityogenes chalcographus	0.036	0.037	0.074	0.034
	Dalotia coriaria	0.035	0.037	0.147	0.181
	Crypturgus pusillus	0.034	0.036	0.217	0.852
Harvester normal - Gouged					
	Placusa depressa	0.048	0.033	0.098	0.008
	Pityogenes chalcographus	0.036	0.037	0.172	0.049
	Placusa tachyporoides	0.032	0.033	0.239	0.019
Gouged - Control					
	Placusa depressa	0.065	0.024	0.128	0.001
	Dalotia coriaria	0.037	0.039	0.202	0.088
	Crypturgus pusillus	0.037	0.039	0.274	0.54

Chapter 4: 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 along a climatic gradient in Central Europe. Our study quantified pest control efficacy, operational efficiency, wood properties, and effects on biodiversity of saproxylic beetles, fungi, and bacteria, as well as woodpeckers (higher trophic levels).3. Three passes of Norway Spruce logs through the harvester aggregate substantially reduced bark beetle populations, demonstrating a scalable method for managing pest outbreaks and disturbances at landscape scales. Motor-manual bark gouging and debarking remain 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 two years and we did not observe changes in elemental composition (H, C, and N).

Synthesis and applications: Triple harvester processing and motor-manual bark gouging effectively suppress pests, enabling two options: permanent on-site retention for biodiversity conservation, or up to two years of on-site intermediate storage for bioenergy, buffering economic bottlenecks during landscape disturbances.

4.1 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 (Seidl et al., 2017; Senf et al., 2020; Patacca et al., 2023). 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 (Hilmers et al., 2018; Sommerfeld et al., 2021; Busse et al., 2022).

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*) stands (Hlásny et al., 2021; Patacca et al., 2023). This dynamic is predicted to persist and intensify under future climate change scenarios (Seidl et al., 2017; Mohr et al., 2025). 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 (Marini et al., 2017; Biedermann et al., 2019). Moreover, a significant proportion of *P. abies* stands 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, labor 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 diminish its marketable timber value or energy content as a result of colonization and subsequent decomposition (Barrette et al., 2015). 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 particularly 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 (Ulyshen et al., 2016; Dossa et al., 2018). Economically, blue-staining fungi are of high relevance for bark beetle infested wood, since the aesthetic alterations can lead to significant timber devaluations (Barrette et al., 2015; Böhm et al., 2025).

While fuel wood may represent a secondary assortment in traditional harvests, 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, potential breeding material is moved away from host trees before beetles emerge (Hoch et al., 2020). Simulation studies suggest that, within the first five weeks of colonization, eliminating at least 80% of the beetles (Fahse & Heurich, 2011) or removing 95% of infested or damaged trees—such as wind-thrown logs—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 subsequent 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 fulfill such intensive wood extraction, reduces saproxylic (deadwood-dependent) biodiversity (Georgiev et al., 2020; Thorn, Chao, et al.,

2020; Thorn et al., 2018) and can compromise forest resilience against future disturbances (Leverkus et al., 2021; Lindenmayer et al., 2017). Mechanical bark treatments offer an alternative to salvage logging, pesticide application, and wet storage. The removal or manipulation of bark destroys the breeding habitat of *I. typographus* (preventative) and causes the existing larvae to dry out (therapeutic), allowing for intermediate on-site storage or permanent retention of wood on site (Hagge, Leibl, et al., 2019). This method is primarily recommended 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 (Wermelinger, 2004; Hlásny et al., 2021; Fettig et al., 2022). Manual and motor-manual debarking techniques, such as the debarking spud and chainsaw attachment, effectively reduce *I. typographus* populations (Thorn et al., 2016; Hagge, Leibl, et al., 2019; Zarges et al., 2023), but complete bark removal negatively impacts saproxylic species richness, its community assembly, and ultimately higher trophic levels like woodpeckers (Thorn et al., 2016; Hagge, Leibl, et al., 2019). Compared to complete debarking, a novel chainsaw attachment that gauges the bark off in regular stripes (Fig. 4.1, Fig. A4.1), reduces *I. typographus* populations with less effort, while the remaining intact bark benefits non-target biodiversity (Thorn et al., 2016; Hagge, Leibl, et al., 2019; Zarges et al., 2023). Rapid intervention is critical for addressing landscape-scale disturbances involving large volumes of wood, for which harvesters represent an effective solution by removing and perforating bark with delimbing knives and multiple passes over the logs (Delb et al., 2021). Yet, experimental validation across multiple sites and climatic regions 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 economic and ecological trade-offs, considering the scale of disturbance and variability of central European *P. abies* forests. This will provide the necessary information for two distinctive management scenarios: temporary wood storage in commercial forests, and long-term dead wood retention to support biodiversity conservation goals. We use pest control efficacy, operational efficiency, wood properties, and effects on biodiversity of saproxylic beetles, fungi, and bacteria for the comparison of five mechanical bark treatments and a control. We quantify changes in wood moisture and chemical stability—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 two years on-site. Additionally, we assessed blue-stain fungi to determine potential impacts of bark removal on wood 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 large wood volumes than motor-manual treatments, conventional harvester handling will not manipulate enough bark to regulate numbers of emerging *I. typographus;* (ii) compared to conventional harvester processing, three passes through the harvester aggregate accomplish pest control but come with higher economic costs; (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 abundance; the net calorific value is predicted to decreases with decomposition over time, while decomposition alters the elemental wood composition of carbon, hydrogen and nitrogen content.

4.2 Materials and Methods

4.2.1 Study area and bark treatments

At 20 study sites distributed across the climatic range of *P. abies* (Norway spruce) dominated forests in Germany (Fig. 4.1a, Fig. 4.2), 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 at the respective sites within three 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 got a mechanical bark treatment by professional forest workers (harvester normal, harvester triple, motor-manual gouging, motor-manual debarking, manual debarking; see Table A4.1). 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; Fig. 4.1b). The same device, with a different blade configuration, was used to gouge regularly spaced longitudinal grooves in the bark (Fig. 4.1b, Fig. A4.1). 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 (Fig. A4.3, Fig. A4.4).

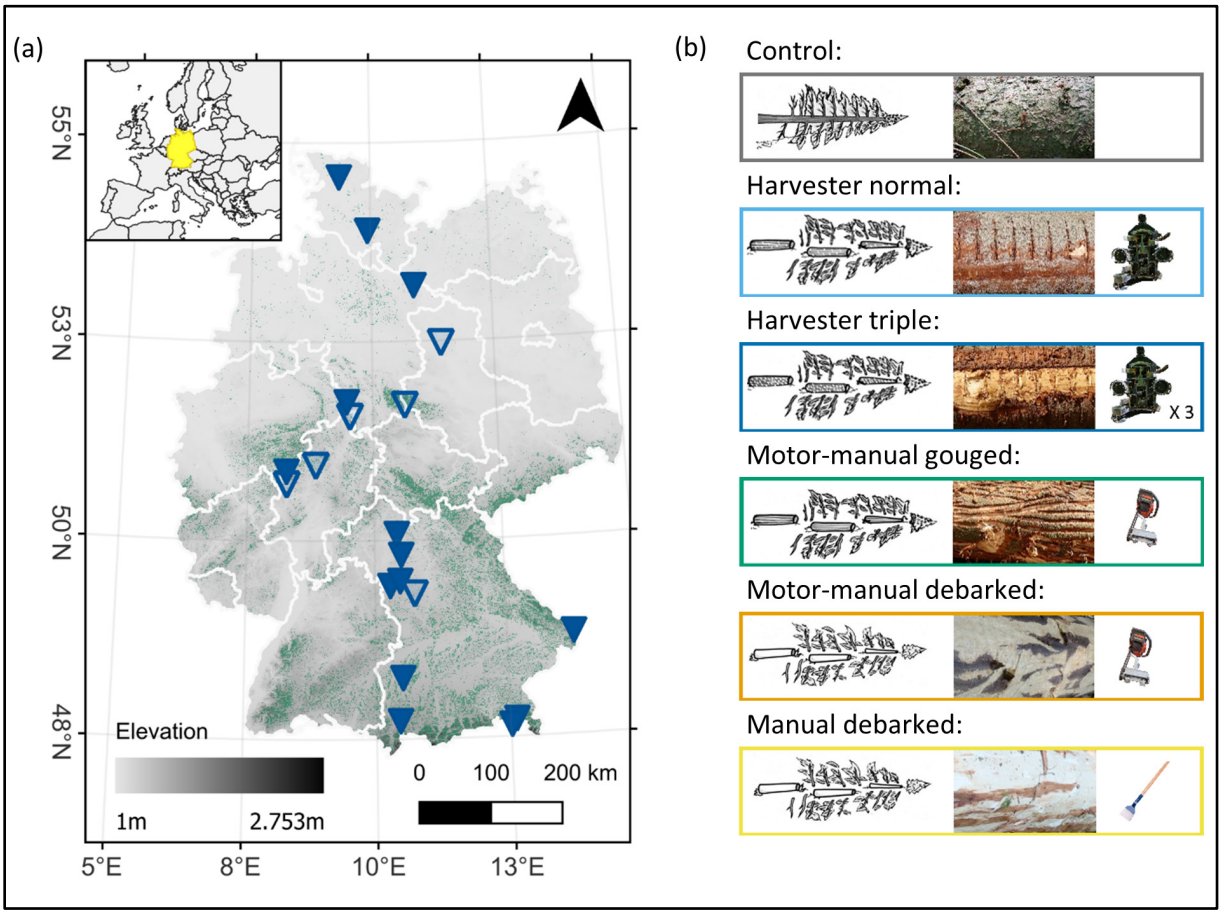

Figure 4.1: Experimental design to test the different bark treatments for *I. typographus* regulation in *P. abies* logs. a) Distribution of the 20 study sites in Germany (empty markers without time study) with grey shading for altitude (NASA JPL, 2013) and green areas for forests dominated by *P. abies* (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.

4.2.2 Sampling

To evaluate pest control 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 ± 0.331 m² (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 (Fig. A4.3). All saproxylic beetles (sensu Schmidl and 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 one 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 pest control and biodiversity analysis due to incomplete data.

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 (Fig. A4.3) 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 A4.1). We analyzed abundances of the ophiostomatoid fungi (*Ophiostomataceae* and *Ceratocystidaceae*), since these families represent a significant guild of tree pathogens that are vectored by bark beetles and cause economically relevant blue-staining of the sapwood (Leonhardt et al., 2019; Wingfield et al., 2017). For this we additionally classified fungal OTUs with the UNTITE v8.3 database (Abarenkov et al., 2024) at a confidence level of 95%.

To evaluate the timber utilization potential, the remaining sawdust was homogenized and wood properties (moisture, carbon, nitrogen, hydrogen content, and net calorific value) were assessed according to established procedures by an external laboratory (see Text A4.2).

4.2.3 Analysis

Pest control 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 reads were modeled 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 at different scales relevant for central European *P. abies* forests, 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 analyze 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 A4.3) with *estimateD* from the iNext package (Hsieh & Chao, 2022).

We used piecewise structural equation modeling from the package piecewiseSEM with the function *psem* (Lefcheck et al., 2024) to analyze direct and indirect effects among bark cover (representing treatment intensity, Fig. A4.4), *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 A4.6). Bark cover was modeled 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 modeled 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 were 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.

4.3 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* (8,535), and *Crypturgus pusillus* (6,757) (complete species list in Table A4.2). The metabarcoding of wood samples revealed a total of 9,402 fungal and 20,171 bacterial OTUs.

4.3.1 Pest control efficacy

Compared to the untreated control, the three times harvester treatment significantly reduced the amount of emerging *I. typographus* by 76 ± 8% ($p = 0.005$, Fig. 4.2a, Table A4.4). 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% ($p < 0.001$; Fig. 4.2a, Table A4.4).

4.3.2 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 ($p < 0.001$, Fig. 4.2b, Table A4.4). 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 ($p < 0.001$, Fig. 2b, Table A4.4). Comparing the (motor-) manual treatments, gouging the bark was the about two times faster method (2.3 ±0.25 m^3 per hour) compared to complete debarking (motor- manual: 1.3 ±0.13 m^3 per hour; manual: 0.7 ± 0.08 m^3 per hour; Fig. 4.2b, Table A4.4).

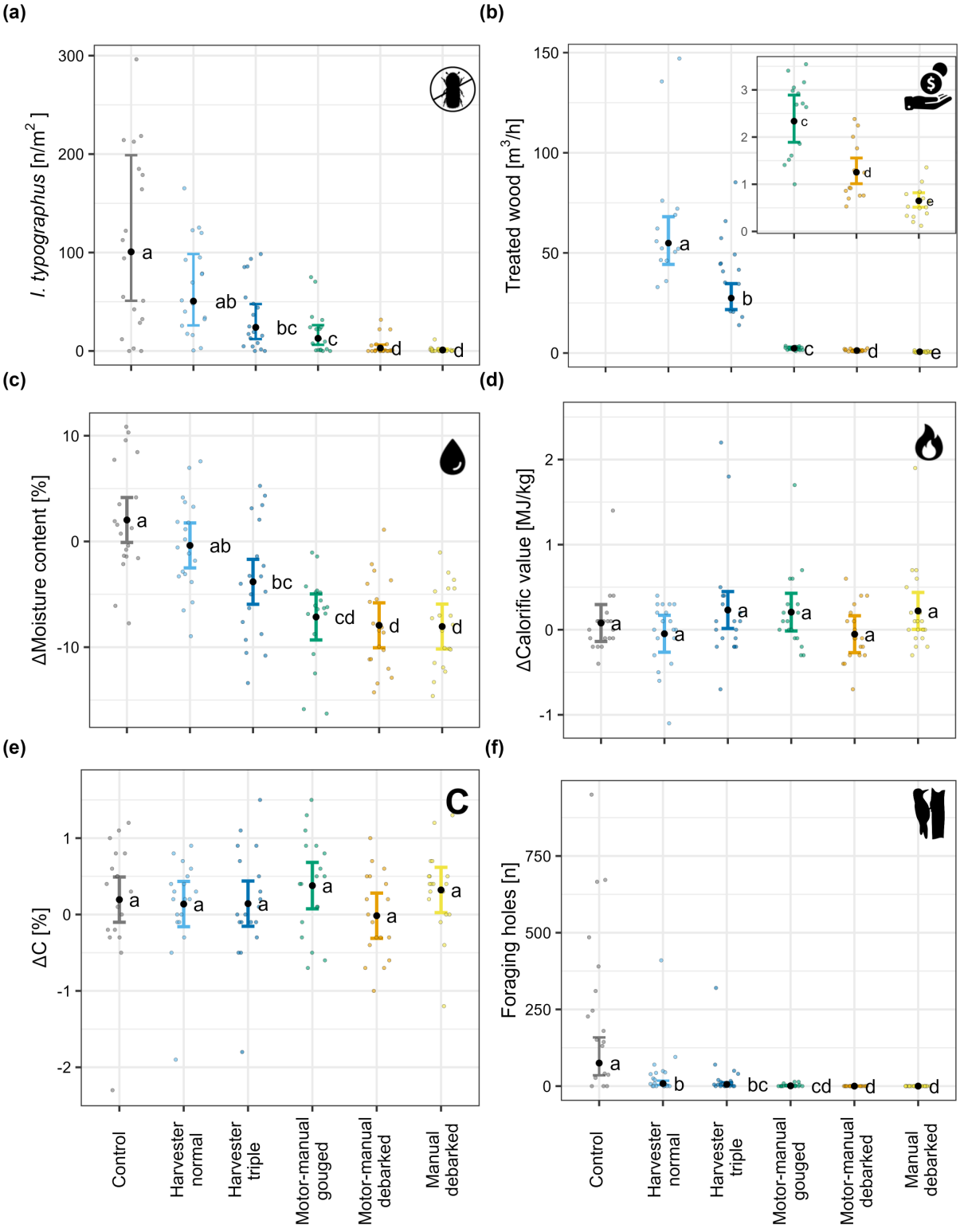

Figure 4.2: Model results for a) pest control of *Ips typographus* (19 sites), b) operational efficiency (14 sites), c) change in moisture content (19 sites), d) change in net calorific value (19 sites), e) change in carbon content (19 sites) and woodpecker foraging holes (19 sites). Black dots indicate 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 colored by treatment.

4.3.3 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 two 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 (Fig. 4.2c, Table A4.4). Change in net calorific value, carbon, nitrogen and hydrogen content did not differ among treatments (Fig. 4.2d and e, Table A4.4, Fig. A4.5). The reads of blue-stain fungi (ophiostomatoids: *Ophiostomataceae* and *Ceratocystidaceae*) did not have a significant difference between treatments ($p > 0.05$; Fig. A4.6).

4.3.4 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.

4.3.5 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 (Fig. 4.3a). 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 ($p < 0.001$, Fig. 4.3b). 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 (Fig. 4.3c). 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 ($p < 0.001$, Fig. 4.3d). The diversity of bacteria OTUs decreased only for gamma diversity in the gouged and completely debarked logs (Fig. 4.3e). 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.

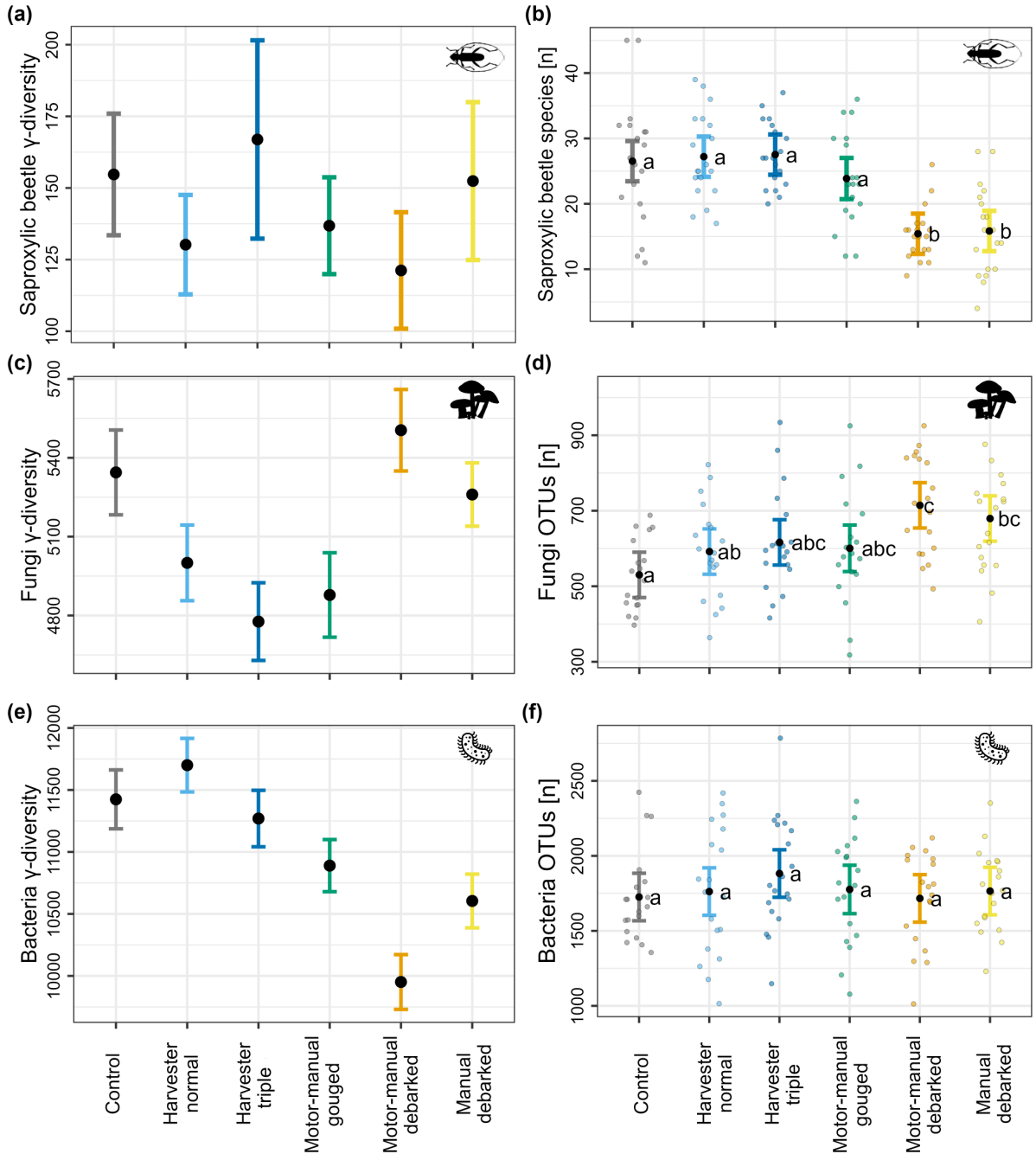

Figure 4.3: Treatment effect on a-b) saproxylic beetle, c-d) fungi and e-f) bacteria OTU richness (number of species/OTUs). Results in the left panels are gamma diversity (black dots) based on coverage-based extrapolation of presence–absence data. Error bars indicate the lower and upper bound of the 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 colored by treatment.

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 (Fig. 4, Table S7).

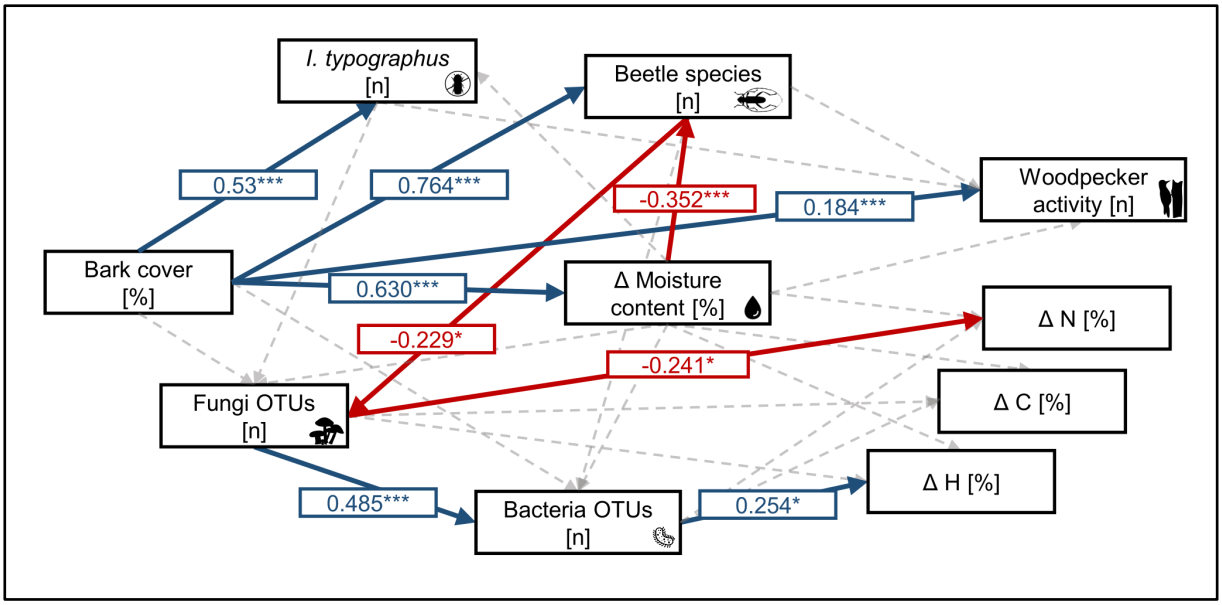

Figure 4.4: Structural equation model with bark cover (%), wood moisture, carbon, hydrogen, nitrogen change (%) over two years, *I. typographus* density, woodpecker activity, saproxylic beetle and fungal/bacterial richness (number of species/OTUs). Blue arrows indicate positive and red arrows negative 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.

4.3.6 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 (Fig. 4.5a). 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 (Figs. 5b and 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 (Fig. 5, Table S5).

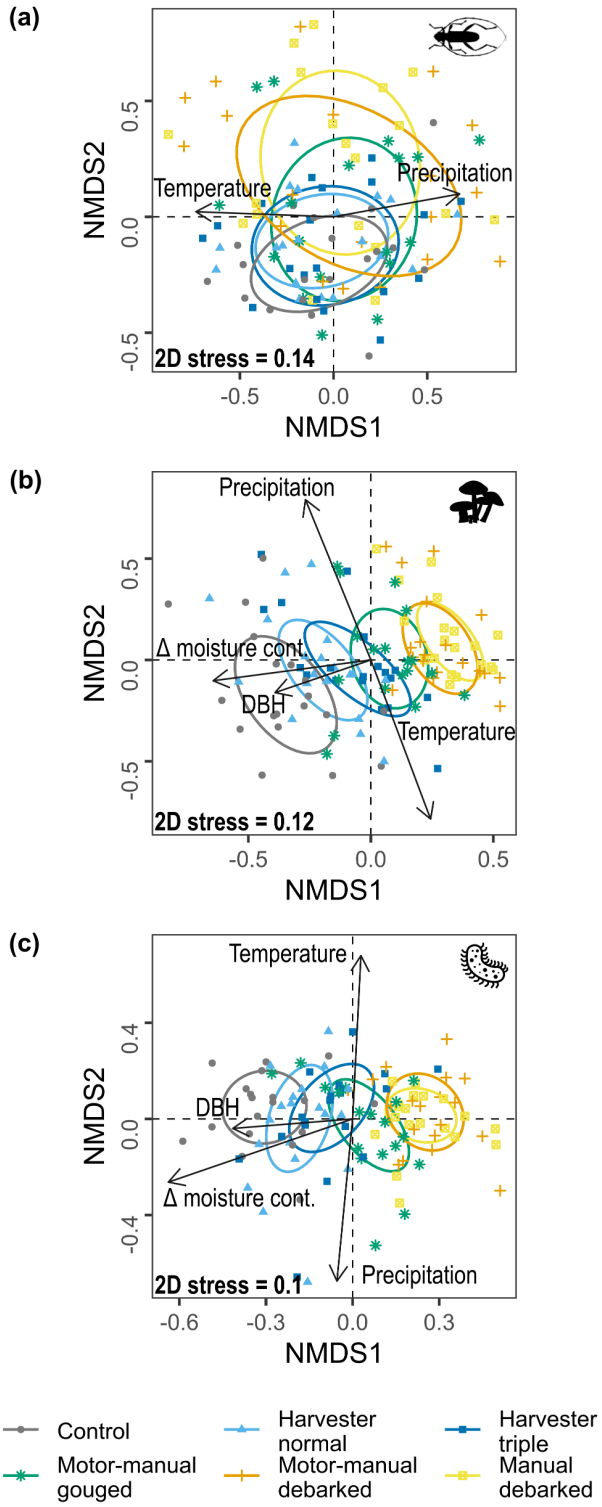

Figure 4.5: Two-dimensional non-metric multidimensional scaling (NMDS) based on presence–absence data Bray-Curtis dissimilarity matrix of a) saproxylic beetle species, b) fungi OTUs and c) bacteria OTUs in *P. abies* logs with different treatment (colors and shapes). With only the significant environmental effects included as vectors.

4.4 Discussion

Our results indicate that bark removal and manipulation represent effective and operationally feasible alternatives to salvage logging for regulating bark beetle populations across Central European *P. abies* forests, 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 while conventional harvester handling is insufficient for pest regulation, three passes through the harvester aggregate successfully reduced bark beetles within the limited timeframes required to manage large volumes of damaged wood during landscape-scale disturbances. In line with our hypotheses, we confirmed for the first time over a large geographical scale that bark removal reduces saproxylic beetle richness, lowers woodpecker activity, increases fungal richness (iii), and influences community assembly of saproxylic taxa (iv). 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 fulfill 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 presence 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 two years, reinforcing the feasibility of using logs for bioenergy, independent of bark treatment, after two years of on-site storage.

4.4.1 Pest control

(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 for harvester-inaccessible disturbances. 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 head), which efficiently remove the complete bark and regulate bark beetles, although only a limited number are currently available (Zarges et al., 2024). The triple harvester 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, Labelle, Wittkopf, et al., 2019). With respect to pest control, 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, Labelle, Wittkopf, 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 or go in the ground for overwintering (Delb et al., 2021; Hoch et al., 2020). The persistence of *I. typographus* emergence into the beginning of the second year of our study indicates that infested logs with bark (control and harvester treatments) can remain a source of high population densities (Fig. S7). Previous studies have reported periods of attractiveness of more than two years (Schroeder, 2010; Wermelinger et al., 2013), however these results were based on windthrown trees, which often remain connected to the root system and therefore dry out more slowly. Consequently, reactive management—such as removal or treatment—has no effect in cut trees after more than one year on-site and should hence be conducted as early as possible after felling or infestation.

4.4.2 Biodiversity

Bark treatments effectively reduce bark beetle populations (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).

4.4.3 Timber utilization

In case the wood is not intended for permanent retention for conservation we show with our results that the wood still has some marketable value after treatment and intermediate on-site storage. However, repeated handling with harvester aggregates is likely to cause damages to the wood fiber 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 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 (Fig S6). Debarking also reduces other economically relevant saproxylic beetle and fungi species (Böhm et al., 2025). Hence, debarking with storage under dry conditions (e.g. sun exposed, no soil contact) helps preserve wood value when disposal options within the supply chain are limited. However, timely removal and appropriate storage of infested wood are critical, as delays increase fungal development and associated wood discoloration, thereby reducing its economic value

(Böhm et al., 2023). The decomposition of deadwood depends on various environmental and species-specific factors and can range between a few years to over a century (Hararuk et al., 2020; Harmon et al., 1986; Petrillo et al., 2016). After two years, the calorific value in our experimental logs did not decrease for all five mechanical bark treatments, indicating its suitability as energy wood. Additionally, the debarked logs had a lower moisture content, reducing the need for pre-drying after storage in the forest. Reducing fuel loads to prevent forest fires is a common motivation for salvage logging even though studies provide mixed results on the effectiveness (reviewed in Leverkus et al., 2020). However, our findings indicate that leaving the bark intact on deadwood can reduce its susceptibility to ignition, not only due to the insulating properties of bark (Renner et al., 2023), but also due to the higher moisture content in the wood we observed under intact bark. 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 three 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 pest control with timber utilization, operational efficiency, and biodiversity conservation. For management practice, harvester-based bark treatments with multiple 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 two years allows for its potential use as a regional renewable energy source.

Following effective bark treatments, two 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 two years to buffer economic constraints during periods of unfavorable timber market conditions after large-scale disturbances.

Appendix

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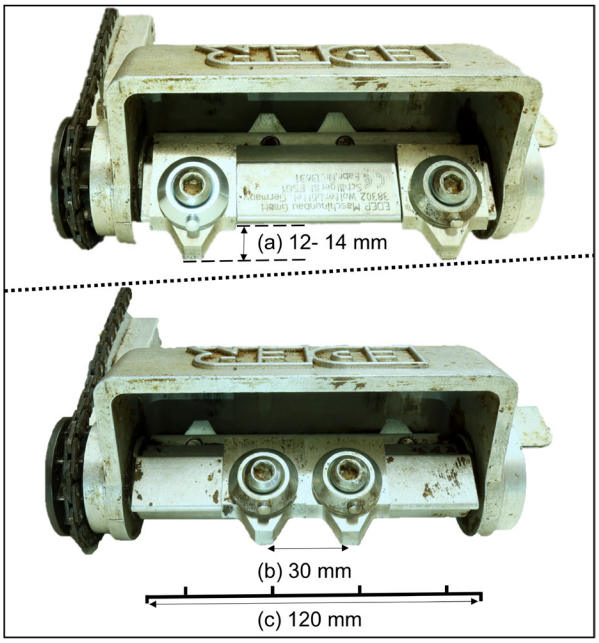

Figure A4.1: Debarking device with the rotating cylinder at two positions equipped with the four modified knifes for bark gouging. Dimensions for a) the adjustable depth for different bark thickness, b) the distance between the tips of the v-shaped knives and c) the width of treatment area are given.

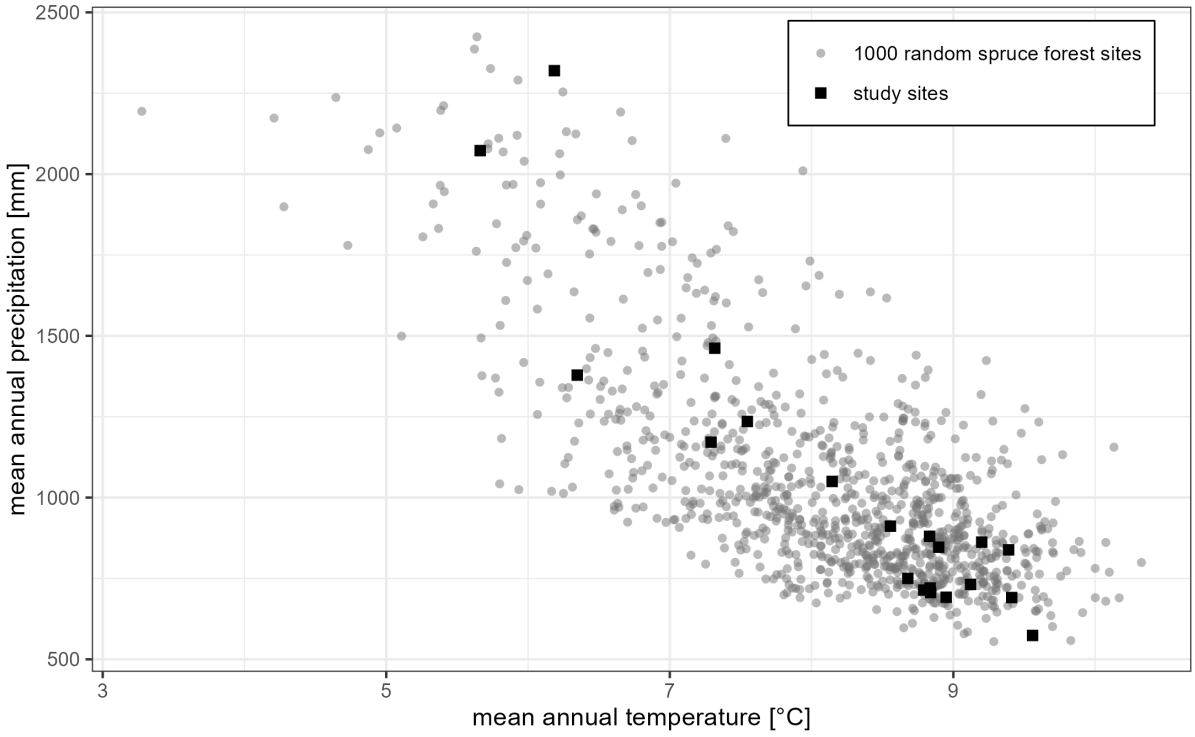

Figure A4.2: Scatterplot comparing the 20 sites (black squares) with temperature and precipitation in 1000 random points across the distribution of *P. abies* forests in German (gray points). Mean annual precipitation and temperature for the period 1990–2020. Data source: Deutscher Wetterdienst (DWD) Open Data Portal (https://opendata.dwd.de) and the German tree species map (Blickensdörfer et al., 2024).

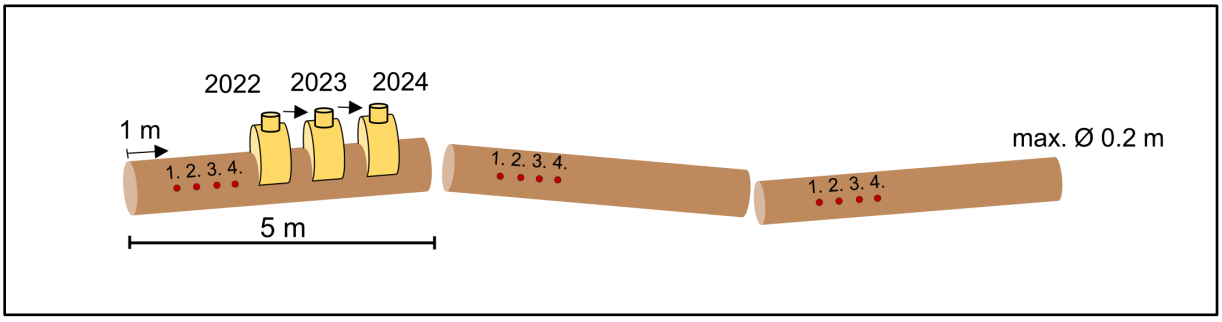

Figure A4.3: Sampling design for each individual log with the two years of emergence traps and the four drilling locations for the thick, middle and thin stem section. Traps were shifted by 50 cm between years. For logs with a greater diameter than the length of the drill, sampling was done from both 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.

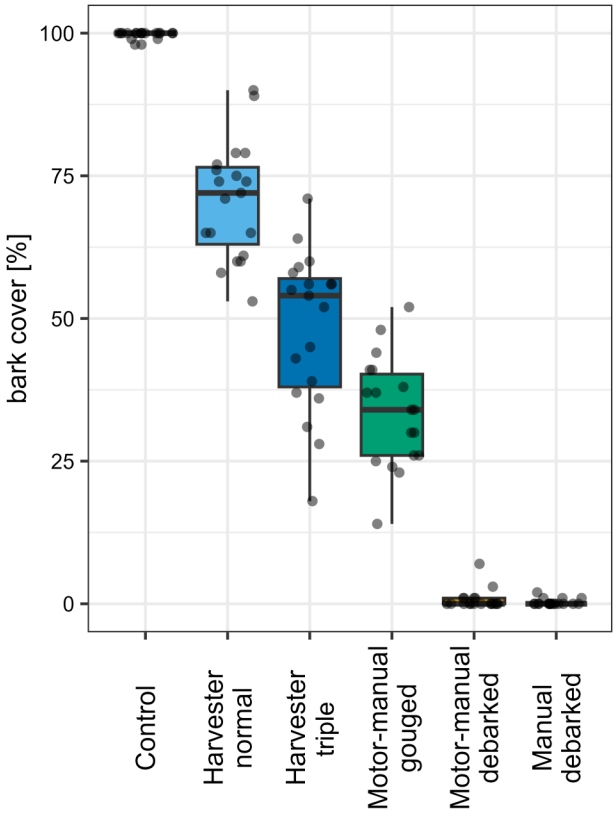

Figure A4.4 Boxplots with the bark cover in percentage of intact bark for each treatment directly after mechanic bark treatments. A transparent sheet with an area of 0.125 m^2 and 25 randomly distributed points was placed at the emergence trap and three drill locations of the first year (2022, Fig. S3). For each point it was assessed if the bark beneath is intact, injured or missing.

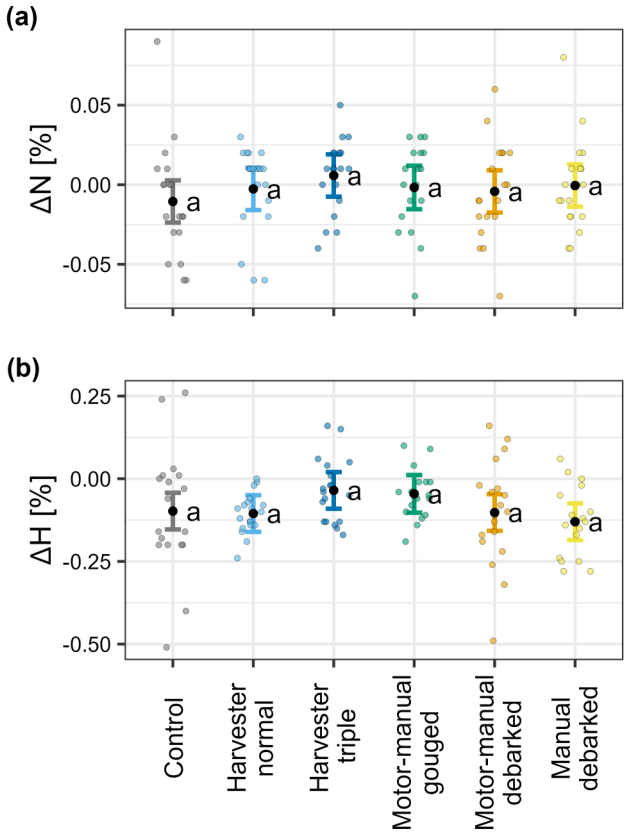

Figure A4.5: Estimated marginal means for the difference between first measurement and after two years (Δ) of a) Nitrogen and c) Hydrogen content in the wood samples. Letters specify significant differences between treatments with Tukey adjustments for multiple testing at a significance level of $p < 0.05$. Error bars indicate 95% CI and colored dots show the observed data for each site.

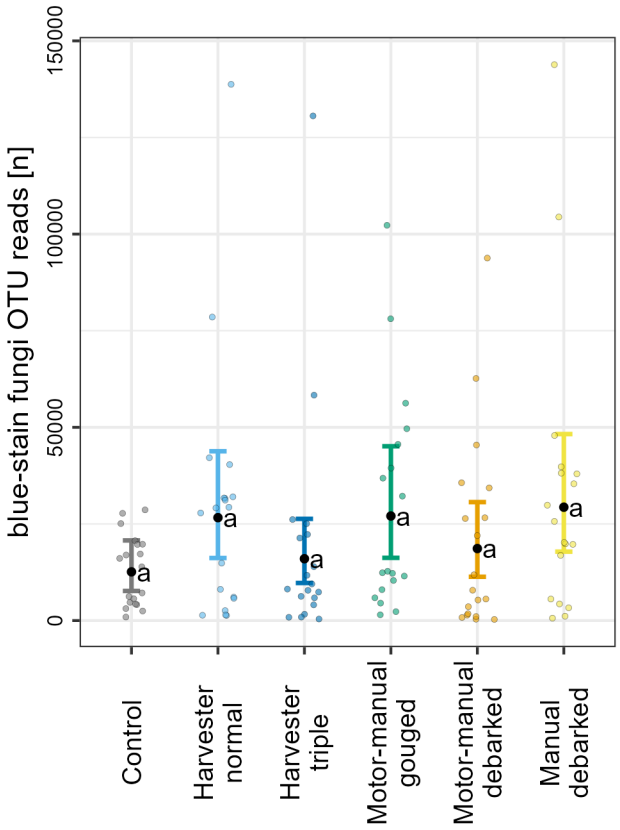

Figure A4.6: Number of reads for blue-stain fungi (ophiostomatoids: *Ophiostomataceae* and *Ceratocystidaceae*) after excluding OTUs detected in the initial drill samples to focus on post-treatment colonization. Read counts were then pooled across the remaining three sampling periods for each site and 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 colored dots show the observed data for each site.

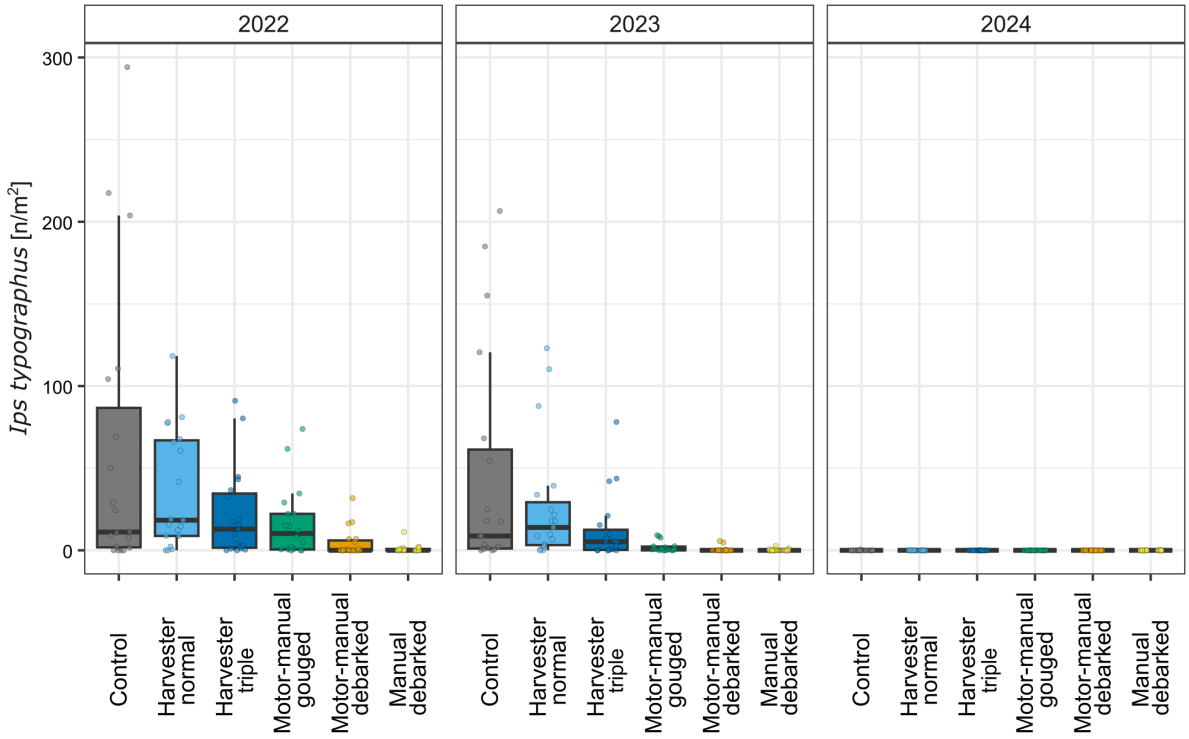

Figure A4.7: Emerging *Ips typographus* (individuals per m^2) from the experimental logs with different bark treatments for bark beetle reduction in the three sampling years (2022, 2023, 2024).

Table A4.1: Summary of mean diameter at breast height (DBH) and tree volume (± standard deviation) for each treatment and overall.

Treatment	**DBH [cm]**	**SD DBH [cm]**	**Volume [m^3]**	**SD Volume [m^3]**
Control	43	8	1.55	0.76
Harvester normal	37	4	0.95	0.34
Harvester triple	39	6	1.16	0.46
Motor-manual gouged	35	6	0.87	0.47
Motor-manual debarked	34	7	0.82	0.65
Manual debarked	33	8	0.73	0.55
Overall	**37**	**7**	**1.01**	**0.61**

Table A4.2: 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.

Family	*Species*	Autor, year	Control	Harvester normal	Harvester triple	Motor-manual gouged	Motor-manual debarked	Manual debarked	Total
Carabidae	*Tachyta nana*	(Gyll., 1810)	3	1	2	1	1	1	**9**
Histeridae	*Plegaderus vulneratus*	(Panzer, 1797)	68	24	35	19	6	2	**154**
Histeridae	*Plegaderus caesus*	(Herbst, 1792)	1	0	1	0	0	0	**2**
Histeridae	*Plegaderus dissectus*	Er., 1839	48	7	13	4	1	3	**76**
Histeridae	*Abraeus granulum*	Er., 1839	0	0	1	0	0	0	**1**
Histeridae	*Paromalus flavicornis*	(Herbst, 1792)	33	25	30	8	11	5	**112**
Histeridae	*Paromalus parallelepipedus*	(Herbst, 1792)	17	21	6	11	4	0	**59**
Histeridae	*Platysoma lineare*	Er., 1834	9	3	4	1	0	1	**18**
Leiodidae	*Anisotoma humeralis*	(F., 1792)	0	0	0	1	0	0	**1**
Leiodidae	*Anisotoma glabra*	(F., 1787)	0	0	0	0	0	1	**1**
Leiodidae	*Anisotoma orbicularis*	(Herbst, 1792)	1	0	0	0	0	0	**1**
Leiodidae	*Agathidium nigripenne*	(F., 1792)	0	0	2	0	0	0	**2**
Staphylinidae	*Neuraphes carinatoides*	Rtt., 1909	2	0	3	0	0	1	**6**
Staphylinidae	*Stenichnus godarti*	(Latr., 1806)	9	11	7	7	1	2	**37**
Staphylinidae	*Microscydmus minimus*	(Chaud., 1845)	1	0	0	0	1	0	**2**
Ptiliidae	*Ptenidium turgidum*	C. Thoms., 1855	2	0	1	0	0	1	**4**
Ptiliidae	*Ptinella aptera*	(Guér.Mén., 1839)	0	2	1	2	0	0	**5**
Ptiliidae	*Pteryx suturalis*	(Heer, 1841)	10	15	6	13	13	14	**71**
Staphylinidae	*Siagonium quadricorne*	Kirby.Sp., 1815	1	0	3	2	1	1	**8**
Staphylinidae	*Scaphisoma agaricinum*	(L., 1758)	8	15	5	3	15	1	**47**
Staphylinidae	*Phloeocharis subtilissima*	Mannerh., 1830	5	9	6	7	3	2	**32**
Staphylinidae	*Acrulia inflata*	(Gyll., 1813)	1	1	2	5	4	1	**14**
Staphylinidae	*Phyllodrepa melanocephala*	(F., 1787)	2	0	0	2	2	1	**7**
Staphylinidae	*Hypopycna rufula*	(Er., 1840)	1	0	0	0	0	0	**1**
Staphylinidae	*Dropephylla linearis*	(Zett., 1828)	0	0	1	0	0	1	**2**

Family	*Species*	Autor, year	Control	Harvester normal	Harvester triple	Motor-manual gouged	Motor-manual debarked	Manual debarked	Total
Staphylinidae	*Dropephylla ioptera*	(Steph., 1834)	8	1	18	16	2	6	**51**
Staphylinidae	*Phloeonomus pusillus*	(Grav., 1806)	40	62	61	59	56	49	**327**
Staphylinidae	*Phloeonomus punctipennis*	C. Thoms., 1867	1	0	1	0	0	0	**2**
Staphylinidae	*Phloeonomus minimus*	(Er., 1839)	0	0	1	0	0	1	**2**
Staphylinidae	*Xylostiba monilicornis*	(Gyll., 1810)	2	0	0	1	1	0	**4**
Staphylinidae	*Phloeostiba plana*	(Payk., 1792)	1	0	1	0	2	2	**6**
Staphylinidae	*Phloeostiba lapponica*	(Zett., 1838)	0	1	3	1	1	3	**9**
Staphylinidae	*Coryphium angusticolle*	Steph., 1834	0	0	1	2	0	2	**5**
Staphylinidae	*Nudobius lentus*	(Grav., 1806)	28	23	30	4	3	1	**89**
Staphylinidae	*Atrecus affinis*	(Payk., 1789)	14	4	3	6	2	1	**30**
Staphylinidae	*Gabrius splendidulus*	(Grav., 1802)	36	48	24	19	10	10	**147**
Staphylinidae	*Quedius xanthopus*	Er., 1839	9	10	9	13	2	1	**44**
Staphylinidae	*Quedius plagiatus*	Mannerh., 1843	2	2	3	0	2	1	**10**
Staphylinidae	*Sepedophilus testaceus*	(F., 1792)	3	3	0	2	1	2	**11**
Staphylinidae	*Gyrophaena boleti*	(L., 1758)	0	3	0	0	0	0	**3**
Staphylinidae	*Placusa complanata*	Er., 1839	14	7	1	6	0	1	**29**
Staphylinidae	*Placusa depressa*	Mäklin, 1845	84	110	77	46	30	8	**355**
Staphylinidae	*Placusa tachyporoides*	(Waltl, 1838)	1	2	26	26	22	71	**148**
Staphylinidae	*Placusa incompleta*	Sjöb., 1934	3	8	30	6	13	10	**70**
Staphylinidae	*Placusa atrata*	(Mannerh., 1830)	0	0	4	3	0	0	**7**
Staphylinidae	*Placusa pumilio*	(Grav., 1802)	0	0	0	1	1	0	**2**
Staphylinidae	*Homalota plana*	(Gyll., 1810)	1	0	1	1	0	1	**4**
Staphylinidae	*Anomognathus cuspidatus*	(Er., 1839)	0	0	0	1	0	0	**1**
Staphylinidae	*Silusa rubiginosa*	Er., 1837	0	0	0	0	0	1	**1**
Staphylinidae	*Leptusa pulchella*	(Mannerh., 1830)	16	12	13	13	14	8	**76**
Staphylinidae	*Leptusa fumida*	(Er., 1839)	4	3	1	3	3	1	**15**
Staphylinidae	*Euryusa castanoptera*	Kr., 1856	0	0	0	1	0	0	**1**
Staphylinidae	*Bolitochara obliqua*	Er., 1837	19	14	3	3	1	0	**40**

Family	*Species*	Autor, year	Control	Harvester normal	Harvester triple	Motor-manual gouged	Motor-manual debarked	Manual debarked	Total
Staphylinidae	*Bolitochara bella*	Märkel, 1844	0	0	2	0	0	0	**2**
Staphylinidae	*Bolitochara mulsanti*	Sharp, 1875	0	0	0	1	0	0	**1**
Staphylinidae	*Bolitochara tecta*	Grav., 1802	1	0	0	0	0	0	**1**
Staphylinidae	*Dinaraea aequata*	(Er., 1837)	1	0	0	0	0	0	**1**
Staphylinidae	*Dadobia immersa*	(Er., 1837)	1	7	8	2	1	1	**20**
Staphylinidae	*Atheta picipes*	(C. Thoms., 1856)	2	1	24	9	1	1	**38**
Staphylinidae	*Phloeopora teres*	Grav., 1802	1	0	0	0	0	0	**1**
Staphylinidae	*Phloeopora testacea*	(Mannerh., 1830)	7	16	9	5	4	2	**43**
Staphylinidae	*Phloeopora corticalis*	(Grav., 1802)	19	6	8	3	2	4	**42**
Staphylinidae	*Phloeopora scribae*	Epplh., 1884	5	6	6	0	1	0	**18**
Staphylinidae	*Dexiogyia corticina*	(Er., 1837)	0	0	0	1	0	0	**1**
Staphylinidae	*Bibloporus bicolor*	(Denny, 1825)	22	18	16	13	3	10	**82**
Staphylinidae	*Bibloporus minutus*	Raffray, 1914	8	2	0	1	0	1	**12**
Staphylinidae	*Bibloporus mayeti*	Guilleb., 1888	1	0	0	2	0	0	**3**
Staphylinidae	*Euplectus nanus*	(Reichb., 1816)	14	11	14	8	1	9	**57**
Staphylinidae	*Euplectus kirbii*	Denny, 1825	0	0	1	0	0	0	**1**
Staphylinidae	*Euplectus kirbii*	Rtt., 1884	0	0	1	0	0	0	**1**
Staphylinidae	*Euplectus piceus*	Motsch., 1835	2	2	0	1	0	0	**5**
Staphylinidae	*Euplectus punctatus*	Muls.Rey, 1861	15	7	12	4	0	2	**40**
Staphylinidae	*Euplectus karstenii*	Reichb., 1816	3	1	2	0	0	2	**8**
Staphylinidae	*Euplectus mutator*	Fauvel, 1895	0	0	1	0	0	1	**2**
Staphylinidae	*Leptoplectus spinolae*	(Aubé, 1844)	0	1	0	0	0	0	**1**
Staphylinidae	*Plectophloeus nubigena*	(Rtt., 1877)	19	10	5	0	1	2	**37**
Staphylinidae	*Plectophloeus nitidus*	(Fairm., 1858)	1	2	0	1	1	0	**5**
Staphylinidae	*Plectophloeus fischeri*	(Aubé, 1833)	3	2	1	1	0	1	**8**
Staphylinidae	*Tyrus mucronatus*	(Panzer, 1803)	3	3	4	4	0	1	**15**
Cantharidae	*Malthinus frontalis*	(Marsh., 1802)	1	0	0	0	0	0	**1**
Cantharidae	*Malthodes mysticus*	Kiesw., 1852	3	0	1	0	0	0	**4**

Family	*Species*	Autor, year	Control	Harvester normal	Harvester triple	Motor-manual gouged	Motor-manual debarked	Manual debarked	Total
Dasytidae	*Aplocnemus nigricornis*	(F., 1792)	1	0	0	1	0	2	**4**
Dasytidae	*Dasytes plumbeus*	(O. Müller, 1776)	1	0	0	2	2	0	**5**
Cleridae	*Thanasimus formicarius*	(L., 1758)	17	8	4	6	2	6	**43**
Cleridae	*Thanasimus femoralis*	(Zett., 1828)	0	1	0	0	1	0	**2**
Trogossitidae	*Nemozoma elongatum*	(L., 1761)	2	6	0	0	1	0	**9**
Trogossitidae	*Thymalus limbatus*	(F., 1787)	0	0	1	0	0	0	**1**
Elateridae	*Ampedus erythrogonus*	(P. W. Müller, 1821)	0	0	0	0	1	0	**1**
Elateridae	*Ampedus balteatus*	(L., 1758)	1	3	1	3	0	1	**9**
Elateridae	*Ampedus sanguineus*	(L., 1758)	5	2	4	3	1	0	**15**
Elateridae	*Ampedus pomorum*	(Herbst, 1784)	3	1	4	8	2	0	**18**
Elateridae	*Ampedus triangulum*	(Dom, 1924)	0	1	0	0	0	0	**1**
Elateridae	*Ampedus nigrinus*	(Herbst, 1784)	0	0	1	0	2	0	**3**
Elateridae	*Melanotus villosus*	(Geoffr., 1785)	0	0	1	7	0	0	**8**
Elateridae	*Melanotus castanipes*	(Payk., 1800)	4	4	4	21	1	1	**35**
Elateridae	*Denticollis linearis*	(L., 1758)	0	0	1	0	0	0	**1**
Elateridae	*Diacanthous undulatus*	(DeGeer, 1774)	1	2	1	1	0	0	**5**
Eucnemidae	*Hylis olexai*	Palm, 1955	0	0	1	1	0	0	**2**
Eucnemidae	*Hylis foveicollis*	(C. Thoms., 1874)	0	1	0	0	0	1	**2**
Throscidae	*Aulonothroscus brevicollis*	(Bonv., 1859)	1273	1451	367	344	29	40	**3504**
Buprestidae	*Phaenops cyanea*	(F., 1775)	0	1	0	0	0	0	**1**
Cerylonidae	*Cerylon fagi*	C. Brisout, 1867	0	0	0	1	0	0	**1**
Cerylonidae	*Cerylon histeroides*	(F., 1792)	86	45	60	19	16	11	**237**
Cerylonidae	*Cerylon ferrugineum*	Steph., 1830	17	14	8	8	6	11	**64**
Nitidulidae	*Epuraea neglecta*	(Heer, 1841)	0	0	1	0	0	0	**1**
Nitidulidae	*Epuraea pallescens*	(Steph., 1835)	2	13	24	20	26	170	**255**
Nitidulidae	*Epuraea laeviuscula*	(Gyll., 1827)	0	3	0	0	0	0	**3**
Nitidulidae	*Epuraea thoracica*	Tourn., 1872	0	4	14	23	0	0	**41**
Nitidulidae	*Epuraea angustula*	Sturm, 1844	0	1	2	0	0	0	**3**

Family	*Species*	Autor, year	Control	Harvester normal	Harvester triple	Motor-manual gouged	Motor-manual debarked	Manual debarked	Total
Nitidulidae	*Epuraea marseuli*	Rtt., 1873	7	14	3	7	8	4	**43**
Nitidulidae	*Epuraea pygmaea*	(Gyll., 1808)	0	0	2	5	3	1	**11**
Nitidulidae	*Ipidia binotata*	Rtt., 1875	17	18	19	1	7	1	**63**
Nitidulidae	*Glischrochilus quadripunctatus*	(L., 1758)	0	1	0	0	0	0	**1**
Nitidulidae	*Pityophagus ferrugineus*	(L., 1761)	2	6	5	3	2	1	**19**
Monotomidae	*Rhizophagus grandis*	Gyll., 1827	0	1	0	0	0	0	**1**
Monotomidae	*Rhizophagus depressus*	(F., 1792)	12	10	17	15	11	11	**76**
Monotomidae	*Rhizophagus ferrugineus*	(Payk., 1800)	0	0	2	0	0	0	**2**
Monotomidae	*Rhizophagus parallelocollis*	Gyll., 1827	0	1	0	0	0	0	**1**
Monotomidae	*Rhizophagus dispar*	(Payk., 1800)	43	33	46	17	34	30	**203**
Monotomidae	*Rhizophagus bipustulatus*	(F., 1792)	8	6	2	3	1	1	**21**
Monotomidae	*Rhizophagus nitidulus*	(F., 1798)	2	2	11	0	3	1	**19**
Monotomidae	*Rhizophagus fenestralis*	(L., 1758)	4	3	0	0	1	0	**8**
Cucujidae	*Pediacus depressus*	(Herbst, 1797)	4	2	13	3	7	8	**37**
Cucujidae	*Pediacus dermestoides*	(F., 1792)	0	0	0	0	1	0	**1**
Silvanidae	*Silvanus bidentatus*	(F., 1792)	9	26	53	20	37	13	**158**
Silvanidae	*Silvanus unidentatus*	(Olivier, 1790)	3	0	1	0	0	1	**5**
Silvanidae	*Uleiota planatus*	(L., 1761)	12	8	4	2	10	2	**38**
Silvanidae	*Dendrophagus crenatus*	(Payk., 1799)	1	0	1	1	2	0	**5**
Cryptophagidae	*Cryptophagus cylindrellus*	C. Johnson, 2007	0	0	0	0	0	1	**1**
Cryptophagidae	*Cryptophagus dorsalis*	C. Sahlb., 1819	0	2	2	0	0	0	**4**
Cryptophagidae	*Micrambe pilosula*	(Er., 1846)	0	1	2	0	0	2	**5**
Cryptophagidae	*Micrambe abietis*	(Payk., 1798)	0	7	5	8	5	9	**34**
Cryptophagidae	*Atomaria ornata*	Heer, 1841	0	0	0	1	0	0	**1**
Cryptophagidae	*Atomaria turgida*	Er., 1846	1	0	0	1	0	2	**4**
Cryptophagidae	*Atomaria bella*	Rtt., 1875	0	10	11	11	2	1	**35**
Cryptophagidae	*Atomaria lohsei*	C. Johnson & A. Strand, 1968	4	4	10	5	4	4	**31**

Family	*Species*	Autor, year	Control	Harvester normal	Harvester triple	Motor-manual gouged	Motor-manual debarked	Manual debarked	Total
Laemophloeidae	*Placonotus testaceus*	(F., 1787)	0	0	0	1	0	0	**1**
Laemophloeidae	*Cryptolestes duplicatus*	(Waltl, 1839)	0	1	1	1	0	0	**3**
Laemophloeidae	*Cryptolestes corticinus*	(Er., 1846)	0	1	0	0	0	0	**1**
Laemophloeidae	*Leptophloeus alternans*	(Er., 1846)	2	0	1	3	0	0	**6**
Latridiidae	*Latridius hirtus*	Gyll., 1827	1	0	1	3	0	0	**5**
Latridiidae	*Enicmus rugosus*	(Herbst, 1793)	6	1	5	3	3	1	**19**
Latridiidae	*Enicmus testaceus*	(Steph., 1830)	0	1	0	2	0	2	**5**
Latridiidae	*Stephostethus alternans*	(Mannerh., 1844)	1	0	1	2	0	0	**4**
Latridiidae	*Corticaria longicornis*	(Herbst, 1783)	7	5	6	7	9	9	**43**
Latridiidae	*Corticaria foveola*	(Beck, 1817)	0	0	1	0	0	0	**1**
Latridiidae	*Corticaria longicollis*	(Zett., 1838)	0	1	1	0	1	0	**3**
Latridiidae	*Corticarina lambiana*	(Sharp, 1910)	0	0	1	0	0	0	**1**
Latridiidae	*Corticarina parvula*	Mannerh., 1844	1	1	0	1	0	1	**4**
Mycetophagidae	*Litargus connexus*	(Geoffr., 1785)	4	1	1	0	1	0	**7**
Mycetophagidae	*Mycetophagus quadripustulatus*	(L., 1760)	0	0	2	0	0	0	**2**
Mycetophagidae	*Mycetophagus atomarius*	(F., 1787)	0	0	0	0	1	0	**1**
Zopheridae	*Bitoma crenata*	(F., 1775)	48	5	12	2	3	1	**71**
Zopheridae	*Colydium elongatum*	(F., 1787)	2	0	1	0	0	0	**3**
Corylophidae	*Orthoperus atomus*	(Gyll., 1808)	2	2	3	2	8	9	**26**
Corylophidae	*Orthoperus corticalis*	(L. Redt., 1845)	2	2	5	21	10	3	**43**
Endomychidae	*Symbiotes gibberosus*	(Lucas, 1846)	1	2	0	2	1	2	**8**
Endomychidae	*Mycetina cruciata*	(Schaller, 1783)	0	20	0	7	0	0	**27**
Endomychidae	*Endomychus coccineus*	(L., 1758)	1	0	0	0	0	0	**1**
Sphindidae	*Aspidiphorus orbiculatus*	(Gyll., 1808)	1	1	0	0	0	0	**2**
Ciidae	*Sulcacis nitidus*	(F., 1792)	0	1	3	0	0	0	**4**
Ciidae	*Sulcacis fronticornis*	(Panzer, 1805)	1	0	0	0	0	0	**1**
Ciidae	*Cis jacquemartii*	Mellié, 1848	1	0	0	0	0	0	**1**
Ciidae	*Cis glabratus*	Mellié, 1848	0	0	1	0	0	0	**1**

Family	*Species*	Autor, year	Control	Harvester normal	Harvester triple	Motor-manual gouged	Motor-manual debarked	Manual debarked	Total
Ciidae	*Cis micans*	(F., 1792)	0	0	1	0	0	0	**1**
Ciidae	*Cis boleti*	(Scop., 1763)	1	1	0	1	2	0	**5**
Ciidae	*Cis punctulatus*	Gyll., 1827	4	0	0	0	0	0	**4**
Ciidae	*Cis dentatus*	Mellié, 1848	0	0	0	1	0	0	**1**
Ciidae	*Cis bidentatus*	(Olivier, 1790)	1	1	0	1	0	0	**3**
Ciidae	*Cis festivus*	(Panzer, 1793)	0	0	0	0	1	0	**1**
Ciidae	*Ennearthron cornutum*	(Gyll., 1827)	1	0	0	0	0	0	**1**
Ciidae	*Hadraule elongatula*	(Gyll., 1827)	0	0	1	0	0	0	**1**
Ptinidae	*Dryophilus pusillus*	(Gyll., 1808)	0	0	1	0	0	1	**2**
Ptinidae	*Ernobius mollis*	(L., 1758)	1	0	0	0	0	2	**3**
Ptinidae	*Microbregma emarginatum*	Duft., 1825	2	0	0	0	0	0	**2**
Ptinidae	*Hadrobregmus denticollis*	(Creutzer, 1796)	0	0	0	1	0	0	**1**
Ptinidae	*Hadrobregmus pertinax*	(L., 1758)	0	0	1	0	0	0	**1**
Ptinidae	*Ptilinus pectinicornis*	(L., 1758)	0	1	0	0	0	0	**1**
Prostomidae	*Prostomis mandibularis*	(F., 1801)	0	0	1	0	0	0	**1**
Scraptiidae	*Anaspis frontalis*	(L., 1758)	0	0	0	1	0	0	**1**
Scraptiidae	*Anaspis maculata*	(Geoffr., 1785)	0	1	0	0	0	0	**1**
Scraptiidae	*Anaspis septentrionalis*	Champion, 1891	1	0	0	0	0	2	**3**
Scraptiidae	*Anaspis thoracica*	(L., 1758)	0	0	1	0	0	0	**1**
Scraptiidae	*Anaspis ruficollis*	(F., 1792)	1	2	2	4	2	3	**14**
Scraptiidae	*Anaspis rufilabris*	(Gyll., 1827)	0	0	0	0	0	1	**1**
Scraptiidae	*Anaspis flava*	(L., 1758)	1	1	1	0	1	0	**4**
Aderidae	*Euglenes oculatus*	(Payk., 1798)	5	2	0	1	0	0	**8**
Aderidae	*Anidorus nigrinus*	(Germar, 1842)	1	1	6	2	1	0	**11**
Aderidae	*Anidorus sanguinolentus*	(Kiesw., 1861)	0	0	0	1	0	0	**1**
Melandryidae	*Wanachia triguttata*	(Gyll., 1810)	4	0	0	0	4	0	**8**
Melandryidae	*Serropalpus barbatus*	(Schaller, 1783)	1	0	1	2	0	0	**4**
Tetratomidae	*Hallomenus binotatus*	(Quensel, 1790)	0	0	1	1	0	1	**3**

Family	*Species*	Autor, year	Control	Harvester normal	Harvester triple	Motor-manual gouged	Motor-manual debarked	Manual debarked	Total
Tenebrionidae	*Corticeus unicolor*	Pill.Mitt., 1783	10	2	0	1	2	1	**16**
Tenebrionidae	*Corticeus fraxini*	(Kugel., 1794)	0	3	0	0	1	0	**4**
Tenebrionidae	*Corticeus bicolor*	(Olivier, 1790)	0	0	1	0	0	0	**1**
Tenebrionidae	*Corticeus linearis*	F., 1790	8	2	0	1	0	0	**11**
Cerambycidae	*Arhopalus rusticus*	(L., 1758)	0	0	2	2	0	0	**4**
Cerambycidae	*Tetropium castaneum*	(L., 1758)	24	2	16	30	11	12	**95**
Cerambycidae	*Tetropium fuscum*	(F., 1787)	26	9	15	7	0	0	**57**
Cerambycidae	*Rhagium mordax*	(DeGeer, 1775)	0	0	0	1	0	0	**1**
Cerambycidae	*Rhagium inquisitor*	(L., 1758)	3	5	1	4	0	0	**13**
Cerambycidae	*Stictoleptura rubra*	(L., 1758)	2	0	0	2	0	2	**6**
Cerambycidae	*Acanthocinus griseus*	(F., 1792)	24	21	13	0	0	0	**58**
Curculionidae	*Phloeotribus spinulosus*	(Rey, 1883)	0	0	0	0	1	0	**1**
Curculionidae	*Hylastes brunneus*	(Er., 1836)	0	0	2	5	0	0	**7**
Curculionidae	*Hylastes cunicularius*	Er., 1836	2	2	3	3	3	1	**14**
Curculionidae	*Hylurgops palliatus*	(Gyll., 1813)	742	529	60	29	11	3	**1374**
Curculionidae	*Tomicus minor*	(Hartig, 1834)	0	0	0	0	0	1	**1**
Curculionidae	*Tomicus piniperda*	(L., 1758)	0	1	0	0	0	0	**1**
Curculionidae	*Polygraphus poligraphus*	(L., 1758)	13	2	0	0	0	1	**16**
Curculionidae	*Crypturgus cinereus*	(Herbst, 1794)	171	204	685	24	3	11	**1098**
Curculionidae	*Crypturgus subcribrosus*	Eggers, 1933	4431	2663	1086	265	25	65	**8535**
Curculionidae	*Crypturgus hispidulus*	C. Thoms., 1870	797	400	293	90	16	27	**1623**
Curculionidae	*Crypturgus pusillus*	(Gyll., 1813)	1110	1597	3976	61	7	6	**6757**
Curculionidae	*Dryocoetes autographus*	(Ratz., 1837)	222	204	233	86	32	16	**793**
Curculionidae	*Dryocoetes hectographus*	Rtt., 1913	1	0	1	0	0	0	**2**
Curculionidae	*Cryphalus asperatus*	(Gyll., 1813)	0	1	0	0	1	1	**3**
Curculionidae	*Pityophthorus pityographus*	(Ratz., 1837)	0	1	1	0	0	0	**2**
Curculionidae	*Gnathotrichus materiarius*	(Fitch, 1858)	0	24	1	0	0	0	**25**
Curculionidae	*Taphrorychus bicolor*	(Herbst, 1794)	0	0	0	0	0	1	**1**

Family	***Species***	**Autor, year**	**Control**	**Harvester normal**	**Harvester triple**	**Motor-manual gouged**	**Motor-manual debarked**	**Manual debarked**	**Total**
Curculionidae	*Pityogenes chalcographus*	(L., 1760)	2177	1170	324	111	29	75	**3886**
Curculionidae	*Orthotomicus laricis*	(F., 1792)	0	0	0	0	1	0	**1**
Curculionidae	*Ips typographus*	(L., 1758)	4726	2503	1495	1276	197	56	**10253**
Curculionidae	*Cyclorhipidion bodoanum*	(Rtt., 1913)	5	1	0	1	0	0	**7**
Curculionidae	*Anisandrus dispar*	(F., 1792)	0	1	0	0	0	0	**1**
Curculionidae	*Xyleborinus saxesenii*	(Ratz., 1837)	30	30	0	3	1	34	**98**
Curculionidae	*Xylosandrus germanus*	(Blandf., 1894)	35	37	90	14	22	33	**231**
Curculionidae	*Trypodendron lineatum*	(Olivier, 1795)	30	78	165	1	32	1	**307**
Curculionidae	*Rhyncolus ater*	(L., 1758)	7	9	6	26	6	20	**74**
Curculionidae	*Pissodes harcyniae*	(Herbst, 1795)	0	0	0	1	0	0	**1**
Curculionidae	*Trachodes hispidus*	(L., 1758)	8	4	4	5	5	3	**29**
Curculionidae	*Hylobius abietis*	(L., 1758)	0	1	1	8	0	0	**10**
Dryophthoridae	*Dryophthorus corticalis*	(Payk., 1792)	0	0	0	0	0	1	**1**

Table A4.3: 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.

	Extrapolation value	Control	Harvester normal	Harvester triple	Motor-manual gouged	Motor-manual debarked	Manual debarked
Beetles	91%	89%	91%	89%	90%	85%	81%
Fungi	90%	80%	84%	85%	83%	85%	85%
Bacteria	95%	89%	89%	90%	89%	91%	90%

Table A4.4: 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 two years, together with model estimates for the observed number of woodpecker foraging holes, saproxylic beetle species, fungal, and bacterial OTUs.

	EMM	SE	df	Lower 95% CI	Upper 95% CI	Grouping letter
***I. typographus* per m^2 [n]**						
Control	100.71	34.96	Inf	51.00	198.86	a
Harvester normal	50.60	17.20	Inf	26.00	98.50	ab
Harvester triple	24.02	8.40	Inf	12.10	47.66	bc
Motor-manual gouged	12.85	4.68	Inf	6.29	26.24	c
Motor-manual debarked	2.93	1.18	Inf	1.33	6.43	d
Manual debarked	1.00	0.42	Inf	0.44	2.29	d
Treated wood [m^3/h]						
Harvester normal	54.89	5.86	44.34	44.26	68.07	a
Harvester triple	27.42	3.19	47.43	21.70	34.66	b
Motor-manual gouged	2.34	0.25	43.81	1.89	2.89	c
Motor-manual debarked	1.25	0.13	44.33	1.01	1.56	d
Manual debarked	0.65	0.08	47.22	0.51	0.82	e
Change in Moisture content [%]						
Control	2.03	1.07	84.45	−0.09	4.16	a
Harvester normal	−0.38	1.07	84.45	−2.50	1.75	ab
Harvester triple	−3.82	1.07	84.45	−5.94	−1.69	bc
Motor-manual gouged	−7.14	1.09	86.91	−9.32	−4.97	cd
Motor-manual debarked	−7.93	1.07	84.45	−10.06	−5.80	d
Manual debarked	-8.05	1.07	84.45	−10.17	−5.92	d

	EMM	SE	df	Lower 95% CI	Upper 95% CI	Grouping letter
Change in net calorific value [MJ/kg]						

Control	0.08	0.11	65.08	−0.14	0.30	a
Harvester normal	−0.05	0.11	65.08	−0.26	0.17	a
Harvester triple	0.23	0.11	65.08	0.01	0.45	a
Motor-manual gouged	0.21	0.11	67.95	−0.01	0.43	a
Motor-manual debarked	−0.05	0.11	65.08	−0.27	0.16	a
Manual debarked	0.22	0.11	65.08	0.00	0.44	a
Change in carbon [%]						
Control	0.19	0.15	92.57	-0.10	0.49	a
Harvester normal	0.14	0.15	92.57	-0.16	0.43	a
Harvester triple	0.14	0.15	92.57	-0.15	0.44	a
Motor-manual gouged	0.38	0.15	94.44	0.07	0.68	a
Motor-manual debarked	−0.02	0.15	92.57	-0.31	0.28	a
Manual debarked	0.32	0.15	92.57	0.02	0.62	a
Woodpecker activity [n]						
Control	75.11	28.31	75.34	35.28	158.66	a
Harvester normal	8.49	3.22	72.79	3.83	17.66	b
Harvester triple	5.66	2.30	73.31	2.35	12.25	bc
Motor-manual gouged	0.97	0.69	76.41	-0.02	2.94	cd
Motor-manual debarked	0.03	0.36	73.25	-0.48	1.05	d
Manual debarked	0.06	0.37	74.08	-0.48	1.14	d
Saproxylic beetle species richness [n]						
Control	20.74	1.41	85.47	17.93	23.55	a
Harvester normal	20.89	1.41	85.47	18.09	23.7	a
Harvester triple	21.21	1.41	85.47	18.4	24.02	a
Motor-manual gouged	19.71	1.45	87.87	16.84	22.59	a
Motor-manual debarked	12.05	1.41	85.47	9.24	14.86	b
Manual debarked	12.32	1.41	85.47	9.51	15.13	b
Fungi OTU richness [n]						
Control	530.16	30.26	94.58	470.08	590.24	a
Harvester normal	591.89	30.26	94.58	531.81	651.98	ab
Harvester triple	616.26	30.26	94.58	556.18	676.35	abc
Motor-manual gouged	600.56	31.04	96.26	538.94	662.17	abc
Motor-manual debarked	714.37	30.26	94.58	654.29	774.45	c
Manual debarked	679.42	30.26	94.58	619.34	739.50	bc

	EMM	**SE**	**df**	**Lower 95% CI**	**Upper 95% CI**	**Grouping letter**
Bacteria OTU richness [n]						
Control	1725.74	79.32	67.74	1567.44	1884.03	a
Harvester normal	1762.11	79.32	67.74	1603.81	1920.40	a
Harvester triple	1882.37	79.32	67.74	1724.07	2040.66	a

Motor-manual gouged	1776.31	80.98	70.63	1614.82	1937.79	a
Motor-manual debarked	1716.53	79.32	67.74	1558.23	1874.82	a
Manual debarked	1765.42	79.32	67.74	1607.13	1923.72	a

Table A4.5: 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 *P. abies* logs within the forest stand. p-values were adjusted with *Bonferroni* correction for multiple testing.

	Comparison		R2	Adj. p-value	
Saproxylic beetles	**overall**	**1.82**	**0.08**	**0.016**	*
	Control-Harvester normal	0.99	0.03	1	
	Harvester triple-Control	1.39	0.04	1	
	Motor-manual gouged-Control	1.97	0.05	0.112	
	Motor-manual debarked-Control	**3.11**	**0.08**	**0.016**	*
	Manual debarked-Control	**2.97**	**0.08**	**0.016**	*
	Harvester triple-Harvester normal	0.61	0.02	1	
	Harvester normal-Manual debarked	**2.65**	**0.07**	**0.016**	*
	Harvester normal-Motor-Manual debarked	2.43	0.06	0.064	*
	Harvester normal-Motor-manual gouged	1.51	0.04	1	
	Harvester triple-Motor-manual gouged	1.25	0.03	1	
	Harvester triple-Manual debarked	**2.29**	**0.06**	**0.016**	
	Harvester triple-Motor-manual debarked	1.98	0.05	0.208	
	Manual debarked-Motor-manual debarked	0.72	0.02	1	
	Manual debarked-Motor-manual gouged	1.6	0.04	0.559	
	Motor-manual debarked-Motor-manual gouged	1.48	0.04	1	
Fungi OTUs	**overall**	**2.378**	**0.100**	**0.016**	*
	Control-Harvester normal	**1.523**	**0.041**	**0.016**	*
	Control-Harvester triple	**2.277**	**0.059**	**0.016**	*
	Control-Motor-manual debarked	**4.144**	**0.103**	**0.016**	*
	Control-Manual debarked	**4.271**	**0.106**	**0.016**	*
	Control-Motor-manual gouged	**2.505**	**0.067**	**0.016**	*
	Harvester normal-Harvester triple	**1.315**	**0.035**	**0.016**	*
	Harvester normal-Manual debarked	**3.607**	**0.091**	**0.016**	*
	Harvester normal-Motor-manual debarked	**3.117**	**0.080**	**0.016**	*
	Harvester normal-Motor-manual gouged	**1.749**	**0.048**	**0.016**	*
	Harvester triple-Manual debarked	**2.869**	**0.074**	**0.016**	*
	Harvester triple-Motor-manual debarked	**2.317**	**0.060**	**0.016**	*
	Harvester triple-Motor-manual gouged	**1.307**	**0.036**	**0.016**	*
	Manual debarked-Motor-manual debarked	**1.079**	**0.029**	**0.032**	*
	Manual debarked-Motor-manual gouged	**1.941**	**0.053**	**0.016**	*
	Motor-manual debarked-Motor-manual gouged	**1.512**	**0.041**	**0.016**	*

	Comparison	F.Model	R2	Adj. p-value	
Ba	**overall**	**2.577**	**0.107**	**0.016**	*
	Control-Harvester normal	**1.336**	**0.036**	**0.016**	*

Control-Harvester triple	**1.994**	**0.052**	**0.016**	*
Control-Motor-manual debarked	**4.969**	**0.121**	**0.016**	*
Control-Manual debarked	**5.064**	**0.123**	**0.016**	*
Control-Motor-manual gouged	**2.653**	**0.070**	**0.016**	*
Harvester normal-Harvester triple	**1.218**	**0.033**	**0.016**	*
Harvester normal-Manual debarked	**3.868**	**0.097**	**0.016**	*
Harvester normal-Motor-manual debarked	**3.865**	**0.097**	**0.016**	*
Harvester normal-Motor-manual gouged	**1.791**	**0.049**	**0.016**	*
Harvester triple-Manual debarked	**2.935**	**0.075**	**0.016**	*
Harvester triple-Motor-manual debarked	2.907	0.075	0.096	
Harvester triple-Motor-manual gouged	1.351	0.037	0.096	
Manual debarked-Motor-manual debarked	**1.116**	**0.030**	**0.016**	*
Manual debarked-Motor-manual gouged	**1.766**	**0.048**	**0.016**	*
Motor-manual debarked-Motor-manual gouged	**1.779**	**0.048**	**0.016**	*

Table A4.6: Linear mixed models with the study sites as random effect which were combined for the piecewise structural equation modelling (SEM).

Response variable	Predictors	Model	R^2_m	R^2_c
I. Typographus per m^2 [n]	bark cover + Δ moisture content	glmer.nb()	0.44	0.59
Δ moisture content [%]	bark cover	lme()	0.40	0.52
Woodpecker activity [n]	bark cover + *I. typographus* + Δ moisture content + beetle richness	glmer.nb()	0.33	0.35
Beetle species richness [n]	Δ moisture content + bark cover	lme()	0.36	0.49
Fungi OTU richness [n]	Δ moisture content + bark cover + beetle richness + *I. Typographus* + bacteria richness	lme()	0.18	0.34
Bacteria OTU richness [n]	Δ moisture content + bark cover + beetle richness	lme()	0.24	0.45
Δ carbon [%]	Δ moisture content + beetle richness + fungi richness + bacteria richness	lme()	0.04	0.20
Δ hydrogen [%]	Δ moisture content + beetle richness + fungi richness + bacteria richness	lme()	0.07	0.16
Δ nitrogen [%]	Δ moisture content + beetle richness + fungi richness + bacteria richness	lme()	0.05	0.07

Table A4.7 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.

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Standardized estimate
***I. Typographus* per m² [n]**	**bark cover [%]**	**0.05**	**0.00**	**113**	**9.62**	**0.000**	**0.530**
I. Typographus per m² [n]	Δ moisture content [%]	−0.04	0.03	113	−1.27	0.203	−0.067
Δ moisture content [%]	**bark cover [%]**	**0.10**	**0.01**	**93**	**9.56**	**0.000**	**0.630**
Woodpecker activity [n]	*I. Typographus* per m² [n]	0.00	0.01	113	−0.55	0.580	−0.012
Woodpecker activity [n]	**bark cover [%]**	**0.08**	**0.01**	**113**	**6.31**	**0.000**	**0.184**
Woodpecker activity [n]	Δ moisture content [%]	−0.04	0.06	113	−0.63	0.530	−0.013
Woodpecker activity [n]	Beetle species richness [n]	0.08	0.04	113	1.88	0.060	0.038
Beetle species richness [n]	**Δ moisture content [%]**	**−0.49**	**0.14**	**92**	**−3.58**	**0.001**	**−0.352**
Beetle species richness [n]	**bark cover [%]**	**0.17**	**0.02**	**92**	**8.28**	**0.000**	**0.764**
Bacteria OTU richness [n]	Δ moisture content [%]	−9.37	6.15	90	−1.52	0.131	−0.165
Bacteria OTU richness [n]	bark cover [%]	1.85	1.14	90	1.63	0.107	0.200
Bacteria OTU richness [n]	**Fungi OTU richness [n]**	**1.17**	**0.21**	**90**	**5.60**	**0.000**	**0.485**
Bacteria OTU richness [n]	Beetle species richness [n]	5.96	4.13	90	1.44	0.152	0.146
Fungi OTU richness [n]	Δ moisture content [%]	−2.04	2.90	90	−0.70	0.483	−0.086
Fungi OTU richness [n]	bark cover [%]	−0.80	0.63	90	−1.27	0.206	−0.209
Fungi OTU richness [n]	*I. Typographus* per m² [n]	−0.04	0.28	90	−0.14	0.886	−0.016
Fungi OTU richness [n]	**Beetle species richness [n]**	**−3.88**	**1.87**	**90**	**−2.07**	**0.041**	**−0.229**
Δ carbon [%]	Δ moisture content [%]	−0.01	0.01	90	−0.98	0.331	−0.094
Δ carbon [%]	Fungi OTU richness [n]	0.00	0.00	90	0.62	0.535	0.073
Δ carbon [%]	Bacteria OTU richness [n]	0.00	0.00	90	−1.59	0.115	−0.182
Δ carbon [%]	Beetle species richness [n]	0.01	0.01	90	1.26	0.211	0.131
Δ hydrogen [%]	Δ moisture content [%]	0.00	0.00	90	−0.23	0.821	−0.022
Δ hydrogen [%]	Fungi OTU richness [n]	0.00	0.00	90	−0.57	0.568	−0.068
Δ hydrogen [%]	**Bacteria OTU richness [n]**	**0.00**	**0.00**	**90**	**2.23**	**0.029**	**0.254**

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Standardized estimate
Δ hydrogen [%]	Beetle species richness [n]	0.00	0.00	90	0.85	0.398	0.089
Δ nitrogen [%]	Δ moisture content [%]	0.00	0.00	90	−0.94	0.349	−0.092
Δ nitrogen [%]	**Fungi OTU richness [n]**	**0.00**	**0.00**	**90**	**−2.03**	**0.045**	**−0.241**
Δ nitrogen [%]	Bacteria OTU richness [n]	0.00	0.00	90	1.82	0.073	0.202
Δ nitrogen [%]	Beetle species richness [n]	0.00	0.00	90	−1.54	0.127	−0.160

Text A4.1: Methods Metabarcoding

Wetlab:

Species identification of organic material in wood samples was performed using DNA metabarcoding following the basic protocol of (Hausmann et al., 2020). Each sample was dried at 60 °C for at least eight hours and subsequently homogenised in a FastPrep96 machine (MP Biomedicals) using sterile steel beads to generate a homogeneous mixture of wood. Prior to DNA extraction, 1 mg of each homogenate was weighed into sample vials and processed using adapted volumes of lysis buffer with the Quick-DNA Fecal/Soil Microbe Kit (Zymo Research Europe GmbH, Freiburg, Germany) following the manufacturer's instructions. Three negative controls (NC) were used – one DNA extraction NC, one PCR NC and one ligation NC along with the samples. NCs were used to filter out reads within the NC filtering step in the bioinformatic postprocessing of the FASTQ files. NCs ran with PCR grade water within the steps. To eliminate PCR inhibitors that might be present within the samples, polyvinylpyrrolidone (PVP) was added to the DNA extraction buffers, and if initial PCRs did not succeed, further cleaning steps of the extracted DNA were performed. For amplification of the target regions and preparation of the MiSeq libraries, a 2-step PCR was performed. Illumina-ready primers derived from the primer pairs by (Toju et al., 2012) (ITS3_KYO2 5′ - GATGAAGAACGYAGYRAA- 3’ ITS4_KYO2 5′ - RBTTTCTTTTCCTCCGCT- 3′) and (Thijs et al., 2017) (341f 5′ - CCTACGGGNGGCWGCAG- 3’ 785r 5′ - GACTACHVGGGTATCTAATCC- 3′) were used, with forward and reverse HTS primers equipped with complementary sites for the Illumina sequencing tails. In a subsequent PCR reaction, index primers with unique i5 and i7 inline tags and sequencing tails were used for amplification of indexed amplicons. Afterwards, equimolar amplicon pools were created and size selected using preparative gel electrophoresis. The pooled DNA was purified using MagSi-NGSprep Plus beads (Steinbrenner Laborsysteme GmbH, Wiesenbach, Germany). A bioanalyzer (High Sensitivity DNA Kit, Agilent Technologies) was used for a final check of the bp distribution and concentration of the amplicons before the creation of the final library. High-throughput sequencing (HTS) was performed on an Illumina MiSeq using v2 (2*250 bp, 500 cycles, maximum of 20 mio reads) chemistry (Illumina) aiming for ~250.000 raw reads before merging. Samples ran on complete flow cell in combination with other samples from other jobs/other amplicons.

Bioinformatics

Preprocessing of raw Illumina reads - ITS and 16S

Taking as input the demultiplexed sample FASTQ R1 and R2 file pairs, paired-end reads were merged using the -fastq_mergepairs utility of USEARCH v11.0.667_i86linux32 (Edgar, 2010) with the parameters -fastq_maxdiffs 99, -fastq_pctid 75, -fastq_trunctail 0 (see https://www.drive5.com/usearch/manual/merge_options.html for the description of options used). Merged reads were re-labeled using the sample filenames, and prepared for adapter trimming by reverse complementing and then concatenating the result with original reads. The reverse complementing was carried out using the --fastx_revcomp utility of VSEARCH v2.28.1_linux_x86_64 (Rognes et al., 2016) (for the details on the utilities and options used, see https://github.com/torognes/vsearch/releases/download/v2.28.1/vsearch_manual.pdf). These concatenated files were then subjected to two rounds of adapter trimming (i.e. single-

end mode) using CUTADAPT (M. Martin, 2011) with default parameters (maximum of 10% mismatches allowed - see https://cutadapt.readthedocs.io/en/stable/reference.html for details). Reads that did not contain the appropriate adapter sequences were filtered out in this step using CUTADAPT's --discard-untrimmed option. Next, quality filtering was performed using the VSEARCH --fastq_filter utility, allowing a maximum of 1 expected error along the length of the sequence and a minimum read length of 150 bases (parameters: --fastq_maxee 1, --minlen 150). Then, each sample file was dereplicated using the --derep_fulllength VSEARCH utility, keeping only a single copy of each unique sequence (parameters: --sizeout, --relabel Uniq). Cleaned and dereplicated sample files were concatenated into one large FASTA file, which was then dereplicated again using --derep_fulllength, and also filtered for sequences occurring only once in the entire dataset (i.e. dataset-wide singletons) with the parameters --minuniquesize 2, --sizein, --sizeout, --fasta_width 0. A pre-clustering step (at 98% identity) was employed before attempting chimera filtering, using the VSEARCH utility --cluster_size and the centroids algorithm (parameters: --id 0.98, --strand plus, --sizein, --sizeout, --fasta_width 0, --centroids). Chimeric sequences were then detected and filtered out using the VSEARCH --uchime_denovo utility and the parameters: --sizein, --sizeout, --fasta_width 0, --nonchimeras). Then, a perl script obtained from the authors of VSEARCH (see https://github.com/torognes/vsearch/wiki/VSEARCH-pipeline) was used to regenerate the concatenated FASTA file, but without the subsequently detected chimeric sequences. The resulting chimera-filtered file was then used to cluster the reads into operational taxonomic units (OTUs) again using the --cluster_size with the centroids algorithm, but this time at 97% identity (parameters: --id 0.97, --strand both, --sizein, --sizeout, --fasta_width 0, --centroids). In the same step, the OTU table matrix was constructed from the resulting clustered UC file by employing the --otutabout parameter. To reduce the risk of false positives, another cleaning step excluded read counts in the OTU table based on negative control samples. If the number of reads for the OTU in any sample was less than the maximum for that OTU among negative controls, those reads were excluded from further analysis.

BLAST

BLAST searches were performed by means of the blastn utility of NCBI BLAST+ v.2.10.0 (https://ftp.ncbi.nlm.nih.gov/blast/executables/blast+/) and the parameters -task megablast -max_target_seqs 1 -max_hsps 1 -evalue 10 -word_size 28 -outfmt "6 sacc pident salltitles qseqid length evalue qcovs staxids". For each query OTU, matches with the highest Hit-%-ID (the percentage of identical base pairs of the OTU query sequence with its closest counterpart in the reference database) were kept.

ITS reference database construction & annotation

OTU sequences were blasted against (1) a preformatted database downloaded on 21 July 2023 from ftp://ftp.ncbi.nlm.nih.gov/blast/db/, and (2) a custom database built from data downloaded from BOLD (www.boldsystems.org) (Ratnasingham & Hebert, 2007, 2013). To construct the BOLD BLAST reference, data was downloaded from the BOLD database on 11 July 2023 using the public data API (http://www.boldsystems.org/index.php/resources/api) in a combined TSV file format. The combined TSV file was then filtered to keep only the records that: (1) had a sequence (field 72, "nucleotides"); (2) had a sequence that did not hold exclusively one or more "-"

(hyphens); had a sequence that did not contain non-IUPAC characters; and (3) belonged to ITS/ITS1/ITS2 (the pattern "ITS" in either field 70 (markercode) or field 80 (marker_codes)). Finally, a FASTA file annotated with (1) a Process ID (field 1, processid), (2) taxonomy (fields 10, 12, 14, 16, 18, 20, 22: phylum_name, class_name, order_name, family_name, subfamily_name, genus_name, species_name), (3) geolocation data (fields 47, 48, 55), and (4) GenBank ID (field 71, genbank_accession) was created from the filtered combined TSV file. This FASTA file was then converted into a BLAST database using the makeblastdb utility of NCBI BLAST+. The CSV files containing BOLD and NCBI BLAST results were combined with the OTU table matrix of read counts per sample and OTU generated by the bioinformatic pre-processing pipeline. The CSVs included: (1) OTU query ID; (2) BOLD Process ID, (3) NCBI Accession ID, (4) NCBI taxonomy ID, (5) BOLD and NCBI BLAST Hit-%-ID values; (6) BOLD and NCBI Grade-%-ID values; (7) lengths of the top BLAST hit sequences from BOLD and NCBI; (8) geolocation data from BOLD (latitude, longitude, country), (9) record description data from NCBI, and (10) phylum, class, order, family, genus and species annotations from BOLD and NCBI. OTUs were additionally classified into taxa using the Ribosomal Database Project (RDP) naïve Bayesian classifier (Wang et al., 2007), which was trained to species hypothesis (SH) level using UNITE + INSD full dataset for eukaryotes (v8.3 - https://unite.ut.ee/repository.php). To facilitate resolving unclear identifications, OTUs were further annotated with a field showing all taxa related to the UNITE SH that was detected by RDP. Finally, the NCBI taxonomy toolkit TaxonKit (https://github.com/shenwei356/taxonkit) was used to annotate the OTUs with the taxonomic information from NCBI (downloaded from https://ftp.ncbi.nlm.nih.gov/pub/taxonomy/ on 21 July 2023).

16S reference database construction & annotation

As in the case of ITS, OTU sequences were blasted against the same preformatted NCBI reference downloaded from their FTP server. Additionally, the Silva NGS web interface (https://ngs.arb-silva.de/silvangs/Index.html) was used to annotate OTUs with taxonomic information up to the genus level (Web Front-End v.1.9.10, analysis pipeline v.1.4.9, Silva reference version r138.1, last updated on 14 March 2023). OTUs were also classified using a 16S-trained RDP classifier (training set 18, July 2020; http://dx.doi.org/10.1128/AEM.00062-07). The BLAST results from NCBI, including the Accession and taxonomy IDs, Hit-%-ID and Grade-%-ID values, target sequence length, and entry description, were exported and annotated with the NCBI taxonomy by means of TaxonKit. The information on Silva release, ID, %similarity, reference ID, as well as detected kingdom, phylum, class, order, family, and genus were exported from SilvaNGS and joined with the NCBI BLAST results, RDP classifier results, and the OTU table matrix.

Text A4.2: Methods Wood properties

Moisture content

First the content of every bag was homogenized, a test portion was extracted and used for water content determination according to ISO 18134-2:2017 "Solid biofuels—Determination of moisture content—Oven dry method Part 2: Total moisture — Simplified method" as double determination at 105°C ± 2°C. Because of the lower sample amount the analysis could not be performed exactly according to the standard. For this, a sample amount of minimum 600g (2x300g) would be needed.

The external laboratory performed the double determination using a reduced sample amount of about 2x 15g to 30g and by drying the samples approx. for 15 hours in a Binder drying chamber FED 115.

Calorific value

Determination of calorific value was determined according to ISO 18125:2017 "Solid biofuels—Determination of calorific value" using calorimeters IKA C6000 and CKIC 5E-C5508. For this, approx. 0,5g of milled sample material was pressed to a pellet and used for calorimetric analysis in adiabatic mode at 25°C. According to standard a maximal deviation of 120J/g within the double determination was accepted. In cases of higher deviation, a third determination was performed, and the mean value of the 3-time analysis was used for further calculations. Over 90% of the samples fulfilled the maximum deviation of 120 J/g within the double determination.

The gross calorific value was calculated from the corrected temperature rise and the effective heat capacity of the calorimeter, with allowances made for contributions from ignition energy, combustion of the fuse(s) and for thermal effects from side reactions such as the formation of nitric acid. Furthermore, correction was applied to account for the difference in energy between the aqueous sulphuric acid formed in the bomb reaction and gaseous sulfur dioxide, i.e. the required reaction product of sulphuric in the biofuel. The corresponding energy effect between aqueous and gaseous hydrochloric acid can be neglected due to the usually low value for the correction regarding solid biofuels. As acid correction from gross calorific value to net calorific value, 10J/g were set. This value was calculated using the typical sulphur and nitrate concentrations given in the literature (e.g. ISO 17225-1 Solid biofuels — Fuel specifications and classes, Part 1: General requirements; Table B.1 — Typical values for virgin wood materials, without or with insignificant amounts of bark, leaves and needles and the Institute for Bioenergy database).

The net calorific value at constant pressure of the biofuel was obtained by calculation from the gross calorific value at constant volume determined on the analysis sample. The calculation of the net calorific value at constant volume requires information about the moisture and hydrogen contents of the analysis sample (see ISO 18125:2017 clause 4.2.).

Elemental analysis

Carbon, hydrogen and nitrogen content of the samples were determined according to ISO 16948:2015 "Solid biofuels—Determination of total content of carbon, hydrogen and

nitrogen" using an Elementar Vario Macro Cube. The measuring system was calibrated with phenylalanine.

Chapter 5 – General discussion and synthesis

The main objective of this thesis was to advance the understanding of mechanical bark treatments for European spruce bark beetle (*Ips typographus*) regulation by evaluating their practical applicability from both economic and ecological perspectives. Across three research chapter, pest control efficacy, operational efficiency, biodiversity, and wood properties were assessed to provide a robust scientific basis for integrating bark treatments into forest protection and conservation strategies. The findings demonstrate that mechanical bark treatments are operationally feasible alternatives to salvage logging, although their effectiveness and applicable scenarios depend on the method, scale, and management objectives.

With bark gouging, effective pest control can be achieved even under low treatment accuracy, while conserving saproxylic beetle diversity compared to (motor-)manual complete debarking (Chapters 2, 3, and 4). It was the most time-efficient alternative for handheld devices (Chapters 2 and 4). By contrast, conventional harvester processing alone was insufficient for regulating *I. typographus* emergence (Chapters 3 and 4). As operationally scalable solutions during landscape-scale disturbances with large wood volumes, debarking heads and three passes through the conventional harvester aggregate (harvester triple) both achieved sufficient bark beetle reductions and maintained saproxylic diversity (Chapters 3 and 4). Net calorific wood value remained stable over two years regardless of treatment type, confirming the bioenergy potential of treated wood after on-site storage (Chapter 4). Additionally, bark removal reduced woodpecker activity, the number of saproxylic beetle species, and wood moisture, while richness of fungi was highest in logs with removed bark (Chapter 4).

Together, these findings establish a comprehensive framework ranging from motor-manual techniques for small-scale and inaccessible sites to harvester-based solutions for landscape-scale disturbances, reconciling forest protection with biodiversity conservation. Ultimately, depending on management objectives, two scenarios can be supported for the application of bark treatments as alternatives to salvage logging for forest protection:

1) Intermediate on-site storage to overcome temporal bottlenecks in work and machinery capacities during landscape-scale disturbances generating large volumes of damaged or infested wood.

2) Permanent on-site deadwood retention and enrichment to promote biodiversity and ecological functioning. This approach contributes to fulfill conservation goals in protected areas, as well as integrated conservation strategies in managed forests (multifunctional forestry).

5.1 Bark treatments as alternatives to salvage logging

The effectiveness of salvage and sanitation logging to regulate *I. typographus* outbreaks in Central European *P. abies* forests is limited by the rarely achievable removal thresholds required for bark beetle regulation at the landscape scale (Dobor et al., 2020), logistical bottlenecks during landscape-scale events, and the economic consequences of timber oversupply on regional wood markets (Jandl, 2020; Toth et al., 2020). Bark treatments that render logs unsuitable for *I. typographus* reproduction decouple pest control from immediate transport dependencies and hence provide forest managers greater operational flexibility than salvage logging. Integrating bark treatments into reactive forest protection strategies at larger scales is increasingly relevant due to accelerated larval development under warmer temperatures (Wermelinger & Seifert, 1998) and increasing intensity and frequency of forest disturbance (Seidl et al., 2017), which demand treatment of larger volumes of damaged trees within shorter timeframes.

5.1.1 Pest control efficacy and operational feasibility of bark treatments

The key variables for the assessment of pest control interventions for *I. typographus* regulation are not only the reduction of emerging beetles relative to natural population densities (pest control efficacy), but also the volume of breeding material that can be treated or removed within the limited timeframes (Hoch et al., 2020). A highly effective treatment is of limited value if its throughput (operational efficiency) is insufficient to process the available breeding substrate before beetles emerge. Bark treatments primarily reduce available breeding areas through phloem removal and desiccation. At the same time intraspecific competition increases in the remaining bark pieces that are large enough for bark beetles to extend their larval galleries. Higher densities result in lower offspring fitness and dispersal capacity (Anderbrant et al., 1985; Salle et al., 2005), as well as greater susceptibility to pathogens (Wegensteiner & Weiser, 1996). Additionally, bark treatments offer a practical solution for the treatment of logging residues, such as freshly cut stumps

and crown material, which can attract and be a source for emerging bark beetles (Schroeder, 2013).

Salvage logging is commonly conducted with harvesters since they can process large volumes efficiently and provide safety advantages for the operators, which is particularly relevant in windthrown forest stands (Sanginés de Cárcer et al., 2021). Despite causing partial bark bruising and phloem disruption, conventional harvester aggregate processing did not reduce emerging *I. typographus* populations (Chapters 3 and 4). This contrasts with earlier results by Delb et al. (2021), who reported variable pest control efficacy after conventional harvester processing between 38 and 81%. The discrepancy likely reflects variability in bark perforation depending on log diameter, season, bark thickness, and aggregate configurations, underscoring that conventional harvester processing is too inconsistent to be relied upon as a pest control measure.

To achieve effective regulation, more intensive mechanical bark removal and manipulation is needed. This can be accomplished either by three passes through the conventional aggregate, which achieved 76% emergence reduction (Chapter 4), or with the specialized debarking head, where only 7.9% of beetles emerged relative to untreated controls (Chapter 3). Both results approach or exceed the simulated threshold of 80% beetle reduction considered necessary to lower epidemic outbreak risk and prevent colonization of undamaged trees (Fahse & Heurich, 2011). The additional economic and time costs are comparable for both treatments, as the use of debarking heads also requires three passes with the aggregate (Heppelmann, Labelle, Wittkopf, et al., 2019; Mergl et al., 2021). Consequently, both processing methods are approximately ten times faster than motor-manual alternatives, although they can treat only half the wood compared to conventional processing in the same time (Chapter 4, Mergl et al., 2021). For the 15.6 million m³ of harvested wood with insect infestation in Germany in 2024 (Statistisches Bundesamt, 2025a), this would correspond to approximately 290,000 extra machine hours required to treat the entire volume with three passes through the aggregate. The effectiveness of the harvester-based treatments depends on seasonal timing, since the bark removal with the delimbing knives is most effective in spring and early summer when sap flow is high (Delb et al., 2021; Heppelmann, Labelle, Wittkopf, et al., 2019). Differences in moisture contents during the growing season did not have an effect on debarking, and the highest bark removal typically occurs in the middle sections of treated logs, with bark pieces mostly remaining at the edges (Mergl et al., 2021).

Complete (motor-)manual debarking achieved the highest pest control efficacy (Chapters 2 and 4), consistent with earlier findings by Thorn et al. (2016) and Hagge, Leibl, et al. (2019). Although these devices are well-suited for challenging terrain, they come with the limitation that not more than 3.2 $m^3$of wood can be treated per hour (Chapters 2 and 4). With motor-manual bark gouging, twice the volume of manual debarking can be treated in alpine terrain (Chapter 2), and was the fastest motor-manual method when tested across German forest landscape conditions (Chapter 4). Importantly, perfect treatment accuracy is not required for effective pest regulation, which lowers the operational threshold under real-world conditions where terrain, operator experience, and time constraints introduce variability (Chapter 2). This flexibility, enables more extensive treatment of susceptible material in remote areas. The relatively low acquisition cost (~400€) is particularly relevant for small, privately owned forests, where reactive pest control measures are often lacking. Bark gouging can therefore also contribute to the overall reduction of outbreak risk at the landscape scale. Nevertheless, overall efficacy may decline with reduced accuracy, and high pest control can only be expected when logs are treated shortly after colonization onset (Frühbrodt et al., 2026).

5.1.2 Intermediate storage after bark treatments

When pest control can be guaranteed, on-site bark treatment provides additional flexibility since it allows for an intermediate storage on site without risking uncontrolled bark beetle population development. In case the wood is stored on-site and is intended for later economic recovery, the effect of decomposition and colonization on timber quality as well as bioenergy use potential can cause significant economic losses. While wood used for bioenergy typically represents a secondary assortment in traditional harvests of *P. abies* forests, the large volumes generated during landscape-scale disturbances, together with unfavorable market conditions, make its utilization in the bioenergy sector a potentially viable economic option (Barrette et al., 2015; Camia et al., 2021). Results from Chapter 4 indicate that the net calorific value remained stable across all five mechanical treatments over two years of on-site storage. This suggests that bioenergy potential can be maintained during intermediate storage regardless of bark cover, supporting the use of timber as a reliable regional energy source and reducing both transport costs and dependence on international export prices. Debarked logs also exhibited lower moisture content than logs without bark treatment after two years (Chapter 4), reducing transport weight and pre-drying requirements, which could partially offset the higher treatment costs (Heppelmann, Labelle, Wittkopf, et al., 2019).

Multiple overpasses with the conventional harvester aggregate and the debarking head can increase damage to the wood fiber, which reduces the yield for quality timber (Labelle et al., 2019; Nuutinen et al., 2010). Increased surface roughness and the exposure of internal wood fibers might also provide additional entry points and a larger surface area for fungal spores to settle and proliferate into the timber. Additionally, the reduction of saproxylic insects in debarked logs is associated with reduced wood-boring activity, resulting in lower technical damage and a reduced risk of introduction of sap-staining fungi (Böhm et al., 2025). Most relevant for sap staining are blue-stain fungi, which are transmitted during bark beetle colonization (Linnakoski et al., 2016). Although blue-stain fungi do not compromise the structural integrity of the wood, the resulting discoloration can lead to lower timber value due to downgrading to a lower timber quality class (Böhm et al., 2023; Hoch et al., 2020). However, no effect of bark treatments on their abundance was observed over the two years in Chapter 4. The fact that logs with removed bark dried out faster may create unfavorable conditions for the growth of wood-staining and wood-decomposing fungi, as moisture levels below the fiber saturation point (~30%) limit fungal decay activity in wood (Brischke & Alfredsen, 2020). This further underlines the importance of dry storage without soil contact when the wood is intended for economic recovery.

5.2 Trade-offs for biodiversity from bark removal

Beyond intermediate on-site storage as a logistical strategy, effective bark treatments can reconcile pest control objectives with forest conservation goals by allowing for permanent retention of deadwood resources. Since bark structures the nutritional environment and is a biotic and abiotic barrier, its removal intensity shapes which species can colonize, how communities assemble, how decomposition proceeds, and which higher trophic levels the retained wood can support.

Consistent with previous results (Frühbrodt et al., 2026; Hagge, Leibl, et al., 2019; Thorn et al., 2016), complete bark removal reduced saproxylic beetle species richness, while bark gouging maintained diversity across all three research chapters. Chapter 4 confirmed these patterns across 20 sites along the full climatic range of *P. abies* forests in Germany, demonstrating their generalizability for a larger landscape. As the first three-year study on bark treatment effects on saproxylic biodiversity, Chapter 4 also included species with development cycles exceeding one year and those using (previously) bark-beetle-infested logs for overwintering. This is providing a more complete picture of the saproxylic

community than single-season assessments allow, particularly since the first three years are critical to structure the decomposer community (Lettenmaier et al., 2025). Bark removal and manipulation also reduced overall beetle abundance, a decline that can cascade to higher trophic levels, as reflected in the observed reduction of woodpecker foraging activity (Chapter 4).

The debarking head did not reduce non-target beetle species richness in Chapter 3. However, since both treatments remove approximately 90% of the bark, their long-term effects on biodiversity are likely similar to the results of complete debarking in Chapter 4, in which on average 10 fewer saproxylic beetle species were observed at the site level compared to bark gouging, harvester triple, normal harvester, and the control. This reduction is consistent with the species-energy hypothesis, which predicts that the available energy richness is a primary determinant of how many species can be supported by a system (Wright, 1983). Bark, and the underlying phloem in particular, is the most energy-rich and nutrient-dense component of deadwood (Dossa et al., 2016; Stokland et al., 2012). Many early colonizing saproxylic species depend directly on this resource for oviposition, nutrition, or shelter (Ulyshen, 2018). Thus, the loss in beetle richness with complete bark removal reflects not only habitat loss but the removal of a nutritional resource that structures the initial assemblages. However, the gamma diversity finding of Chapter 4 indicates that complete bark removal is not reducing saproxylic beetle species richness on the landscape scale, supporting the use of debarking heads for large-scale disturbances under conditions of particularly high bark beetle pressure.

The saproxylic beetle species assemblages of completely (harvester-)debarked logs diverged significantly from control logs, while bark gouging and treatments with the conventional harvester had near-natural assemblages (Chapters 3 and 4). Completely debarked logs exhibited higher dispersion and greater variability between sites. This suggests that complete bark removal weakened the deterministic environmental filtering associated with specialized early colonizers, making colonization less deterministic (Chase & Myers, 2011; Vellend, 2010). Without bark as a biotic barrier, differences in assemblages are likely governed more by the surrounding regional species pool and which species arrive first (priority effect), rather than niche requirements determining which species can establish. This would favor generalist species capable of exploiting bare wood over the specialized early colonizers dependent on bark. Since early colonization history shapes the community trajectories throughout decomposition, the ecological consequences of bark treatments are likely to

propagate beyond the initial colonization process (Fukami et al., 2010; Lettenmaier et al., 2025).

Despite the established role of bark beetles and other phloem-feeding insects as vectors of a variety of fungi (Linnakoski et al., 2016; Ulyshen, 2018), *I. typographus* abundance did not increase fungal richness. Instead, fungal richness was highest in completely debarked logs, where richness of bacteria decreased on the landscape scale (Chapter 4). This is consistent with bark functioning as a physical protective layer that limits access of fungi to the wood, and its removal opening the log surface for fungal colonization (Dossa et al., 2018; Hagge, Bässler, et al., 2019). Microbial assemblages differed significantly between treatments, driven by the lower moisture content in logs without bark. Hence, while bark removal directly increases fungal richness, it simultaneously alters the abiotic conditions. This provides a mechanistic explanation for the assemblage shifts previously observed by Hagge, Bässler, et al. (2019), extending them across the full climatic range of Central European *P. abies* forests.

Taken together, these findings demonstrate that bark treatments are not only a pest control measure with biodiversity side effects, but active interventions in the long-term decomposition trajectories of retained deadwood. The intensity of bark removal determines which assembly processes operate and which species are able to colonize (Chapter 4). While debarking treatments contribute the most to pest regulation (see 5.1.1), bark gouging and three passes through the harvester aggregate preserve a higher ecological integrity of the deadwood resource through the retained bark. These approaches therefore represent the most suitable compromise when permanent deadwood retention and biodiversity conservation are management priorities.

5.3 Bark treatments for permanent deadwood retention

The ecological consequences of bark removal determine primarily at the log level which species colonize, how communities assemble, and how decomposition proceeds. However, the significance of retaining deadwood after bark treatments on-site extends beyond individual logs to the broader functioning and resilience of forest ecosystems. Deadwood supports complex food webs in which the substrate quality, structural complexity, and microclimate drive community composition and diversity (Kriegel et al., 2023; Seibold et al., 2016). Changes have cascading effects on the decomposition and colonization process

(Harmon, 2021; Stokland et al., 2012), as observed in Chapter 4. The moisture-mediated shifts in microbial communities and associated changes in nitrogen immobilization and hydrogen cycling demonstrate that the intensity of bark removal not only shapes colonization dynamics but modulates the functional trajectory of retained deadwood within the broader ecosystem nutrient cycle.

Deadwood represents a significant carbon pool (Martin et al., 2021), and the deadwood-dependent food webs channel a substantial proportion of forest ecosystem biomass, sustaining the decomposition processes that maintain nutrient and carbon cycling between disturbance events (Seibold et al., 2021). Bark treatments did not significantly affect carbon content across treatments (Chapter 4), indicating that it has no effect on climate change mitigation potentials. Additionally, deadwood generated by disturbance events is not only a pest hazard or timber reserve, but a biological legacy that drives the reorganization of forest ecosystems after disturbance, supporting saproxylic biodiversity, decomposition processes, nutrient cycling, and microclimate stabilization over decades (Franklin et al., 2000; Harmon, 2021; Stokland et al., 2012). The findings on the biodiversity demonstrate that bark treatments provide an operational pest control response, able to retain these legacies for saproxylic beetles, fungi, and bacteria after disturbances.

As disturbance events become more frequent and severe (Seidl et al., 2017), the recovery window for forest ecosystems between successive events shortens, making the retention of biological legacies increasingly critical. Salvage logging following bark beetle outbreaks and windthrows removes these legacies at a moment of high ecological vulnerability (Leverkus et al., 2021). Consequently, in combination with climate-change-induced changes to site conditions, forests may be pushed toward the critical thresholds beyond which transitions to alternative stable states become likely (Johnstone et al., 2016, Fig. 1). By retaining these functional legacies rather than removing them through salvage logging after disturbances, bark treatments help to preserve the structural complexity that facilitates forest recovery and maintains ecosystem resilience (Cerioni et al., 2024; Seidl, Rammer, et al., 2014).

Beyond resilience, the biodiversity consequences of management intensity are equally significant. Consistent with the intermediate disturbance hypothesis (Connell, 1979; Jentsch et al., 2022), salvage logging acts as a second high-intensity intervention that compounds the original disturbance, removing the legacy on which the saproxylic biodiversity depends

(Thorn et al., 2018). In this sense, bark treatments provide a form of disturbance moderation, by suppressing pest populations and preserving the structural legacies that support biodiversity and ecological processes. Logs retained on site can serve as connectivity elements within the landscape mosaic and as persistent substrates for later successional communities (Lindenmayer et al., 2017; Müller et al., 2019). Bark gouging and three passes through the harvester, by contrast, retain deadwood at intermediate intervention intensity, preserving the structural heterogeneity that sustains diverse saproxylic communities (Chapters 2, 3, and 4). Complete bark removal techniques are also suitable for deadwood retention, albeit with reduced saproxylic species richness and a shift in assemblage composition away from specialized early colonizers.

Overall, the deadwood legacies preserved on site through bark treatments provide a foundation for climate change adaptation, ecosystem functioning, ecological resilience, and biodiversity in disturbed forest ecosystems. Bark treatments should therefore be embedded within broader management and policy frameworks that acknowledge disturbance as an opportunity for adaptation and biodiversity conservation by balancing pest control objectives and conservation goals.

5.4 Integrating bark treatments into forest ecosystem management

In commercial forestry, diebacks are seen as economic damage and as a potential source of pest insects. Consequently, salvage logging remains the dominant post-disturbance management response in Central European forests (Leverkus et al., 2021; Lindenmayer et al., 2012). Yet its ecological costs and operational constraints are increasingly difficult to reconcile with biodiversity conservation and sustainable forest management objectives under accelerating disturbance regimes (Leverkus et al., 2018; Müller et al., 2019). Over the last three decades, deadwood has received increasing attention and has been progressively integrated into sustainable forest management strategies and certification programs (Thorn, Seibold, et al., 2020; Vítková et al., 2018). The findings of this thesis identified specifically bark gouging and three passes through the harvester aggregate as feasible pest control alternatives to the controversial immediate wood removal (see 1.7). Both approaches thereby enable 1) intermediate on-site storage to buffer logistical and economic bottlenecks and 2) permanent deadwood retention to support biodiversity, ecosystem functioning, and resilience. While permanent retention ensures habitat continuity for saproxylic species, storing logs on site for up to two years provides not only economic flexibilities but can also

benefit species with short life cycles, as well as bark beetle antagonists. In addition, conducting bark treatments within forest stands retains essential nutrients, thereby supporting nutrient cycling and stand productivity (Vos et al., 2023; Yan et al., 2017). Consequently, bark treatments provide a practical mechanism for integrating pest control with multifunctional forest management objectives and conservation goals (Fig 5.1).

The operational feasibility of bark treatments depends on accessibility for harvesters and the wood volume that needs to be treated within the limited timeframes. In terrain without harvester access, like steep mountain forests, on-site wood retention is largely determined by extraction constraints and valuable protective functions from retained deadwood (Caduff et al., 2022; Ringenbach et al., 2022). In this context and when the volumes of wood that need to be treated are small, motor-manual bark gouging is the most suitable bark treatment, offering the best balance of pest control efficacy, operational efficiency, and saproxylic biodiversity conservation. Where terrain permits harvester access and wood volumes exceed motor-manual processing and transport capacities, harvester-based treatments represent an operationally scalable alternative to salvage logging for effective bark beetle regulation (see 5.1.1). Where maximum pest control efficacy is the primary objective, the specialized debarking head achieves higher bark removal rates and greater emergence reduction than three passes through the conventional aggregate (Chapter 3), but similar long-term consequences to biodiversity as with complete debarking (Fig. 5.1).

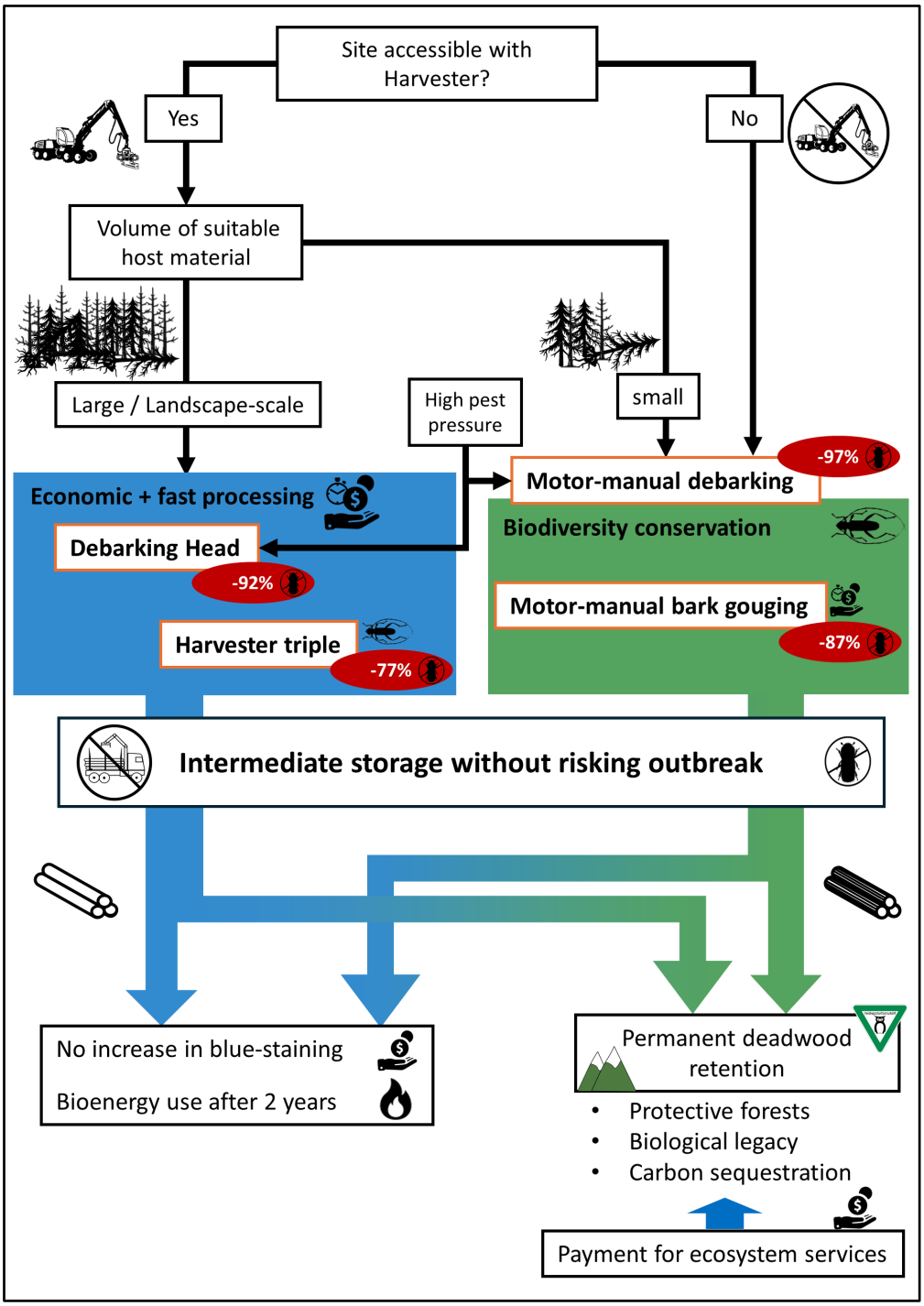

Figure 5.1: Graphical overview of bark treatments (orange) and their respective pest control efficacies for the regulation of *Ips typographus*, based on the results from the research chapters. The scheme integrates decision pathways based on site accessibility, host material volume, and pest pressure, supporting economic (blue) and ecological (green) management objectives.

A practical, landscape-scale solution would be a combination of salvage logging and bark treatments to offset operational costs with timber sale, while preserving biological legacies after a disturbance event. For instance, removing half of the wood while treating the

remaining half with (harvester-based) bark treatments increases machine hours by approximately 50% compared to salvage logging alone while allowing for a disproportionate preservation (~73%) of unique species richness relative to the salvaged area (Thorn, Chao, et al., 2020). In this context, three passes through the conventional harvester aggregate are particularly suitable, as it is widely available, reduces bark beetle emergence, maintains saproxylic biodiversity, and preserves both wood quality and bioenergy potential during on-site storage (Chapter 4).

Permanent retention of logs after bark treatment aligns with the principles of retention forestry, which aim to maintain biological legacies within managed stands (Fedrowitz et al., 2014). Retaining deadwood as disturbance legacies fits within the frameworks of adaptive forest management, closer-to-nature forest management, forest landscape restoration, and specifically into natural disturbance-based management, all of which advocate preserving natural disturbance outcomes to maintain biodiversity, resilience, and adaptive capacity (Kuuluvainen et al., 2021; Spathelf et al., 2018; Stritih et al., 2026). For the management of disturbed forest ecosystems, not only biomass but also species diversity, functional diversity, and structural diversity must be integrated into management strategies to ensure adaptive potential and the stable provision of ecosystem services (Lefcheck et al., 2015; Mori et al., 2017). Bark treatments therefore provide not only a pest control tool but also enable the integration of climate change adaptation and biodiversity conservation into forest disturbance management responses.

Conservation areas are where conflicts between pest control obligations and biodiversity conservation goals are most acute, and where the case for bark treatments over salvage logging is therefore strongest for maintaining the ecological legacy of bark beetles as ecosystem engineers. In national park buffer zones and Natura 2000 habitat areas, pest control requirements coexist with legally binding obligations to maintain habitat structure, deadwood volumes, habitat continuity, and saproxylic biodiversity that salvage logging cannot fulfill without compromises (Lindenmayer et al., 2017; Müller et al., 2019; Thorn et al., 2018). Bark gouging and three passes through the harvester aggregate can reconcile this conflict by achieving sufficient pest reduction while maintaining saproxylic beetle diversity and deadwood structural integrity at natural levels, as demonstrated across all three research chapters. The use of debarking heads, due to their concomitant effects on assemblages, should be reserved for conservation areas with highly susceptible landscapes (e.g. high host tree shares) and high bark beetle densities.

The increasing role of disturbance in forest dynamics requires management strategies that adapt to more variable and uncertain disturbance regimes rather than focusing exclusively on disturbance prevention (Messier et al., 2019; Kuuluvainen et al., 2021). Bark treatments are well positioned within this paradigm, providing scalable and operationally flexible pest control solutions that are compatible with both economic recovery and conservation objectives. Consistent with the latest framework of the Convention on Biological Diversity (CBD, 2022) and the objectives of the EU Biodiversity Strategy for 2030 (European Commission, 2020), the Nature Restoration Regulation (Nature Restoration Regulation, 2024) establishes the first legally binding targets to achieve an increasing trend in deadwood and organic carbon stocks in Europe's forest ecosystems. The EU Forest Strategy for 2030 supports these objectives by promoting forest management that enhances biodiversity and resilience (European Commission, 2021). Deadwood retention after disturbances through bark treatments provides a practical mechanism to contribute to these policy objectives, while financial reimbursements are available to forest owners through existing payment schemes for ecosystem services and climate-adapted forest management (FNR, 2026). However, realizing the full potential of bark treatments within these frameworks requires adaptive management approaches that explicitly monitor biodiversity, carbon, and pest regulation outcomes across treatment types and adjusting guidelines in response to changing disturbance regimes (Messier et al., 2019; Huth et al., 2025).

5.5 Conclusions and future directions

The structural vulnerability of Central European *P. abies* forests and the intensification of disturbance regimes have pushed forest management to its operational limits in recent years, motivating the need for new approaches for disturbance management. This thesis demonstrates that mechanical bark treatments provide a scientifically grounded and operationally flexible alternative to salvage logging, reconciling bark beetle management with conservation goals and economic objectives. The findings demonstrate that effective *I. typographus* regulation does not require immediate wood removal, and that bark-treated deadwood retained on-site can function as a biological legacy.

All bark treatments, except the conventional harvester processing, reduced *I. typographus* emergence sufficiently to lower the likelihood of epidemic population dynamics and subsequent standing tree attacks. At the same time, economically relevant wood properties were preserved over two years. This supports intermediate on-site storage to overcome

logistical bottlenecks during landscape-scale disturbances, thereby reducing economic risks associated with reactive pest management. Bark removal intensity governs the trade-off between pest control efficacy and biodiversity conservation. Bark gouging and three passes through the conventional harvester aggregate achieved sufficient pest reduction and preserved saproxylic beetle diversity, making them the preferred methods when permanent deadwood retention for biodiversity conservation is the objective. Complete debarking maximizes pest control but reduces saproxylic beetle richness at the log level. However, the extrapolated gamma diversity results indicate that this reduction does not translate into species loss at the landscape scale, thereby supporting their application under high bark beetle pressure.

Integrating the pest control results into landscape-level outbreak simulations will help to further refine bark removal thresholds under different disturbance intensities and forest landscape compositions. Development of harvester aggregates replicating the bark gouging principle of bark removal in stripes could combine the operational efficiency necessary for landscape-scale disturbances with high pest reduction and positive effects for saproxylic biodiversity. To bridge the remaining gap between research evidence and management practice, bark treatments need to be integrated into forest protection guidelines, management policies, practitioner training, and payment schemes for ecosystem services, to realize their full potential across private, state-owned, commercial, and conservation forests.

While species assemblage changes following bark treatments are well documented, their functional consequences remain to be fully understood. Long-term assessments will help to clarify the effect of bark cover on colonization trajectories and the succession of saproxylic communities beyond the initial colonization process. Trait-based analyses of functional diversity could further identify which ecological roles and functional guilds are lost or preserved through different bark treatments. Particularly, parasitoids, predatory beetles, and entomopathogenic fungi as natural antagonists of *I. typographus* represent important biocontrol mechanisms for resilience against future outbreaks. Identifying bark treatments that preserve this natural regulation mechanism would provide a further advantage in comparison to salvage logging.

After effective pest control, bark-treated deadwood is no pest hazard and can increase on-site retention to sustain forest ecosystem functioning and resilience. This opens a practical pathway to integrate deadwood retention into post-disturbance management across both conservation areas and commercial forests. It supports multifunctional forest management

objectives by contributing to ecosystem functioning, resilience, and biodiversity. Disturbances can thereby become an opportunity rather than a setback to meet deadwood retention and biodiversity targets, providing a practical mechanism for climate change adaptation.

Ultimately, this thesis contributes to a broader shift in how forest ecosystems and disturbances are perceived—from a resource-driven management paradigm focused mostly on economic yield, toward a recognition that biodiversity and ecological functioning are the foundation of forest resilience and the long-term provision of ecosystem services. Dead trees and disturbances are not only a loss of economic investment but a valuable biological legacy that can maintain ecosystem functionality and resilience for decades. Equipping forest managers with novel practical tools to implement this perspective will be essential for maintaining productive, resilient, and biodiverse forests in the face of accelerating global change.

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Appendix B – Use of large language models

In the preparation of this dissertation, I used large language models (including ChatGPT, Claude, and Gemini) for linguistic support, particularly to improve wording, grammar, and stylistic clarity, as well as for technical support in programming, including assistance with identifying and resolving errors and refining R scripts.

Furthermore, ChatGPT and Gemini were used to assist in the creation of selected graphical elements (disturbance and treatment icons) included in Figures 1.4, 1.5, and 5.1. These graphical elements were reviewed and, where necessary, modified.

Large language models were not used to generate, develop, or substantially shape the scientific arguments, interpretation of results, or conclusions presented in this dissertation. Full responsibility for the content of this dissertation remains with me.