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Habitat on the move

Translocation of deadwood and associated species as a novel conservation tool

Olov Tranberg

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Olov Tranberg
Faculty of Forest Sciences
Department of Wildlife, Fish, and Environmental Studies
Umeå

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Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies, Umeå, Sweden

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Habitat on the move - Translocation of deadwood and associated species as a novel conservation tool

Abstract

Restoration of degraded habitat is frequently used in ecological compensation, although it often faces challenges of long delivery times of features important for biodiversity, such as old large dead trees, and difficulties for target species to find and colonize restored areas. Conservation translocation of entire communities of substrates and species is a novel method used in ecological compensation and restoration, to mitigate negative effects of land-use on biodiversity. In a large-scale field experiment in boreal forests of Sweden, I tested a possible way to circumvent the uncertainty of restoration efforts; translocation of deadwood substrates from an impact area to a compensation area. My research focused on the effects of deadwood translocation on several saproxylic organism groups and habitat availability. I assessed how abundance, species richness and assemblages of beetles, bryophytes and lichens were influenced by translocation to a compensation area. By translocating different types of deadwood, the method showed potential in quickly providing habitats important for biodiversity, as well as translocating species to the compensation area. However, the outcomes vary depending on species group. Increased species richness and richer assemblages of saproxylic beetles were noted, especially in areas with high density of translocated deadwood. Sessile species responded differently with unchanged species richness for lichens and increased richness for bryophytes. However, challenges such as differing deadwood composition between impact and compensation sites, and the need for higher efforts to achieve landscape-level compensation, indicate that the method requires further refinement. These findings suggest that deadwood translocation could be a cost-efficient tool in ecological restoration, yet underscore the importance of continued evaluation to optimize methods and fully realize the benefits for biodiversity.

Keywords: biodiversity, deadwood, conservation translocation, ecological compensation, ecological restoration, saproxylic organisms

Habitat på väg - Translokering av död ved och associerade arter som ett nytt naturvårdsverktyg

Sammanfattning

Restaurering används ofta inom ekologisk kompensation, men ställs inför flera utmaningar; dels långa leveranstider av substrat som är viktiga för biologisk mångfald, såsom gamla grova döda träd, dels problem för målarter att hitta och kolonisera restaurerade områden. Translokering av habitat tillsammans med de artsamhällen som lever där är en ny metod som föreslagits för att minska de negativa effekterna på biologisk mångfald till följd av expansiv markanvändning. I ett storskaligt fältexperiment i boreal skog i Sverige testade jag en möjlig metod för att lösa detta problem, genom att translokera ovanliga dödvedssubstrat från ett område som skulle exploateras för gruvexpansion till ett kompensationsområde. Jag undersökte hur vedlevande skalbaggar, mossor och lavar påverkades av att translokeras samt tillgången på habitat efter flytt. Metoden att translokera död ved visade potential att snabbt tillhandahålla typer av substrat som är viktiga för biologisk mångfald samt att flytta arter från påverkansområdet till kompensationsområdet och att responsen varierar beroende på artgrupp. Translokeringen hade positiva effekter på artrikedom och artsammansättning hos skalbaggar, särskilt i ytor med hög densitet av translokerad ved. Sessila arter reagerade olika, med oförändrad artrikedom för lavar och ökad för mossor. Skillnader i samansättningen av olika typer av död ved mellan påverkans- och kompensationsområde, samt behovet av mer omfattande insatser för att uppnå kompensation på landskapsnivå, indikerar att metoden behöver vidareutvecklas. Resultaten visar att translokering av död ved kan vara ett kostnadseffektivt verktyg inom ekologisk restaurering, men betonar vikten av fortsatt utvärdering för att optimera metoderna och fullt ut realisera följderna för biodiversitet.

Nyckelord: biologisk mångfald, död ved, ekologisk kompensation, ekologisk restaurering, translokering, vedlevande organismer

Dedication

Te skârpmâkką̊n, göllkuą̊n, tzwärgą̊n, ettersnâllą̊n,
å öll âr kuser söm beddzä ti ską̊jâm.

To the longhorn beetles, ladybugs, spiders, dragonflies,
and all other creatures that live in the forest.

[Transtrandsmål, local dialect of Transtrand area, Dalarna]


Photo: Olov Tranberg

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Tranberg, O., Hekkala, A-M., Lindroos, O., Löfroth, T., Jönsson, M., Sjögren, J. & Hjältén, J. (2024). Translocation of deadwood in ecological compensation: A novel way to compensate for habitat loss. AMBIO, 53: 482-496. https://doi.org/10.1007/s13280-023-01934-0.

II. Tranberg, O., Löfroth, T., Hekkala, A-M., Jönsson, M., Holmström, L., Sjögren, J & Hjältén, J. (2024). Translocating deadwood in ecological compensation benefit saproxylic beetles, but effects are dependent on substrate density. (submitted).

III. Jönsson, M., Tranberg, O., Hekkala, A-M., Gibb, H., Löfroth, T., Work, T., Sjögren, J. & Hjältén, J. (2024). Deadwood translocation as a tool for ecological compensation and restoration of saproxylic beetle communities (manuscript).

IV. Tranberg, O., Löfroth, T., Jönsson, M., Sjögren, J., Hekkala, A-M. & Hjältén, J. (2024). Enhanced bryophyte communities, but challenges for lichens following translocation of deadwood in ecological compensation (manuscript).

The contribution of Olov Tranberg to the papers included in this thesis was as follows:

I. Main author. Received data from co-authors. Designed the study question, preformed the analysis and wrote the manuscript with contributions from the co-authors.

II. Main author. Designed the study question, performed data collection and received additional data from co-authors. Species identification of beetles was performed by external experts. Preformed the analysis and wrote the manuscript with contributions from the co-authors.

III. Co-author. Performed data collection and co-writer of manuscript. Collaborated with main author on idea and design and analyses. Species identification of beetles was performed by external experts.

IV. Main author. Designed the study question, organized data collection, and received additional data from co-authors. Species identification was performed by external experts. Preformed the analysis and wrote the manuscript with contributions from the co-authors.

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Photo: Olov Tranberg

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Abbreviations

BBOP	Business and Biodiversity Offset Program
DC	Decomposition class
GLM	Generalized Linear Models
HDP	High density plots
IUCN	International Union for Conservation of Nature
MDP	Medium density plots
NTP	No translocation plots
OECD	Organisation for Economic Cooperation and Development
SIMPER	Similarity Percentage


Photo: Olov Tranberg


Photo: Olov Tranberg

Photo: Susanna Bergström

1. Introduction

1.1 Ecological compensation

The climate and biodiversity crisis has become two of the most serious challenges of our time, with profound implications for ecosystems, economies, and societies worldwide (Díaz et al., 2019). As global temperatures rise and ecosystems face unprecedented pressure, the urgency for a “green” transition has gained significant attention (Rockström et al., 2017). This shift towards renewable energy and sustainable practices is essential to reduce our dependence on fossil fuels, yet it also brings new challenges. One of the critical issues emerging from this green transformation is the growing demand for minerals and metals essential for renewable technologies, such as batteries and wind turbines (Hund et al., 2023). The extraction of these materials risks further degrading ecosystems that are already under severe stress from deforestation, pollution, and climate change (Newbold et al., 2015).

To simultaneously conserve biodiversity and continue economic development is a major challenge as human society depends on functional ecosystems in numerous ways (Lubchenco, 1998). Thus, finding ways to mitigate negative effect of nature exploitation is therefore of high priority. Ecological compensation, where areas targeted for intensive land-use are compensated with conservation of land elsewhere (BBOP, 2012), potentially provides an approach that links biodiversity conservation and human development associated with economic growth. Although legislation mandating ecological compensation exist today in many countries, ecological compensation is still under development (Blicharska et al., 2022; Josefsson et al., 2021) .

1.1.1 Mitigation hierarchy strategy

The mitigation hierarchy is a framework used globally to minimize the negative impacts of development on biodiversity and ecosystems (Griffiths et al., 2019). It involves a sequential approach that prioritizes avoidance of damage, followed by minimization, restoration, and, as a last resort, compensation (Gauthier et al., 2014). Historically, this strategy was developed in the 1970s in the US in relation to wetland restoration (Damiens et al., 2021) and is closely related to the "polluter pays principle" (OECD, 1992), stating that the part responsible for damage of ecosystems also should bear the cost of reducing such damage. The goal of the mitigation hierarchy framework is to achieve no-net-loss, or even a net gain, in biodiversity (Griffiths et al., 2019). It has been applied in various human development projects where impacts on ecosystems are inevitable, for example establishment of industries, infrastructure and mining. The strategy involves four key steps (Figure 1):

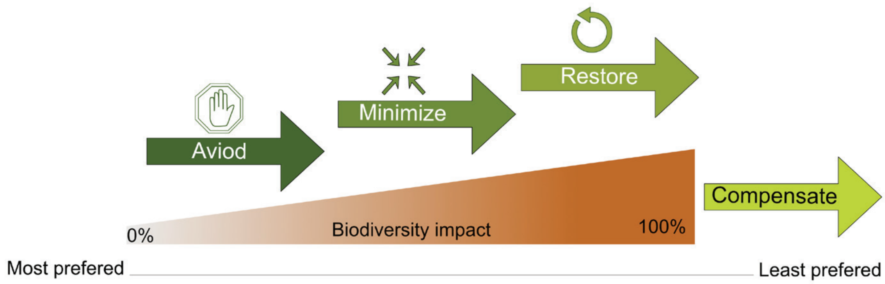

Figure 1. Steps in the mitigation hierarchy in relation to their potential negative impact on biodiversity. Illustration: Olov Tranberg.

Avoidance: This step involves planning and decision-making to prevent any potential negative impacts on biodiversity. This could mean selecting alternative project sites or adopting new technologies to avoid sensitive areas (Kangas and Ollikainen, 2022).

Minimization: When avoidance is not possible, efforts should be made to reduce or minimize the scale and intensity of the impact. This includes modifying operations, reducing the size of intended impact, and using less harmful techniques during extraction or development processes. For example, in forestry operations in Canada, techniques such as selective logging and buffer zones around sensitive habitats are employed to reduce habitat fragmentation (Robichaud and Knopff, 2015; Tupala et al., 2022).

Restoration: This step focuses on restoring ecosystems after they have been impacted. Restoration aims to rehabilitate affected ecosystems to their original state (Hobbs and Norton, 1996). Restoration in boreal ecosystems often involves replanting trees, restoring wetlands, and ecological restoration of habitats. However, restoration in boreal forests can be a lengthy process due to the slow growth rates of trees and the complexity of the ecosystems involved (Halme et al., 2013; Nordlind and Östlund, 2003).

Compensation or biodiversity offsets: When inevitable impacts still remain after all previous steps, ecological compensation is considered. Compensation may involve creating, restoring, protecting or enhancing equivalent ecological values or habitats elsewhere to offset the biodiversity losses in the negatively impacted area (BBOP, 2012; Naturvårdsverket, 2016). In the context of boreal forests, this could involve protecting forest land elsewhere or investing in long-term conservation projects (Weber et al., 2015). Ecological compensation should aim to ensure no-net-loss of biodiversity, but challenges arise in measuring and valuing the biodiversity lost compared to what is gained elsewhere (Lapeyre et al., 2015; Maron et al., 2012).

1.1.2 Ecological compensation in boreal forests

It is important to underscore that ecological compensation as a conservation tool, should only be considered when all preceding steps in the mitigation hierarchy cannot be fulfilled, when preservation is not possible, and the societal benefits of the impact exceed the ecological values. Even so, ecological compensation have during the last decades gained interest as a promising tool (Coralie et al., 2015). Despite the theoretical benefits of ecological compensation, their application is not without challenges (Bull et al., 2013). One of the primary criticisms is the difficulty in achieving no-net-loss of biodiversity (Gibbons and Lindenmayer, 2007). In boreal forests, compensating for the loss of old-growth forest with the protection of younger forests does not equate to the same ecological value, as older forests offer unique habitats and carbon storage capacities that cannot be easily replicated (Stokland et al., 2012). Moreover, there are ethical concerns surrounding the use of ecological compensation as a “license-to-trash”, allowing industries to proceed with developments that cause irreversible damage to ecosystems with the promise of compensation elsewhere (Lapeyre et al., 2015; McKenney and Kiesecker, 2010). Another challenge in implementing ecological compensation in boreal forests is the long recovery time of these ecosystems. Boreal forests grow slowly, and even with extensive restoration efforts, it can take decades for the forests to regain their former structure and ecological functions (Bergeron and Harper, 2009; Fenton, 2016). Therefore, compensation efforts often focus on preserving large, contiguous areas of undisturbed forest or improving the management of already protected areas (Weber et al., 2015).

If compensation offsets have lower conservation value than the impacted area, ecological restoration is often used to improve the quality of the compensation area. While appealing as practical conservation solution, the implementation and success of restoration measures have been questioned (Bell et al., 2015; Kouki et al., 2012; Palmer et al., 1997) highlighting the need for evaluations of ecological compensation in real-world contexts. Until recently, ecological compensation have rarely been used in boreal forests in Sweden and the ecological consequences remain uncertain (Blicharska et al., 2022; Josefsson et al., 2021). Compensatory measures can be required by several different acts of the Swedish environmental code, especially in regard to Natura 2000 areas, National parks or Nature reserves, but also not formally protected areas (Naturvårdsverket, 2016). One of few existing examples of large scale ecological compensation of forest land in northern Sweden is the Mertainen mine expansion in Kiruna (mine expansion permitted, though never executed due to decreased market prices), involving an impact of 1220 hectares of forest and wetland habitats with high conservation value (Koh et al., 2014). The mining company, signed a 50-year agreement with the Jukkasjärvi forest commons to protect an area of 2600 hectares as compensation for the impact. To ensure that compensation matched the ecological value lost in impact, the offset ratio and habitat amount were calculated using a metric called Habitat hectares (Quétier and Lavorel, 2011). Even so, there is a lack of suitable metrics to use in ecological compensation (Moilanen et al., 2009). As exploitation of forest habitats is expected to increase in the future there is now an increased interest in ecological compensation and restoration as a means to mitigate the negative effect of different types of land-use on biodiversity (Griffiths et al., 2019).

Ecological compensation has been criticised for a variety of reasons: conceptual (e.g., choice of currency or metric, definition of no-net-loss, equivalence, time lags, longevity, uncertainty) as well as practical (e.g., compliance, measurement of ecological outcome, uncertainty, monitoring) (Bull et al., 2013). There is still a need for refinement of both the conceptual and practical aspects of ecological compensation. Until now, few studies have evaluated the ecological outcome of compensation actions, especially in boreal forests (Josefsson et al., 2021). Further, it is important to determine which impacts on biodiversity can be compensated for and which cannot (BBOP, 2012). If it is impossible to find habitats of equivalent quality required for compensatory exchange, available options include restoration or recreation of habitats.

1.1.3 Ecological restoration of boreal forests

Ecological restoration of boreal forests involves a combination of strategies aimed at reversing degradation and restoring biodiversity and ecosystem processes (Hjältén et al., 2023). Deadwood is a key component of boreal forests, providing habitat for numerous species, including saproxylic (deadwood dependent, (Speight, 1989)) beetles, fungi, bryophytes and lichens (Siitonen, 2001). In many managed boreal forests, the volume of deadwood has been drastically reduced due to intensive human interventions (Jonsson et al., 2016; Linder and Östlund, 1998). To restore this habitat, deadwood enrichment, which involves adding logs and snags with various methods (e.g., sawing, ring-barking, pushing down trees with excavator) is widely employed (Doerfler et al., 2018). Deadwood creation in situ as a restoration tool, through felling and leaving cut trees, has shown significant benefits for biodiversity, especially for species that rely on decaying wood (e.g., Hägglund et al., 2020; Hekkala et al., 2016; Johansson et al., 2006).

Fire is a natural disturbance that shapes the boreal forest landscape (Zackrisson, 1977), creating a mosaic of different successional stages of habitats. However, fire suppression policies in many regions have altered these natural dynamics, leading to homogenized forest structures (Linder and Östlund, 1998; Zackrisson, 1977). To address this, prescribed burning is used as a restoration tool to mimic natural fire regimes, promoting species adapted to fire-disturbed habitats and creating habitat diversity (Vanha-Majamaa et al., 2007). This technique has been successfully implemented in several experiment in Fennoscandia, where prescribed fires have been shown to increase structural heterogeneity and promote biodiversity recovery (e.g., Fredriksson et al., 2020; Vanha-Majamaa et al., 2007).

Restoring boreal forests is a long-term effort, with many actions requiring decades to centuries to achieve full ecosystem recovery (Hjältén et al., 2023). One of the key challenges is the slow growth rate of boreal trees, which makes it difficult to quickly restore the structural characteristics of old-growth forests (Aakala, 2010).

1.1.4 Deadwood and saproxylic organisms

Deadwood plays an important role in boreal forest ecosystems by providing habitat and resources for a wide range of saproxylic (wood-dependent) organisms, including insects, bryophytes, lichens and polypores (Stokland et al., 2012). The characteristics of deadwood, such as diameter, posture, tree species, and decay stage, are shaping the composition of species communities that depend on it (Gibb et al., 2005; Ranius et al., 2015; Siitonen, 2001; Stokland et al., 2012). These properties influence not only the species that colonize deadwood but also the microhabitats they create, which support specialized species, including many that are rare or endangered (Grove, 2002; Stokland et al., 2012). Larger logs decay more slowly and provide stable moisture and temperature conditions, making them particularly valuable for saproxylic organisms (Stokland et al., 2012). For instance, saproxylic beetles often show preferences for certain types of deadwood with larger diameter logs and advanced decay stages (Gibb et al., 2005). In addition, standing deadwood tends to support different communities than lying deadwood, with standing dead trees often hosting higher abundances of cambium consumers, fungivores, and red-listed species (Andersson et al., 2015; Hjältén et al., 2010; Johansson et al., 2017).

The decay stage of deadwood also significantly impacts its suitability for saproxylic organisms. Early decay stages tend to support species that are adapted to relatively fresh wood, while later stages provide habitat for species specialized in decomposed wood and those that depend on wood living fungi for survival (Abrahamsson et al., 2008; Jonsell et al., 2005; Lee et al., 2014). The presence of decomposer fungi is particularly important for determining the composition of beetle assemblages in deadwood, as fungi modify the structure and chemistry of the wood, creating suitable microhabitats for various invertebrates (Abrahamsson et al., 2008; Jonsell et al., 2005).

Human activities, including forest management and land-use changes, have greatly diminished the availability of high-quality deadwood (Linder and Östlund, 1998), such as large-diameter logs and advanced decay stages that require extensive time to form (Santaniello et al., 2017). The loss of deadwood has been one of the major factor in the decline of numerous saproxylic species (Haddad et al., 2015; Harrison and Bruna, 1999; Tilman et al., 1994; Wilcox and Murphy, 1985). Consequently, conserving and increasing deadwood within forest ecosystems is vital for supporting biodiversity.

Efforts to restore and enrich forest ecosystems with deadwood are important tools to mitigate the adverse effects of land-use changes on saproxylic beetles. Due to the widespread shortage of deadwood in managed forests (Jonsson et al., 2016; Siitonen, 2001), generating additional deadwood can improve both the availability and diversity of habitats and food sources, leading to greater saproxylic beetle diversity (Grove, 2002; Hjältén et al., 2023; Sandström et al., 2019). Restoration initiatives vary in scale, from small-scale interventions like artificial creation of high-stumps and standing dead trees (Hämäläinen et al., 2021; Schroeder et al., 1999), larger efforts such as stand-level heterogenization and deadwood creation (Gossner et al., 2013; Hjältén et al., 2017), to approaches that mimic natural disturbances, such as prescribed burns (Hjältén et al., 2017; Saint-Germain et al., 2004; Toivanen and Kotiaho, 2010).

While these restoration techniques have shown significant benefits for many deadwood-dependent species, including both common and threatened species, not all organisms respond positively. For instance, certain species of bryophytes may experience short-term negative impacts from prescribed burning (Espinosa del Alba et al., 2021), while certain lichens have shown limited positive responses to high-stump creation (Hämäläinen et al., 2021). Additionally, the long delivery times of certain deadwood substrates like kelo wood might lead to potential risk of extinction due to the lack of suitable substrates (Larsson Ekström et al., 2023). Thus, restoration strategies must be carefully tailored to balance the needs of various species and ensure long-term ecosystem functions.

1.1.5 Field-of-Dreams-dilemma

Even if suitable habitat features are generated through restoration efforts, there is an uncertainty about whether target species can successfully disperse to and establish themselves in the restored areas. This uncertainty is commonly referred to as the “Field-of-Dreams dilemma” (Hilderbrand et al., 2005; Palmer et al., 1997). It reflects the idea that simply building a habitat does not guarantee the immediate or successful attraction of desired species, and if not, restoration might fail (Bell et al., 2015; Kouki et al., 2012). While restoration projects hold great promise for enhancing biodiversity in the long term (Heikkala et al., 2016), the slow formation of important habitat features in boreal forests poses an important challenge. Furthermore, replicating certain types of substrates, such as large-diameter dead trees (>50 cm) or advanced decay kelo wood, can be difficult or impossible through traditional restoration methods and take decades (Larsson Ekström et al., 2023; Santaniello et al., 2017). The process of generating such habitat structures is inherently slow, as it involves tree growth, wood decomposition, and species colonization, which can take decades to centuries (Mäkinen et al., 2006; Stokland et al., 2012). This has led to growing concerns about the effectiveness of traditional ecological restoration, with some questioning whether simply generating habitat structures is sufficient to restore biodiversity (Maron et al., 2012). These challenges underscore the need for innovative approaches in ecological restoration to ensure that important habitats are generated in time to support species at risk.

1.1.6 Conservation translocations

One approach of ecological restoration is conservation translocations, defined by International Union for Conservation of Nature (IUCN/SSC, 2013) as: "*Translocation is the human-mediated movement of living organisms from one area, with release in another*". In recent decades, the number of executed translocation have increased, but most assisted translocations focus is on single-species translocations of mammals, birds, reptile and amphibians (Seddon et al., 2014, 2007). In comparison to the total number of species within the taxa, the number of invertebrate reintroduction efforts is low, with approximately 65 projects worldwide recorded as in 2005. (Seddon et al., 2005). In recent decades, a number of successful conservation translocations of invertebrates have been performed (Bellis et al., 2019). For example, translocation and reestablishment projects of the Great Capricorn beetle (*Cerambyx cerdo*) in both Sweden and Poland (Drag and Cizek, 2015) that have shown successful results. Recently, invertebrate translocations via soil inoculation, where soil containing invertebrate communities is transferred to restoration sites, have demonstrate the potential for ecosystem restoration by relocating entire communities ("whole-of-community" rewilding (Contos et al., 2023, 2021)). Bellis et al. (2019) concluded that the most important factor influencing the success of translocation of invertebrates was the number of individuals released at the translocation site. Weather conditions and insufficient habitat quality were the most commonly reasons for translocation failures. The latter is further highlighting the importance and challenges in ecological restoration in replicating specific habitat features, such as old-dead trees of various decomposition stages.

For more sessile species like bryophytes and lichens, several translocation and reintroduction experiments have been performed (e.g., Mallen-Cooper and Cornwell, 2020; Smith, 2014), though a majority of experiments have focused on single species translocations. In a study conducted in Sweden, *Buxbaumia viridis*, a rare bryophyte, was cultivated to assess its establishment and growth. Results showed that establishment success depended heavily on substrate type, pH and moisture (Wiklund, 2003). The success and survival of bryophyte species in translocation efforts, are further influenced by microclimatic conditions, as shown in studies on *Eurhynchium angustirete, Herzogiella seligeri, Barbilophozia lycopodioides* and *Hylocomiastrum umbratum* (Dahlberg et al., 2014; Merinero et al., 2020). Substrate characteristics also affected the success and survival, as shown in experimental transplantation of the threatened liverwoth *Lejeunea cavifolia* (Mežaka, 2023), underscoring the need to consider both microclimatic conditions and substrate quality in conservation translocation efforts.

Most of the existing translocation studies on lichens have focused on assessing environmental influences on lichens (Smith, 2014). Early studies of epiphytic lichen translocation, e.g., Gilbert, (1977) and Hallingbäck, (1990), examined the survival rates of *Bryoria fuscescens* and *Lobaria pulmonaria*. Hazell and Gustafsson (1999), Lidén et al. (2004) and Jansson et al. (2009) stressed the importance of microhabitat factors and dispersal distances in achieving successful translocations of species like *Lobaria pulmonaria, Evernia divaricata, Ramalina dilacerata* and *Usnea longissima*. Overall, even if old-growth forest lichens can survive in new locations, their survival is limited by dispersal ability (Hilmo and Såstad, 2001) and the fact that some species are highly sensitive to environmental changes (Lidén et al., 2004).

Despite the theoretical promise of translocating single-species of invertebrates, bryophytes and lichens, several challenges remain. Species with complex habitat requirements, such as specific microclimatic or substrate preferences (Larsson Ekström et al., 2023), may struggle to survive in translocated environments unless those factors are carefully replicated (Bellis et al., 2019). However, the benefits of species translocations in conservation are clear, particularly in highly fragmented landscapes where preserving original habitats is no longer feasible (Armstrong and Seddon, 2008; Baur, 2014). Although many species frequently form associations involving multiple species or taxa (e.g., lichens (Asplund and Wardle, 2017)), most performed conservation translocations of bryophytes and lichens has up until now been single species translocations (Smith, 2014). As translocation methods continue to improve, conservation translocations will likely become an increasingly valuable tool in biodiversity conservation efforts (Seddon et al., 2014) and due to complexities of ecological communities, efforts should aim to move from single-species translocations to translocation of entire communities (Mallen-Cooper and Cornwell, 2020; Seddon et al., 2014).

1.1.7 Translocations of deadwood

One innovative approach within ecological compensation and conservation translocation is the already mentioned “whole-of-community” translocation of multiple species including their natural habitats. Translocation of old and large diameter deadwood in advanced decay stages, along with associated species living in and on the deadwood has recently been suggested as a novel approach to compensate for habitat and biodiversity loss (Lindroos et al., 2021; Tranberg et al., 2024). Translocation of deadwood and associated species from impact areas, subjected to exploitation, to compensation areas has the potential to solve some of the problems related to the field-of-dreams dilemma as well as long delivery times of deadwood in boreal forests.

To my knowledge, large-scale conservation translocation of deadwood with associated saproxylic species have not been previously evaluated. Deadwood enrichment has previously been performed (e.g., Baber et al., 2016; Gossner et al., 2013; Hjältén et al., 2012), although these experiments have all evaluated enrichment by fresh or recently cut trees of lower variation and quality. While deadwood enrichment and the translocation of more advanced types of deadwood (and its associated species) have rarely been assessed, a few examples on a small scale exists, though knowledge about these small scale implementations are scares and hard to come by.

Figure 2. Translocation of aspen deadwood in Oset-Rynningeviken Nature Reserve, Örebro, 2016. Photo: Per Wedholm.

In a Swedish context, there are a few examples of conservation translocation of deadwood with associated species. In 2016, approximately 100 freshly cut logs of *Populus tremula, Betula pendula, Ulmus glabra* and *Quesrcus robur* were translocated as compensatory measure to a nearby Nature Reserve in Örebro county. Roughly, a third of the logs were mounted as standing deadwood against living trees (Figure 2). Similarly, in 2020, approximately 80 kelo snags with Wolf lichen (*Letharia vulpina*) were translocated to near vicinity of original site, as compensatory measure due to a large-scale wind turbine park establishment in Åndberg, Jämtland county (Figure 3). All snags were mounted to other similar substrates or living trees. In 2021 roughly 60 logs of *Pinus sylvestris* were translocated to Örsbäck Nature Reserve, Västerbotten county as a compensatory measure due to a road construction (Figure 4). None of these examples has undergone scientific evaluation. Overall, the knowledge of deadwood translocation in ecological compensation is scarce and its impact on saproxylic species communities remains unexplored.

Figure 3. Translocation of kelo deadwood with Wolf lichen (*Letharia vulpina*) in Åndberg, Jämtland, October 2020. Photo: Olov Tranberg.

Figure 4. Translocation of large-diameter deadwood into Örsbäck Nature Reserve, Nordmaling, Västerbotten, December 2021. Photo: Olov Tranberg.

Photo: Susanna Bergström

2. Research objectives

The objective of my study is to evaluate the ecological impact of a novel conservation tool in ecological compensation; translocation of deadwood and associated species to compensation areas, by assessing changes in deadwood volumes and diversity, saproxylic beetle, bryophyte and lichen species richness and community composition.

Specifically, I aim to determine whether translocation increases deadwood volumes and diversity to levels equivalent to or beyond those in the impacted area, enhances the richness and abundance of saproxylic beetles, and maintains or enhances bryophyte and lichen diversity over time. Additionally, I examine how factors such as substrate type, habitat amount, and time since translocation influence these biodiversity metrics. I have four specific hypotheses, corresponding to each of the chapters in this thesis:

Paper I – Deadwood volumes, diversity and cost efficiency.

Translocation of deadwood to compensation areas will increase deadwood volumes and maintain deadwood diversity (particularly volumes of large diameter advanced decayed wood) to values equivalent to or beyond those found in the impact area.

Paper II - Implications for saproxylic beetles on plot level.

Translocation of deadwood will increase the species richness and abundance of saproxylic beetles and change assemblage composition in a compensation area compared to plots with no deadwood addition, and the effects will increase with the amount of translocated deadwood.

Paper III – Implications for saproxylic beetles on substrate level.

Translocation of deadwood will lead to enhanced saproxylic beetle communities in a compensation area, with species richness and community composition influenced by substrate type (e.g., tree species, decay stage) and time since translocation. Specifically, we hypothesize that diverse substrate qualities will increase beetle diversity.

Paper IV – Implications for bryophytes and lichens.

Translocation of deadwood will lead to enhanced or maintained bryophyte and lichen diversity in a compensation area, with species assemblages and richness influenced by habitat amount, substrate type, and time since translocation.

3. Methods

3.1 Study area and design

The data for my thesis originated from a newly established research infrastructure belonging to the Aitik ecological compensation project. The research project is located close to Gällivare (WGS84: 67°8'11.3"N 20°40'0.4"E, Figure 5) in Norrbotten county, northern Sweden and include three areas: one impact area (376 ha), one compensation area (397 ha) and one reference area (3563 ha, Ätnarova Experimental Forest). For Paper I, I used previously collected data on biodiversity and forest structures from the impact area (exploited due to mine expansion in 2017, before I started). In addition, I collected new data on biodiversity and forest structures in the compensation area (Paper I-IV). Furthermore, I collected data on biodiversity and forest structures in the reference area (Paper II) that will serve as a landscape reference. This was done to ensure the independence of experimental plots in the compensation area, in case the translocation of deadwood also affects the control plots.

All areas are located within the north boreal vegetation zone (Ahti et al., 1968) and are dominated by Norway spruce (*Picea abies*), older Scots pines (*Pinus sylvestris*) and scattered birch (*Betula pubescens*). Goat willow (*Salix caprea*) and aspen (*Populus tremula*) also occur. All areas have signs of earlier silviculture, i.e., selective felling, but have never been clear-felled. The compensation area have lower conservation values than the impact area, e.g., in terms of quality and volumes of deadwood, very old trees and variation in forest structure (Forsgren et al., 2016).

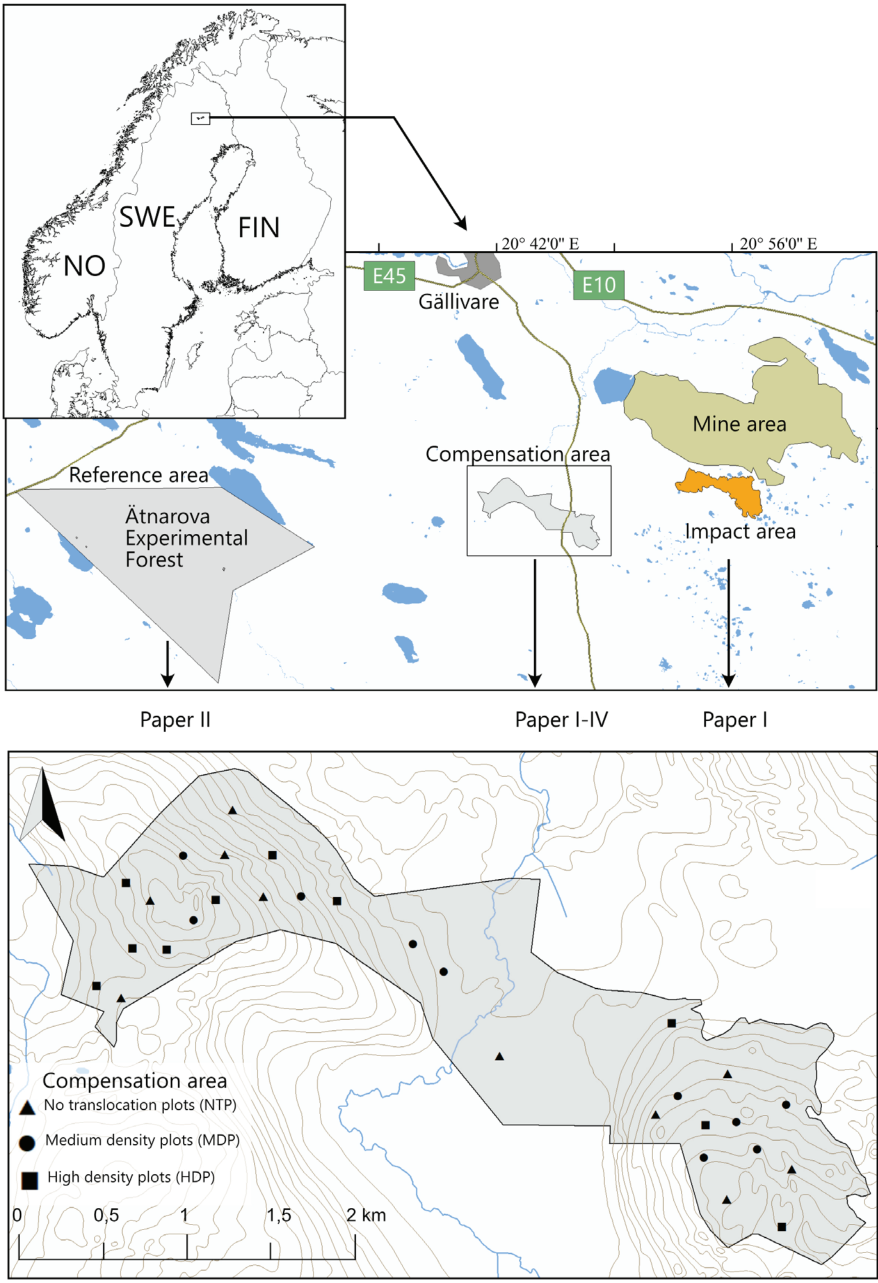

Figure 5. Overview of study areas used in my thesis and corresponding papers. Illustration: Olov Tranberg.

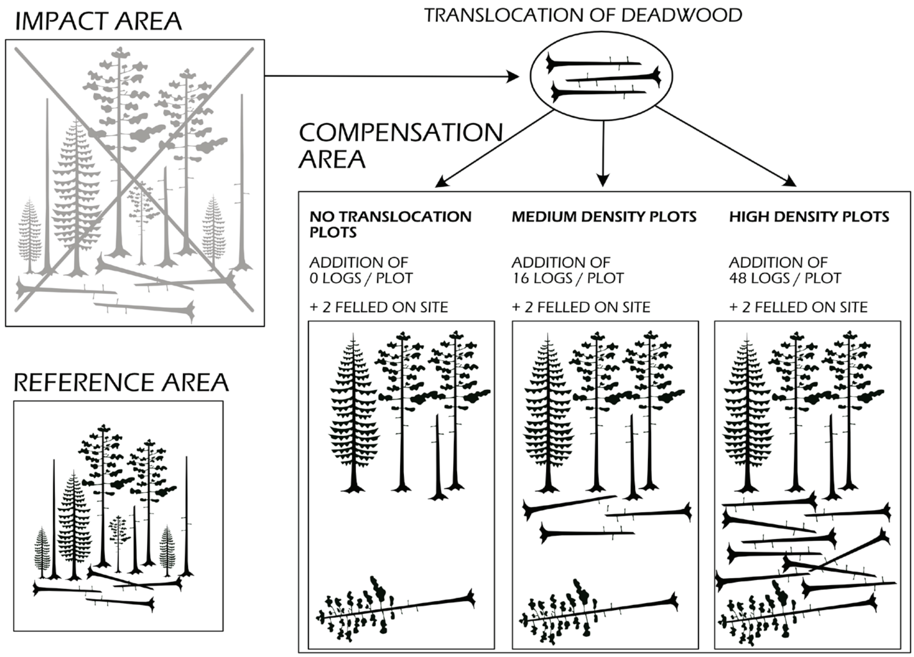

Figure 6. Study design including the exploited impact area and distribution of translocated deadwood into different experimental plots (r = 25 m) in the compensation area (Paper I-IV), additionally showing and reference area (Paper II) receiving no translocated deadwood. Illustration: Olov Tranberg.

The forest in the impact area was felled in early winter 2017. Immediately prior to this, deadwood logs (3-5 m in length and ≥ 15 cm in large end diameter) and felled living trees were translocated from the impact area to the compensation area situated approximately 6 km from the impact area (Figure 5).

Translocated deadwood belonged to four categories of both Norway spruce and Scots pine; 1. felled living trees with high conservation value (nature value trees, NV), 2. dead trees in an early decay stage (DC1, sensu Thomas and Parker (1979)), 3. dead trees in an intermediate decay stage (DC2-3), and 4. standing dead trees (snags). In total eight classes or 637 substrates were translocated (Table 1 and Figure 7). The selected deadwood was translocated to the compensation area and inserted into 30 experimental plots (50 m in diameter), separated by at least 150 m for independence. Ten plots serve as control plots, receiving no translocated logs (No Translocation

Table 1. Experimental setup and corresponding papers, including plot types; NTP (no translocation plots), MDP (medium-density plots), HDP (high-density plots) and deadwood enrichment of deadwood types.

	Impact area (n = 10)	NTP (n = 10)	MDP (n = 10)	HDP (n = 10)	Reference area (n = 10)	Total
Included in Papers	I	I-IV	I-IV	I-IV	II	
Deadwood volume (m^3 ha^{-1}) before translocation	21.1 ± 4.8	9.1 ± 3.9	10.6 ± 3.4	8.8 ± 2.8	29.3 ± 4.9	
Number of translocated logs/plot		0	16 ± 1	48 ± 1	0	637
Translocated deadwood volume to each plot (m^3)		0	6.0 ± 0.9	15.0 ± 1.0	0	
Trees felled on site/plot		2	2	2	0	60
Translocated deadwood types/plot						
Pine NV	-	-	3 ± 1	8 ± 3	-	133
Pine early	-	-	1 ± 1	1 ± 1	-	18
Pine intermediate	-	-	1 ± 1	4 ± 2	-	65
Pine snag	-	-	3 ± 1	5 ± 2	-	97
Spruce NV	-	-	2 ± 1	6 ± 1	-	84
Spruce early	-	-	2	6 ± 2	-	80
Spruce intermediate	-	-	2 ± 1	6 ± 1	-	79
Spruce snags	-	-	2 ± 1	6 ± 1	-	81
Total						637

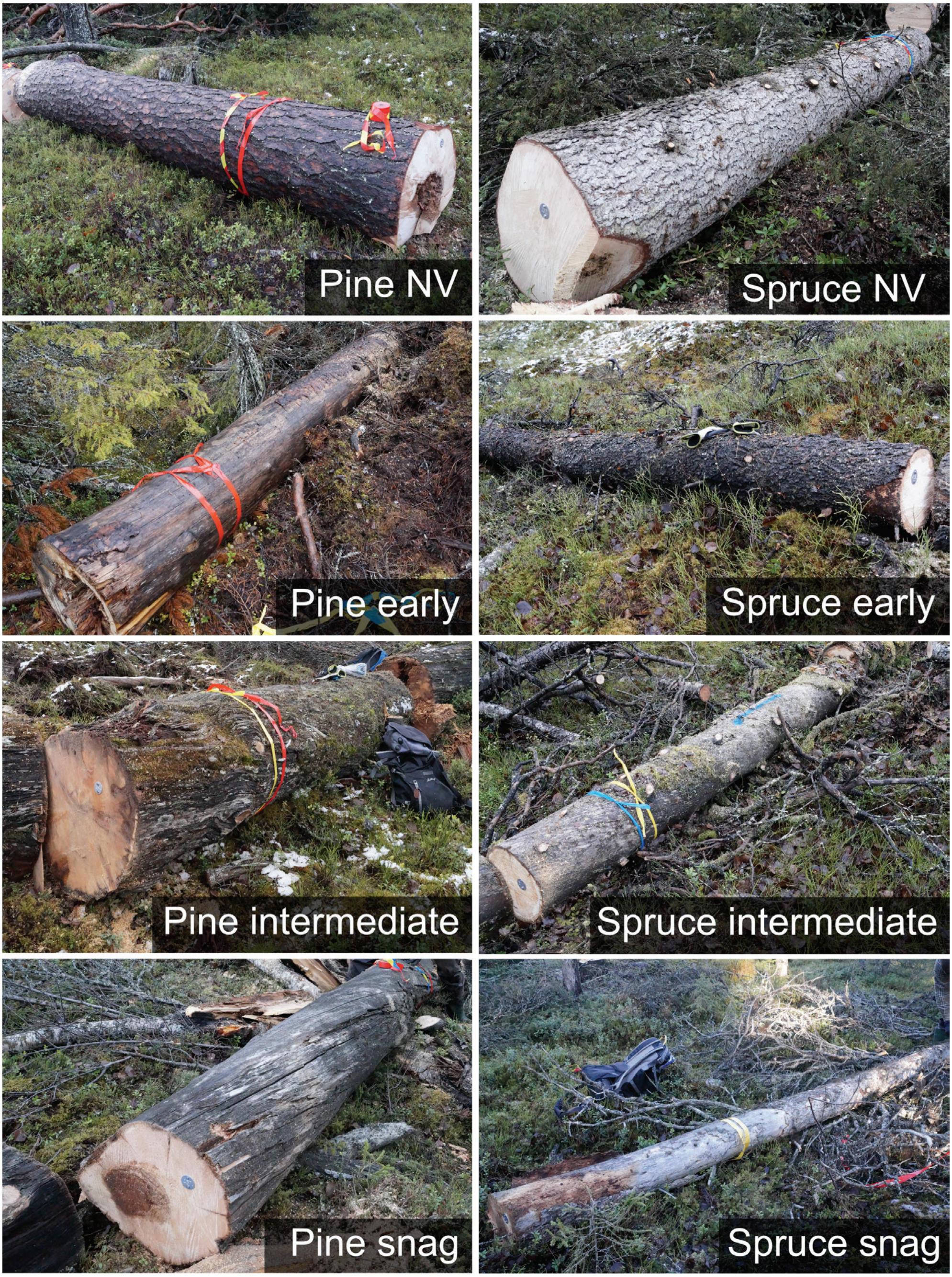

Figure 7. Deadwood types of different decay stages included in the translocation.
Photo: Nordlund Konsult AB.

Plots = NTP), ten plots received 16 deadwood substrates (Medium Density Plots = MDP) and ten plots received 48 deadwood substrates (High Density Plots = HDP). The goal was to insert approximately two of each substrate type in each MDP and approximately six of each substrate type in HDP, but due to insufficient numbers of pine early logs, additional substrates were supplemented from standing dead trees and living trees of pine (Table 1). Further, one living spruce and one pine, were felled on site in all plots, including NTP but excluding plots in the reference area (Figure 6) to provide a continuum of new substrates for translocated species to colonize.

3.1.1 Translocation methods

Translocation of deadwood followed a seven step scheme (Lindroos et al., 2021), also displayed in Figure 8. The first step, identification of areas, involved selecting suitable compensation areas. The second step, identification of substrates, involved surveying the impact area, selecting and marking qualitative substrates of logs, nature values trees, and snags later to be translocated. The third step, logging, involved tree felling and cutting the substrates. The fourth step, marking of logs, involved marking the felled and cut logs. The fifth step, extraction of logs, involved skidding the marked logs out of the impact area. The sixth step, road transportation, involved transporting the extracted logs by truck from the impact area to the compensation area. The seventh and last step, insertion to the compensation area, involved inserting the transported logs into the compensation area.

Figure 8. Translocation scheme; a) identification and marking of substrates, b) tree felling and cutting, c) extraction of logs from impact area, d) road transportation to compensation area, e) insertion to the compensation area and f) one of the experimental plots after insertion. Photo: a-d) Nordlund Konsult AB, e) Joakim Hjältén, f) Olov Tranberg.

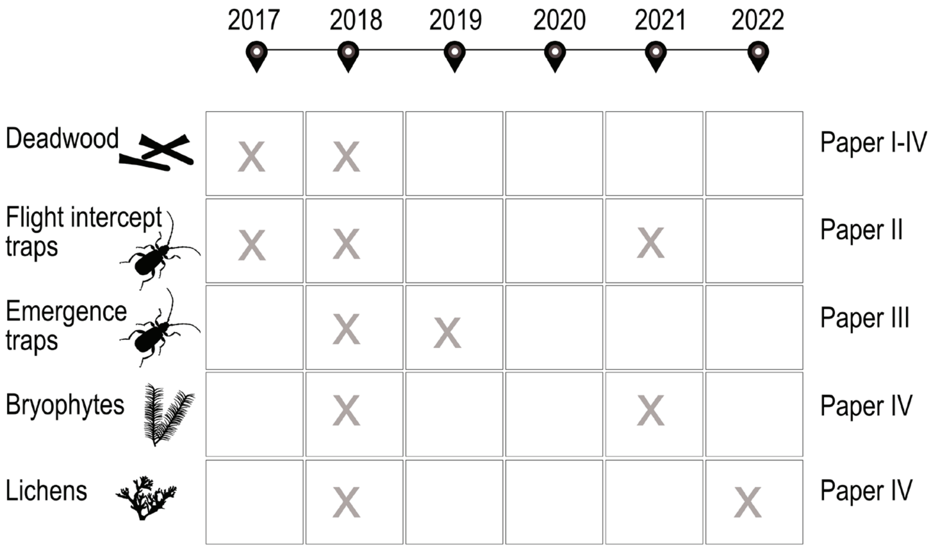

Figure 9. Chronological overview of collection for data used in my thesis, and corresponding papers. Translocation of deadwood from impact to compensation areas took place in late autumn of 2017. Illustration: Olov Tranberg.

3.2 Data collection

3.2.1 Deadwood sampling (Paper I)

Before the translocation in late autumn 2017, deadwood measurements were conducted in both the impact and compensation areas (Figure 9). Deadwood characteristics were assessed within a 25 meter radius plot, including all naturally occurring dead trees with a minimum large-end diameter of ≥ 5 cm. Measurements included base and top diameter, tree species, and trunk length. Posture of each tree was classified as either standing dead or downed logs. Trees with tree base/root originating outside the plots were excluded from measurements. For standing dead trees and snags, height and diameter at breast height (DBH) were measured. The decay class (DC) for coniferous deadwood was determined using classification system from Thomas and Parker (1979), including DC1-5 for downed and DC1-7 for standing deadwood. For broadleaves, decay class was categorized based on wood softness (“hard” or “soft”) following the system by Gibb et al. (2005). Deadwood inventories were repeated in 2018 after translocation, including measurements of both naturally occurring and translocated deadwood.

Figure 10. Flight intercept trap, model IBL-2 in the reference area. Photo: Olov Tranberg.

3.2.2 Insect sampling – Flight intercept traps (Paper II)

Beetle sampling for Paper II was carried out in the compensation area using two flight intercept traps (model IBL-2) within a 10-meter radius of each plot centre. These traps (Figure 10) feature a triangular, semi-transparent plastic barrier with an approximate surface area of 0.35 m^2. Each trap was equipped with a water-draining funnel leading to a 600 ml collection bottle. The collection bottles were filled to about one-third of their capacity with a solution of 50% propylene glycol and 50% water, along with a small amount of detergent to reduce surface tension, following the methodology described by Stenbacka et al. (2010). For each sampling year, the traps were placed in field from late May or early June until mid-September. Sampling was conducted on three separate occasions: prior to translocation in 2017, during the first season after translocation in 2018, and in the fourth season post-translocation in 2021.

After collection, the samples were sorted and identified to the most precise taxonomic level possible, typically to species but occasionally to genus, by expert taxonomists. All specimens were classified as either saproxylic (including both facultative and obligate) or non-saproxylic, with the latter group being excluded from further analysis. Saproxylic species were further categorized into feeding guilds, combining cambivores and woodborers into a single group, based on their nutritional ecology as outlined in Koch, (1992, 1989a, 1989b) and Hagge et al. (2021) and supplemented by expert opinions. Species were also identified as being of conservation concern if they were listed in any of the three most recent Swedish red-lists (SLU Artdatabanken, 2020, 2015, 2010). Based on recommendations from taxonomic experts, specimens identified as *Zilora cfr elongata* were grouped with *Zilora ferruginea*, and those identified as *Orthoperus cfr punctatus* were grouped with *Orthoperus rogeri*. Additionally, some specimens could not be determined to species level and were therefore excluded from further analysis; these included 29 specimens of *Acrotrichis sp*., 2 specimens of *Atomaria sp*., 1 specimen of *Epuraea sp*., and 2 specimens of *Ptinella sp*.

3.2.3 Insect sampling – Emergence traps (Paper III)

Beetle sampling for paper III was conducted in compensation area using trunk emergence traps (Figure 11), capturing adult beetles emerging from a randomly selected sub-sample of 235 translocated logs (two logs of each substrate type in each of the 20 plots containing translocated wood). Sampling was done during the first summer of 2018 after the translocation, and again after one year in 2019. The same 235 logs were sampled in both years, in all 470 samples. The traps were active from May to September each year. Each trap enclosed an average log volume of 0.07 m^3 (SD ±0.05) and was constructed by wrapping a randomly chosen 30 cm section of the log in black polypropylene weed barrier cloth, with a collecting bottle attached. The specific log section sampled was randomly relocated on same log between survey years. The barrier cloth allowed moisture and oxygen to pass through but blocked light. The cloth was secured to the log using plastic bands and staples to prevent insects from entering or escaping the trap, and foam underlay was used to seal the trap's sides. A translucent 250 ml plastic bottle, attached to a hole at the top of the trap and half-filled with 50% propylene glycol, collected the insects. All saproxylic beetles were extracted from the samples and identified to species level by expert taxonomists.

Beetles were classified according to the 2020 Swedish Red List (SLU Artdatabanken, 2020) as either least concern or red-listed. All species were further categorized as either saproxylic (facultative and obligate) or non-saproxylic, with the latter excluded from further analyses. Feeding guilds were assigned as cambivore (including cambium and phloem consumers, and woodborers), fungivore (mycetophagous species), predator (predators and ectoparasitoids), and omnivore for species with multiple feeding guilds. The classification of beetle length (adult mean body length; mm) and feeding guild was based on knowledge of beetle body measurements and nutritional ecology from the literature (Hagge et al., 2021; Koch, 1992, 1989a, 1989b) and expert taxonomists.

Figure 11. Emergence traps mounted on deadwood in the compensation area. Photo: Olov Tranberg.

3.2.4 Bryophyte and lichen sampling (Paper IV)

Deadwood in compensation area were surveyed directly after translocation in summers of 2018 for both bryophytes and lichens, followed by a re-survey in 2021 for bryophytes and 2022 for lichens. All fallen naturally occurring and translocated deadwood logs of Scots pine and Norway spruce with a maximum diameter >10 cm and length >1 m with root end within the plots (radius 50 m) was surveyed for bryophytes and lichens. For the lichen survey on naturally occurring deadwood, only logs with at least some part of the trunk being debarked were included, thick branches were excluded. Species identification was done in the field by experts and each species was noted as presence-absence for each individual log. For bryophytes, all species present on the logs were noted, both obligate saproxylic species (sensu Ódor and van Hees (2004)) and non-saproxylic species. For lichens obligate saproxylic species were included, using a selection based on Spribille et al. (2008) with addition of red-listed species and species that are regional indicators of high conservation value deadwood (personal comment Fredrik Jonsson, 2024). Four lichen species, *Arctoparmelia centrifuga*, *Flavocetraria nivalis*, *Hypogymnia bitteri* and *Micarea melaena* were removed from further analysis following recommendation of species experts due to incomplete survey of these species in field.

3.3 Statistical analysis

3.3.1 Deadwood volumes, diversity and cost efficiency (Paper I)

To assess deadwood volumes for logs I used the formula for a truncated cone, while volumes for standing dead trees (snags) were calculated using specific functions from Näslund (1940) for pine, spruce, and birch in northern Sweden. For high stumps or broken trees, volumes were calculated using the formula for a cylinder. I applied linear regression to test for differences in deadwood volumes between impact area plots and translocation plots, followed by Tukey pairwise comparisons.

Deadwood volumes were calculated at different spatial scales: plot (25-meter radius), stand (1 hectare), and landscape (≤ 500 hectares). This allowed for an assessment of the cost and effort needed for compensation at these scales. Costs of alternative intensities and sizes of areas for compensation measures were calculated using data from Lindroos et al. (2021).

Deadwood diversity was examined by generating 240 unique deadwood types based on possible combinations of tree species, decay class, diameter class, and posture (snag or downed). The diversity patterns were analysed using a permutational multivariate analysis of variance (PERMANOVA) and visualized using non-metric multidimensional scaling (NMDS). Indicator species analysis was used to identify deadwood types with significantly higher occurrences in translocation plots or study areas. All analyses were conducted using R software (R Core Team, 2021).

3.3.2 Implications for saproxylic beetles on plot level (Paper II)

To compare species richness and abundance across the three sampling years (2017, 2018, and 2021) and four treatments (NTP, MDP, HDP and reference area) I used a generalized linear model (GLM) using the "glmmTMB" function from the "glmmTMB" package by Brooks et al. (2024) using R software (R Core Team, 2021). A negative binomial distribution was applied, with treatment, year, and their interaction as fixed factors. Pairwise comparisons between treatments were conducted using a post-hoc Tukey test using the "emmeans" function from the "emmeans" package by Lenth et al. (2023).

To assess differences in species composition between treatments and years, I performed a permutational multivariate analysis of variance (PERMANOVA) in PRIMER (Anderson, 2001; PRIMER, 2007), with treatment, year, and their interaction as fixed factors. I transformed the data using a fourth-root transformation, and Bray-Curtis similarity as a community distance measure. I visualized variations in species composition across different plots and years using non-metric multidimensional scaling (NMDS) with the "metaMDS" function from the "vegan" package by Oksanen et al. (2020). I used Similarity percentage analysis (SIMPER) in PRIMER to determine which species contributed most to differences in beetle assemblages, with a 50% cut-off for all feeding guilds and a 90% cut-off for species of conservation concern and indicator species analysis using the "multipatt" function from the "indicspecies" package by De Cáceres et al. (2022).

3.3.3 Implications for saproxylic on substrate level (Paper III)

To analyse emerging beetles from translocated deadwood we used hierarchical modelling of species communities (HMSC) with the R package Hmsc (Tikhonov et al., 2022). This method, a type of joint species distribution model, allows the integration of species occurrences, environmental variables, and species traits to examine species-to-species associations while controlling for various factors. The analysis focused on presence/absence data from 99 saproxylic species (90% of total occurrences). We excluded species occurring in fewer than three logs and empty traps, reducing the initial 178 species dataset. The model assessed the influence of substrate type, year, and species traits (e.g., feeding guilds, body length) on beetle communities. The probit link function was used, and a latent variable approach accounted for repeated log sampling, enabling the examination of species-to-species associations. Associations were classified as positive, negative, or neutral based on posterior probabilities, with thresholds set at 75%, 25%, and between, respectively. The analysis aimed to determine how species richness, emergence probabilities, and traits varied between substrate types (pine vs. spruce, snags vs. early decay logs, early vs. mid decay logs) and over time (2018 vs. 2019). Predictions were made using 2,000 posterior draws from the model, with differences considered statistically supported at 90% or 95% probability.

Additionally, rarefied species accumulation curves were generated using the iNEXT package (Hsieh and Chao, 2024) to analyse overall species richness across different densities and substrate types, including rare species. The full dataset of 178 species from 235 logs was used, pooled from both years. All analyses were conducted using R software (R Core Team, 2021) (R Core Team 2021).

3.3.4 Implications for bryophytes and lichens (Paper IV)

To evaluate how translocated deadwood contributes to bryophyte and lichen biodiversity at the plot level, I aggregated presence-absence data of each species for each unique plot. Similarly, to assess the impact of habitat diversity (different deadwood substrates) on the success of translocation for bryophytes and lichens, I summed presence-absence data for each individual log at the substrate level, focusing only on translocated deadwood.

At plot level, I assessed differences in species richness using a generalized linear model (GLM) with a Poisson distribution, setting plot treatment, year, and substrate origin (translocated or naturally occurring) as fixed factors. At substrate level, I applied generalized linear models (GLM) using the “glmmTMB” package (Brooks et al., 2024) with a negative binomial distribution to handle zero-inflated count data, which was common in the first year, particularly for certain substrates. The model initially included Plot ID as a random factor, but I removed this due to convergence issues. I conducted pairwise comparisons for species richness across treatments, substrate origins, substrate types, and years using Tukey-adjusted post-hoc tests with the “emmeans” function from the emmeans package (Lenth et al., 2023).

To assess differences in species composition at both plot and substrate levels, I performed PERMANOVA analyses (Anderson, 2001) in PRIMER (PRIMER, 2007), using fixed factors such as treatment, year, and substrate origin. At substrate level, substrate type (eight categories) was also included as a fixed factor. The data were fourth-root transformed, and I used Bray-Curtis similarity for resemblance. Finally, to identify species that contributed most to the differences in assemblage compositions, I conducted SIMPER analysis in PRIMER on fourth-root transformed data, with a cut-off set to 90% explained variation.


Photo: Mari Jönsson

4. Results and discussion

4.1 Deadwood volumes, diversity and cost efficiency (Paper I)

4.1.1 Main results of Paper I

Prior to translocation, compensation area plots had significantly lower deadwood volumes than the impact area plots (1.8 m^3/plot compared to 4.1 m^3/plot, respectively, Figure 12). After translocation, medium- (MDP) and high-density (HDP) plots had significantly higher volumes of deadwood compared to no translocation plots (NTP). Both HDP and MDP reached deadwood volumes higher than those in the impact area ($p<0.001$ for both), with translocated deadwood accounting for the majority of the volume in MDP and HDP plots (76% and 89%, respectively). However, at stand level (one ha), neither MDP nor HDP had significantly different deadwood volumes compared to the impact area. When considering the entire compensation area, translocation did not fully reach deadwood levels found in impact area. The compensation area still had significantly less deadwood overall compared to the impact area, with an average addition of only 0.58 m^3/ha due to translocation, far below the 21.1 m^3/ha found in the impact area. To match the deadwood levels of the impact area, a substantial increase in translocated logs (an additional 7.0-16.6 m^3/ha) would be required, involving a significantly higher effort and cost.

The diversity of deadwood types in the compensation area increased following translocation, but significant differences remained between the impact area and the compensation plots. While translocated substrates contributed to a greater variety of deadwood in MDP and HDP plots, the overall composition did not fully replicate that of the impact area.

To fully compensate for deadwood loss at a landscape level (size of compensation area), reaching deadwood levels of the impact area would require approximately 12.500 logs and a cost of 5.8 million SEK, which is 20 times the effort and cost of the performed translocation, where 637 logs were moved at a cost of 0.3 million SEK.

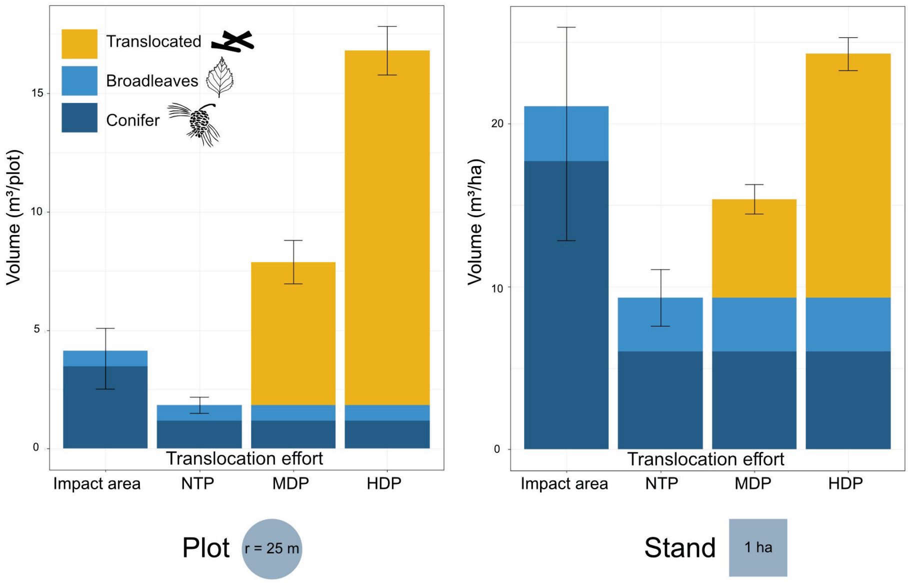

Figure 12. Deadwood volumes in the impact area (far left) and compensation area, the later divided into NTP; no translocation plots (no deadwood addition), MDP; medium-density plots (addition of 16 substrates/plot) and HDP; high-density plots (addition of 48 substrates/plot). Translocated deadwood (yellow) consist only of conifers. Illustration: Olov Tranberg.

4.1.2 Discussion of Paper I

Translocation of deadwood successfully increased the volume and diversity of deadwood in the compensation area, particularly in HDP and MDP plots, where volumes exceeded those in the impact area. However, the overall compensation effort was insufficient to fully match the deadwood levels and composition of the entire impact area, highlighting the need for more extensive translocation efforts to achieve full compensation.

In Paper I, I assessed the effectiveness of deadwood translocation as a novel method for ecological compensation, particularly in addressing the long timeframes typically required for the natural development of large-diameter, high-quality deadwood. The findings indicate that translocating deadwood significantly increased deadwood volumes in experimental plots, achieving levels comparable to or exceeding those found in old-growth forests. This increase in deadwood volume, particularly in medium-density and high-density plots, suggests that translocation can help achieve the threshold volumes necessary to support populations of rare and red-listed saproxylic species.

One of the primary benefits of deadwood translocation is its potential to create “deadwood hotspots” in the landscape, which can serve as sources of dispersal for saproxylic species. This method not only accelerates the development of necessary habitat elements but also preserves species that would otherwise be lost in impact areas, offering them a chance to establish in new habitats. Additionally, translocation increases deadwood without reducing the standing volume of living trees in compensation areas, allowing these trees to mature and contribute to future deadwood availability.

However, in Paper I, I also highlight several challenges and limitations. The composition of deadwood in the compensation area differed from that in the impact area, with certain deadwood types, such as standing dead trees, being underrepresented due to the practical difficulties of maintaining them in a standing position after translocation. The lack of deciduous deadwood, particularly from willow, could result in a lower richness of species associated with these substrates. Moreover, while the method increased the volume and quality of deadwood, it did not necessarily replicate the full diversity of deadwood types present in the impact area.

I also discussed the costs associated with large-scale deadwood translocation. While full compensation at a landscape scale would require significantly more resources, the costs are relatively low compared to the budgets of large-scale exploitation projects. I suggests that further methodological improvements could enhance the cost-efficiency of deadwood translocation while maintaining the desired biodiversity benefits.

In conclusion, deadwood translocation presents a promising tool for ecological compensation and forest restoration, capable of rapidly increasing deadwood volumes to support biodiversity. However, the method requires further refinement and evaluation, particularly in developing techniques to translocate a wider range of deadwood types and maintaining standing deadwood. Monitoring the fate of species communities moved with translocated deadwood is essential for assessing the long-term biodiversity benefits. The broader principle that I emphasized is that preservation of valuable habitats should always be prioritized, with compensatory actions like translocation being pursued only when preservation is not possible.

4.2 Implications for saproxylic beetles on plot level (Paper II)

4.2.1 Main results of Paper II

In total, I caught 31 147 individuals from 440 beetle species, of which 339 species (77%) were saproxylic. The majority of species were fungivores (159 species, 36%), followed by predators (129 species, 29%), and cambivores and woodborers (55 species, 13%).

Translocation of deadwood significantly increased both the species richness and abundance of saproxylic beetles in the compensation areas, both in medium- (MDP) and high-density (HDP) plots (Figure 13). Within high-density plots, species richness increased over time, with significant increases observed from 2017 to 2021. By 2021, species richness in HDP was significantly higher than in no translocation plots (NTP), and both MDP and HDP plots demonstrated greater species richness than the reference area (RA) across multiple feeding guilds.

In terms of abundance, the total number of saproxylic beetles also rose substantially in the translocation plots. One year after translocation in 2018, HDP plots exhibited a higher abundance of all saproxylic beetles compared to NTP. This trend persisted, with the abundance of cambivores and woodborers remaining higher in HDP plots than in MDP plots by 2021. Moreover, the abundance of beetles in translocation plots consistently exceeded that in the reference area, particularly for all saproxylics, fungivores, predators, and cambivores/woodborers.

I also noted significant findings for species of conservation concern, where these species were more abundant in MDP and HDP plots compared to NTP plots, especially in the years following translocation.

Furthermore, the composition of beetle assemblages underwent significant shifts in the translocation plots compared to the reference area.

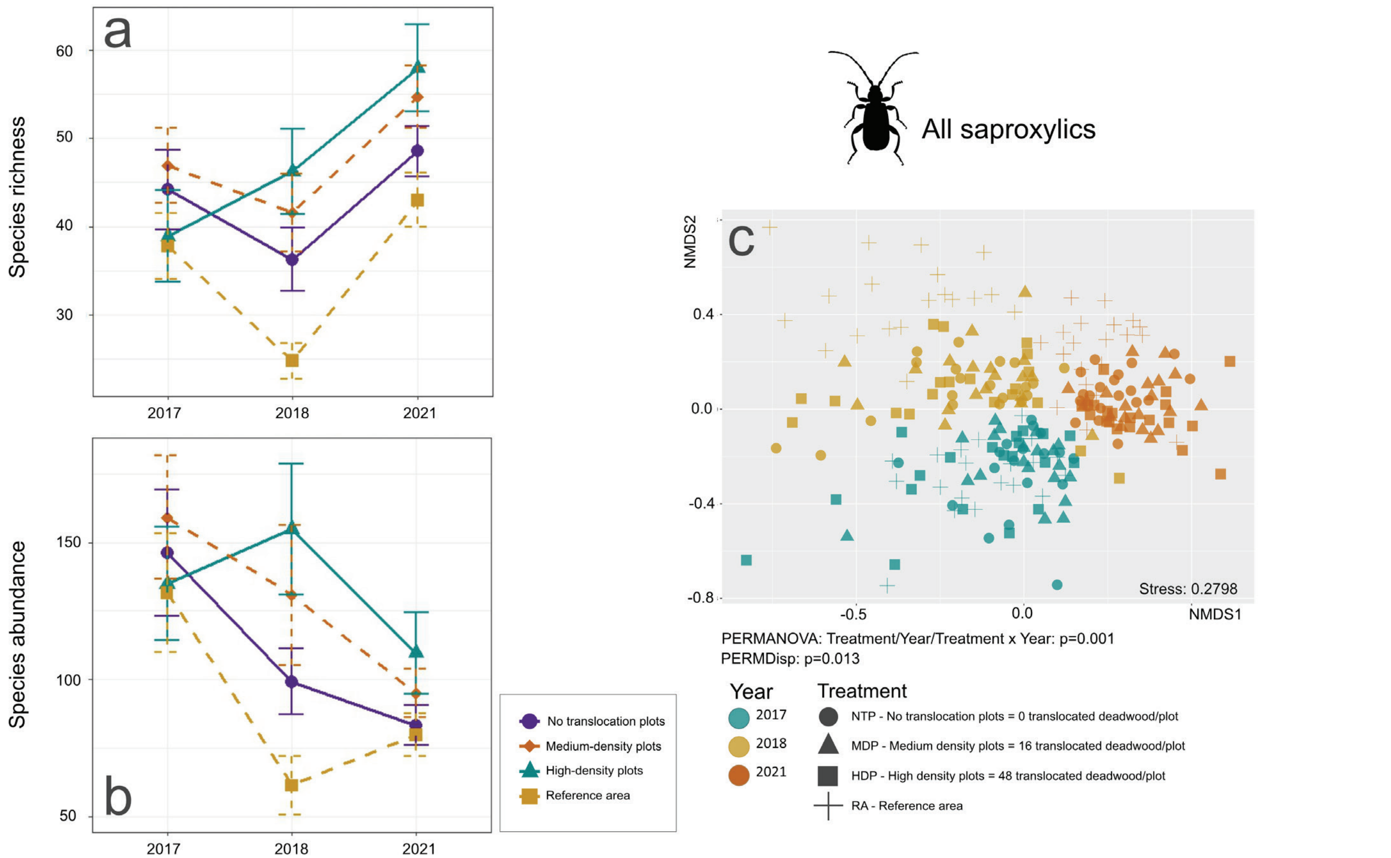

Figure 13. Results for all saproxylic beetles over the sampling years: before translocation in 2017, one year after translocation in 2018, and four years after translocation in 2021. Including; a) species richness, b) abundance and c) assemblage composition. In c) NMDS ordination for the assemblage composition of saproxylic beetles on trap level. The colours indicate the years and symbols treatment groups. Illustration: Olov Tranberg.

4.2.2 Discussion of Paper II

One remark of Paper II is that translocating deadwood to compensation areas, at least temporarily, significantly enhances the species richness, abundance, and diversity of saproxylic beetles. The effects were most pronounced in plots where higher volumes of deadwood were added, with both medium- and high-density plots showing higher levels of species richness metrics compared to no translocation plots and the reference area. Additionally, the translocation altered the assemblage composition of beetle communities.

I revealed a moderate increase in species richness, particularly among cambivores, following the addition of fresh deadwood. This increase aligns with previous research showing that deadwood enrichment, especially with fresh substrates, enhances species richness (e.g., Hägglund and Hjältén, 2018). The translocation of later decay stages was expected to benefit species of conservation concern, often associated to less common deadwood substrates (Ulyshen and Hanula, 2009). However, these species did not show any significant increase in abundance, likely due to their relatively low presence in absolute numbers. Nevertheless, the increase of fungivores within the first year after translocation suggests that including a variety of deadwood types in translocations can support species associated with different successional stages.

I found the strongest effects on species richness and abundance in high-density plots, possibly due to either more species being translocated with the wood or more species being attracted from the surrounding landscape. However, it was not possible to distinguish between these two drivers.

Regarding assemblage composition, I found only partial support for the hypothesis that translocation would lead to significant changes. While treatment had an effect on assemblage composition (18-26 % of the variance), most differences (56-64 % of the variance) were attributed to year. This indicate that beetle assemblages are generally more influenced by inter-annual weather variations (Müller et al., 2023) although that enrichment of deadwood through translocation also had an effect.

I also highlighted the importance of level of deadwood enrichment in influencing species assemblages, with high-density plots showing a higher number of indicator species. Species assemblages in the reference area differed from those in the compensation area, likely due to differences in climatic and habitat conditions, as well as deadwood volume and continuity.

In Paper II, I conclude that deadwood translocation offers a potential approach for restoring habitat elements and enhancing biodiversity that would otherwise take decades to develop. In the short term, translocation increased species richness of saproxylic beetles, with the effect being proportional to the volume of wood translocated. However, I also identifies several caveats. Heterogeneity within the compensation area prior to translocation, and the need for long-term monitoring to ensure survival of benefited invertebrates are important considerations. Additionally, I suggests that deadwood translocation should be tailored to the initial quality of the compensation area to achieve thresholds suitable for target species.

4.3 Implications for saproxylic beetles on substrate level (Paper III)

4.3.1 Main results of Paper III

In the study 1026 individual beetles from 99 saproxylic species were captured (species that occurred on ≥ 3 logs in at least one of the 2018 and 2019 datasets), emerging from 218 translocated logs across 362 trap samples (two years). The most common beetles were fungivores (35 species), predators (35 species), cambivores and woodborers (21 species), and omnivores (8 species).

Species richness was generally low, with an average of 2-3 species per sample each year, slightly greater in 2019 than in 2018. Red-listed species had only a few emerging events, particularly from spruce snags and mid-decay spruce logs in the second year after translocation. The total accumulated species richness was greater on spruce snags and spruce logs in early stages of decay compared to other substrate types and did not level off towards asymptote for most substrate types (Figure 14a). When all substrate types were combined, species richness began to level off towards asymptote at around 200 species (Figure 14b).

Beetle emergence was influenced by the traits of the species and deadwood substrate type, explaining 37% of the variation in emergence patterns. Predators and fungivores had higher emergence probabilities from pine snags and logs in early decay stages, while cambivores were more likely to emerge from spruce substrates. Beetle species with longer body lengths were more common in 2018, particularly from spruce snags, but this trend decreased by 2019 as shorter-bodied predators and fungivores became more dominant.

Species-to-species associations were mostly positive, with small to medium-sized fungivores and predators showing strong associations. The red-listed cambivore *Ernobius explanatus* was negatively associated with several other species, including predators and cambivores.

Rarefaction curves showed slightly greater species richness in high-density translocations compared to medium-density translocations, with species richness more than doubling from 2018 to 2019. Spruce snags and early decay spruce logs had the highest accumulated species richness.

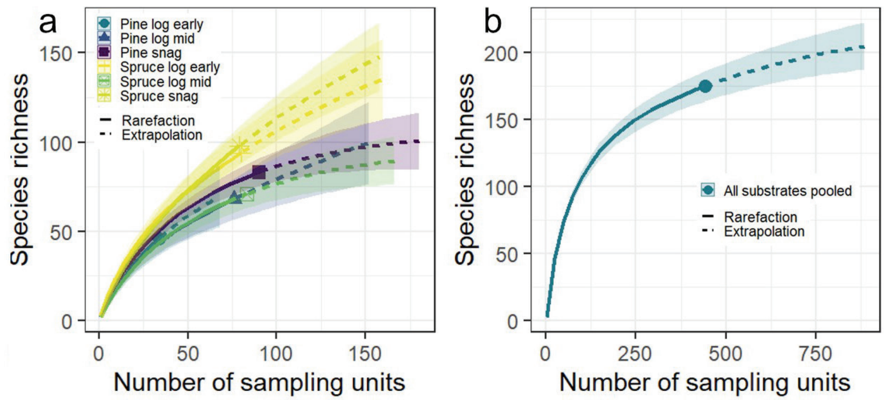

Figure 14. Rarefaction curves showing total species richness of a) substrate types (b) and all substrate types pooled, for year 2018 and 2019 pooled. Y-axis represents observed (full lines) and extrapolated (dashed) species richness. X-axis represents the sample effort in cumulative trap samples. Error bars show 95 % S.E.

4.3.2 Discussion of Paper III

This is one of the first large-scale experiments on deadwood translocation, providing valuable insights into the short-term effects on wood-inhabiting beetle communities. The findings suggest that translocation of diverse deadwood types can enhance beetle species richness, particularly in high-density plots, giving support for including a high diversity of deadwood types. Species richness increased over time, with spruce snags and early decay logs important for supporting a greater richness of beetles, including some red-listed species, while pine substrates held an important role in supporting fungivores and predators.

We demonstrated that beetles with different functional traits, such as body length and feeding guilds, responded differently to translocated deadwood, highlighting the importance of including a variety of deadwood qualities in translocations. The observed positive species-to-species associations within translocated beetle communities suggest that whole-of-community translocations can support complex ecological networks, although planning for these interactions remains challenging.

However, we also pointed out the complexities of balancing diverse species needs in translocation efforts. The success of such translocations depends on carefully considering species' abiotic and biotic dependencies, habitat preferences, and interspecific interactions to provide sufficient amounts and qualities of substrates.

The research underscores the importance of long-term monitoring to fully understand the impacts of deadwood translocation on beetle communities and to assess whether additional restoration strategies are needed. The results indicate that deadwood translocation can be an effective tool for reinforcing wood-inhabiting beetle communities in compensatory forests, but it must be carefully tailored to the specific needs of target species and communities to achieve the best conservation outcomes.

4.4 Implications for bryophytes and lichens (Paper IV)

4.4.1 Main results of Paper IV

I found a total of 52 bryophyte and 38 lichen species, with naturally occurring deadwood hosting a higher number of bryophyte species (47) compared to translocated deadwood (32), while lichen species were nearly evenly distributed between naturally occurring (32) and translocated deadwood (33).

Bryophytes showed a positive response to translocation over time, with species richness increasing from 2018 to 2021. In contrast, lichen species richness had a decreasing trend over the same period, although not significant. Specifically, bryophytes experienced more colonizations (8 new species) and fewer extinctions (1 species) compared to lichens, which had an equal number of colonizations and extinctions (4 species each). The most abundant bryophyte, *Pleurozium schreberi*, increased significantly from being found on 194 logs in 2018 to 780 logs in 2021. The lichen *Xylographa vitiligo* also increased in abundance, from 117 logs in 2018 to 205 in 2022.

The total accumulated species richness was greater on naturally occurring deadwood than translocated deadwood for bryophytes (Figure 15). The composition of species assemblages differed significantly between naturally occurring and translocated deadwood, as well as between medium- and high-density plots, particularly for bryophytes. While the composition on naturally occurring deadwood remained stable, translocated deadwood changed in both bryophyte and lichen assemblages over time.

Substrate type had a significant effect on species richness (Figure 16) and the different deadwood types provided habitat for significantly different assemblages of bryophyte and lichens (8 % of the variation for bryophytes and 86 % for lichens). Further, assemblage composition changed from 2018 to 2021 for with year accounting for 88.7 % of the variation in assemblage. For lichens, assemblages changed from 2018 to 2022 for Pine early, intermediate, and snags ($p = 0.005$, 0.042, and 0.001 respectively) as well as for Spruce intermediate ($p = 0.004$), and year only accounted for 3.7 % of variation in assemblages. For bryophytes, Pine intermediate ($p = 0.014$) and Spruce snags ($p = 0.038$) showed different assemblages also between medium- and high-density-plots.

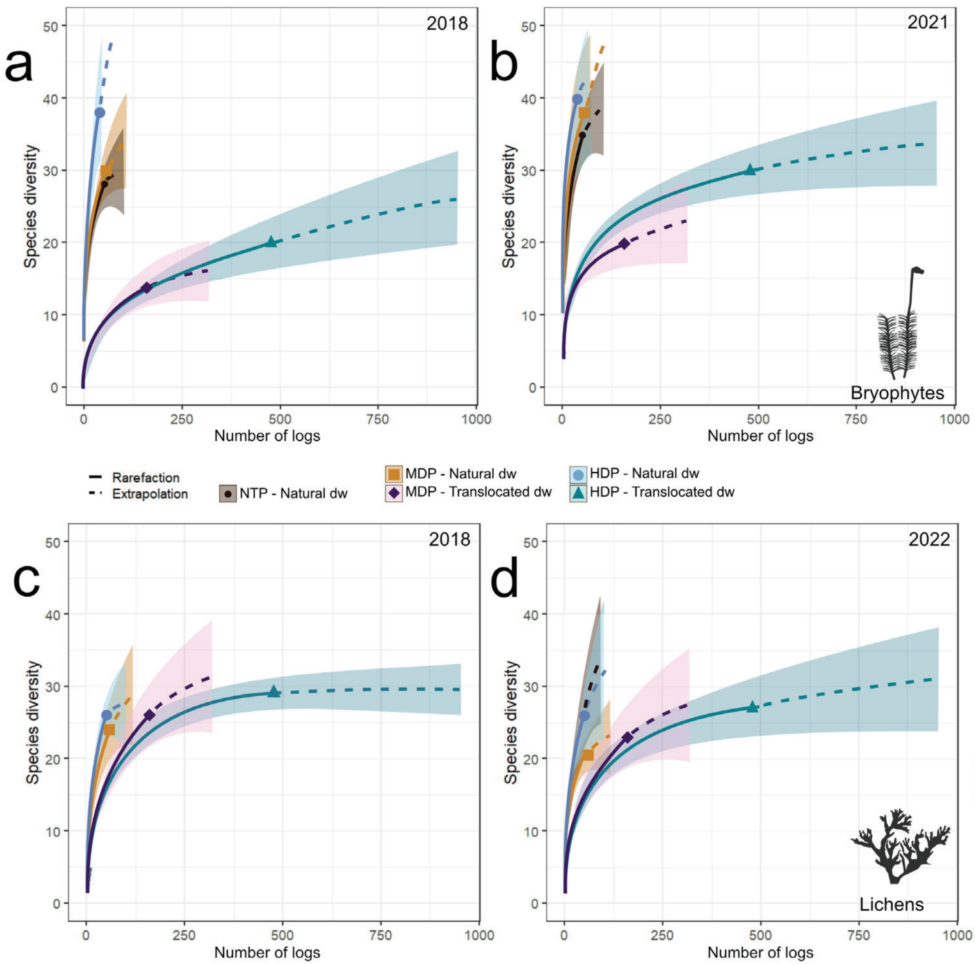

Figure 15. Rarefaction curves showing total species richness for bryophytes (a-b) and lichens (c-d) on plot level, grouped by Naturally occurring (Natural dw) vs Translocated deadwood (Translocated dw) in relation to number of surveyed logs for each year. Treatment on plot level are no translocation plots (NTP, no deadwood addition), medium-density plots (MDP, addition of 16 substrates/plot), and high-density plots (HDP, addition of 48 substrates/plot). Error bars show 95 % S.E. Note that naturally occurring deadwood for lichens in NTP were not surveyed in 2018, hence missing in graph c). Illustration: Olov Tranberg.

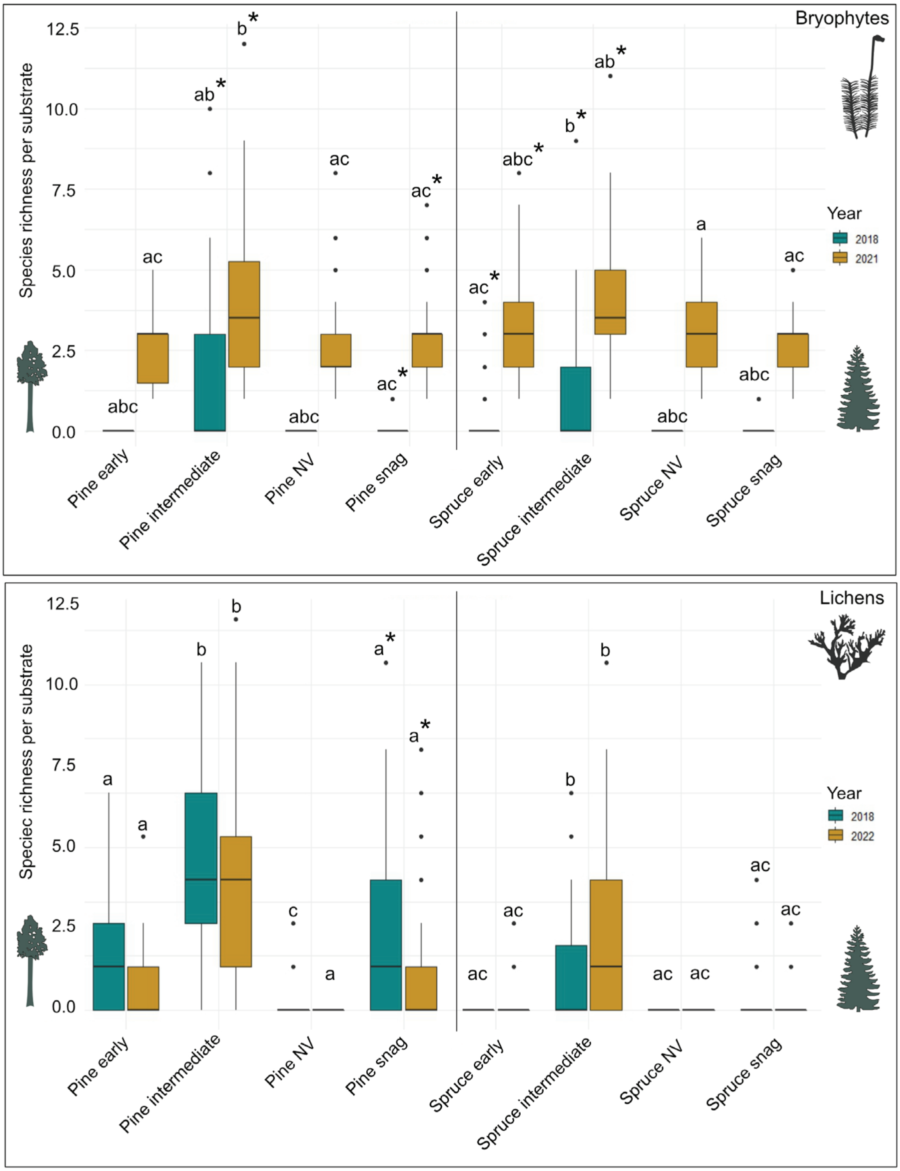

Figure 16. Bryophyte and lichen species richness on translocated deadwood at substrate level, grouped by substrate type. Pairwise comparisons for lichen species richness on substrate level for significant interactions of GLM for each tree species; significance for 'Type within Year' marked with letters for each year group and 'Year within Type' marked with asterisk (*) for significant different substrate richness. Illustration: Olov Tranberg.

4.4.2 Discussion of Paper IV

One conclusion of Paper IV is that translocating deadwood to compensation areas have an impact on bryophyte and lichen diversity, but the effects vary depending on species, substrate type, and the time elapsed since translocation. While translocated deadwood contributed to increased bryophyte species richness over time, lichen species richness tended to decline, though not significantly on translocated logs. The naturally occurring deadwood maintained higher overall species richness and more stable assemblage compositions oven the studied time compared to translocated deadwood, highlighting its importance in preserving biodiversity. The results indicate that while translocation can "life-boat" saproxylic species and enhance diversity, especially in high-density plots, it is not a substitute for naturally occurring deadwood, which remains essential for maintaining long-term ecological stability.

I highlight that bryophytes, particularly generalist and non-wood-dependant species, like *Pleurozium schreberi* and *Hylocomium splendens*, benefitted from the translocation, showing increased colonization across all translocated substrate types. In contrast, lichen species, especially those requiring specific microhabitats, such as *Calicium denigratum* and *C. trabinellum*, experienced declines, particularly on translocated pine kelo wood. This suggests that microclimatic changes, such as increased ground contact of substrates due to changes in deadwood positioning, may have negatively impacted lichen communities.

In Paper IV, I also explored the effects of habitat amount and substrate diversity on translocation success. High-density plots exhibited higher bryophyte richness, indicating that greater volumes and diversity of translocated deadwood can enhance habitat conditions for bryophytes. However, lichen richness did not show a significant response to deadwood density on substrate level, suggesting that lichens may require more specific substrate types or microhabitats that are not provided by increased deadwood volume alone. Type of deadwood significantly influenced both bryophyte and lichen assemblages, affirming the importance of including a variety of substrates in conservation translocations to maintain species diversity.

In this Paper, I underscores the complexities involved in "whole-of-community" translocations. While this approach can help by "life-boating" whole of communities of saproxylic species, it also presents challenges in meeting the diverse habitat needs of multiple species. For conservation strategies to be effective, it is crucial to carefully manage deadwood types according to their specific qualities, ensuring that microclimatic conditions before and after translocation are as similar as possible. This is particularly important for snags, which should remain standing to preserve the microhabitats essential for certain species. This can practically be achieved by leaning logs against other standing trees and securing them with ties for stability (see Figures 2-3 for examples). Overall, it is essential to have clear goals for ecological compensation, such as focusing on “life-boating” specific target species or groups that are rare, specialized, and at higher risk of extinction.

4.5 Translocated species (Paper II-IV)

A total of 221 species of three taxa were found on the translocated deadwood in the first survey following translocation in 2018, including 170 species of invertebrates (emergence traps 2018, all observations, Paper III), 21 bryophyte species (species on translocated deadwood in 2018, Paper IV) and 30 lichen species (species on translocated deadwood in 2018, Paper IV).

In total, 33 078 individuals of 522 invertebrate species were caught, including both compensation and reference area, and all trap types; emergence traps 2018 + 2019 and flight intercept traps 2017 + 2018 + 2021. In general, flight intercept traps contained greater number of species and individuals than emergence traps, although emergence traps had a higher variation of assemblages among traps (Figure 17).

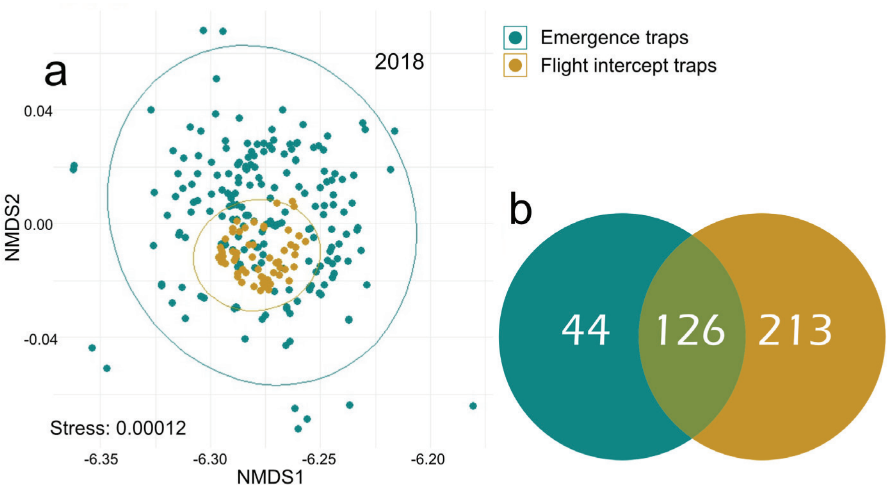

Figure 17. Comparisons of assemblage compositions and species richness for different beetle trap types used in my thesis (Paper II and Paper III) for first year following translocation in 2018; a) NMDS (non-metric multidimensional scaling) of assemblage compositions for emergence traps (Paper III) and flight intercept traps (Paper II), b) Venn diagram for number of caught species by each trap type. Illustration: Olov Tranberg.


Photo: Olov Tranberg

5. Conclusions and management implications

Until now, the ecological consequences of ecological compensation have rarely been assessed (Blicharska et al., 2022; Josefsson et al., 2021), although there is a need to determine which impacts on biodiversity can be compensated for and which cannot (BBOP, 2012). With this thesis, I provide more insights on the ecological effects on both biodiversity and key habitat metrics to be considered.

Overall, my research suggest that translocation of deadwood and associated species to compensation areas is a promising conservation strategy and potentially as a part of a conservation toolbox. However, its effects varies across focal species and substrate types. Addition of deadwood significantly increases deadwood volumes in compensation areas comparable to levels found in old-growth forest, though most pronounced effect are on a smaller scale (Paper I). Even so, the composition of translocated deadwood types differed from the original impact site, with certain substrate types, such as standing dead trees, and dead broadleaf trees, being underrepresented. This limited the effectiveness of translocation for species that rely on specific deadwood qualities. Still, translocation can significantly increase deadwood types that usually takes hundreds of years to form through restoration efforts in situ, for example large-diameter (>50 cm) dead trees. Translocation also offers a cost-effective method to rapidly increase deadwood availability and support species conservation, although it should be seen as complementary to habitat preservation rather than a substitute (Paper I).

During the short time period of my study, I showed that deadwood translocation enhance species richness and abundance, particularly for saproxylic beetles and for bryophytes. The success of translocation was influenced by substrate type and translocation volume added to the compensation area. High-density plots (addition of 48 deadwood substrates/plot), in particular, demonstrated increased species richness, suggesting that translocating large volumes of deadwood can “life-boat” certain species from impact areas by moving species communities along with their habitats (Paper III and IV). Translocation also demonstrated potential to be an important tool in enhancing wood-inhabiting beetle communities in compensation areas (Paper II), although species from different functional guilds respond differently.

While translocated deadwood was shown to enhance both bryophyte and invertebrate species richness over time, the impact on lichen species was less pronounced, with declines observed, especially for species sensitive to microhabitat changes (Paper IV). Deadwood characteristics, such as posture (downed or standing), influence the microclimate inside deadwood, affecting moisture levels, sun exposure and temperatures (Lindman et al., 2022). At translocation these factors are important to consider because translocation can result in changes of the deadwood microclimate and thus impact survival rate of the translocated species. For instance, species that prefer a drier environment may gain a competitive advantage if the translocated deadwood is placed in a sunnier location. Conversely, species that thrive in moist conditions, for example some bryophytes that require high humidity (Furness and Grime, 1982), might outcompete some lichen species that prefer drier conditions, if the translocated deadwood is placed in more humid conditions. Several specialist species, such as the lichen *Calicium denigratum*, declined after translocation, indicating that specific microhabitats were not adequately replicated in translocated substrates, such as keeping snags standing. This can lead to shifts in community composition, where species that were previously subordinate may become dominant, and vice versa. Changed microhabitat conditions can also affect the rate of deadwood decay. Deadwood in moist environments tends to decompose faster due to increased fungal and microbial activity (Fravolini et al., 2016). This can affect the availability of resources for saproxylic organisms, thereby influencing community assemblages and duration of different deadwood types as habitats (Arnstadt et al., 2016), effecting the long-term result and permanence of translocation efforts.

The limitations of conservation translocation in ecological compensation as a conservation tool must be acknowledged. The primary aim of conservation translocations is to restore populations of species within their historical ranges, thereby enhancing ecosystem and biodiversity (Seddon et al., 2014). In complex multi-taxon translocations as in this experiment, the goal extends to the support of multiple species that depend on same habitats, such as those associated with specific deadwood substrates. In this context, we face the challenge of balancing the conservation requirements of several hundred species, and highlight the complexities of achieving positive outcomes for multiple target species simultaneously (Paper III and IV). Some, like the generalist bryophyte *Pleurozium schreberi* or the cambivore beetle *Dryocoetes autographus*, thrive in a variety of deadwood substrates. Other species, such as the lichen *Chaenothecopsis fennica*, have highly specific substrate requirements, making the practical performance of the translocation particularly important for their survival.

This aligns with the umbrella species concept, that conservation focused on focal species with high requirements for habitat quality, will indirectly also benefit many other co-existing species within same habitat community, or in this case deadwood type (Fleishman et al., 2000; Lambeck, 1997). The relative abundance of generalist species suggests they may not require targeted support, emphasizing that the selection of target or focal species for deadwood translocation should prioritize those species that have high habitat demands, are threatened and cannot be effectively conserved through other means. Prioritizing the most sensitive species as conservation targets can create a protective umbrella, or habitat, for a broader range of species, including generalist species, promoting overall ecosystem stability. Even if a focal species is not found in a specific habitat type, for example on kelo wood that host distinct lichen communities (Larsson Ekström et al., 2023), the substrate can still hold an important function in conservation within the umbrella species framework (Lõhmus et al., 2021). The choice of target species, suitable compensation area or ultimate goal of conservation translocation should therefore clearly be defined, since ecological compensation has historically struggled to achieve no-net-loss of biodiversity (Bull et al., 2013; Gibbons and Lindenmayer, 2007). One danger lies in the perception that conservation translocations, particularly when used as a form of ecological compensation, can serve as a remedy for any type of habitat exploitation.

This “license-to-trash” mind-set (Lapeyre et al., 2015; McKenney and Kiesecker, 2010) undermines conservation translocations and promotes a false sense of security that all environmental impacts can be mitigated. The mitigation hierarchy (Gauthier et al., 2014; Griffiths et al., 2019) stresses that compensation should only be considered as a last resort, after all possibilities for avoidance and minimization of damage have been exhausted.

As shown in Paper I and IV, translocated deadwood have a different composition of substrate types compared to naturally occurring deadwood and translocated deadwood also support different richness and assemblages of bryopythes and lichens than those found on naturally occurring deadwood. The fact that translocation of deadwood and associated species enrich the compensation area with other assemblages of species and habitat types, suggests that there is an additive value in using translocation as a compensation strategy. However, these results are dependent on the initial state of the compensation area, which raises question of what habitat structures and species assemblages the assigned compensation area should hold in relation to the possible enrichment value through translocation. In my experiment, the compensation area was selected prior to the scientific assessments with the criteria that it should hold similar habitat, although it intentionally had lower conservation values than the impact area, e.g., in terms of quality and volumes of deadwood, very old trees and variation in forest structure (Enetjärn et al., 2015; Forsgren et al., 2016). When selecting areas suitable to become a compensation area for translocated habitat and species, I formulate two key mechanisms to be considered (Figure 18);

First mechanism is the equivalence and permanence value of translocations, referring to that compensation areas should have relatively equivalent ecological values compared to the biodiversity being lost, to ensure that potential biodiversity gains are comparable (Carreras Gamarra et al., 2018; Laitila et al., 2014). Permanence ensures that these gains are sustained over time by the survival of translocated species. This involves detailed inventories of habitat structures and species assemblages of the impacted area and the compensation area and ensuring, based on ecological knowledge, that that the compensation area can support similar assemblages and ecological processes. Ecosystems that are too dissimilar or degraded, compared to the species introduced through translocations, will result in low equivalence and permanence value, with a high risk of local extinction of translocated species and no gains in biodiversity. Conversely, in comparable ecosystems, translocated species will potentially have a high survival rate

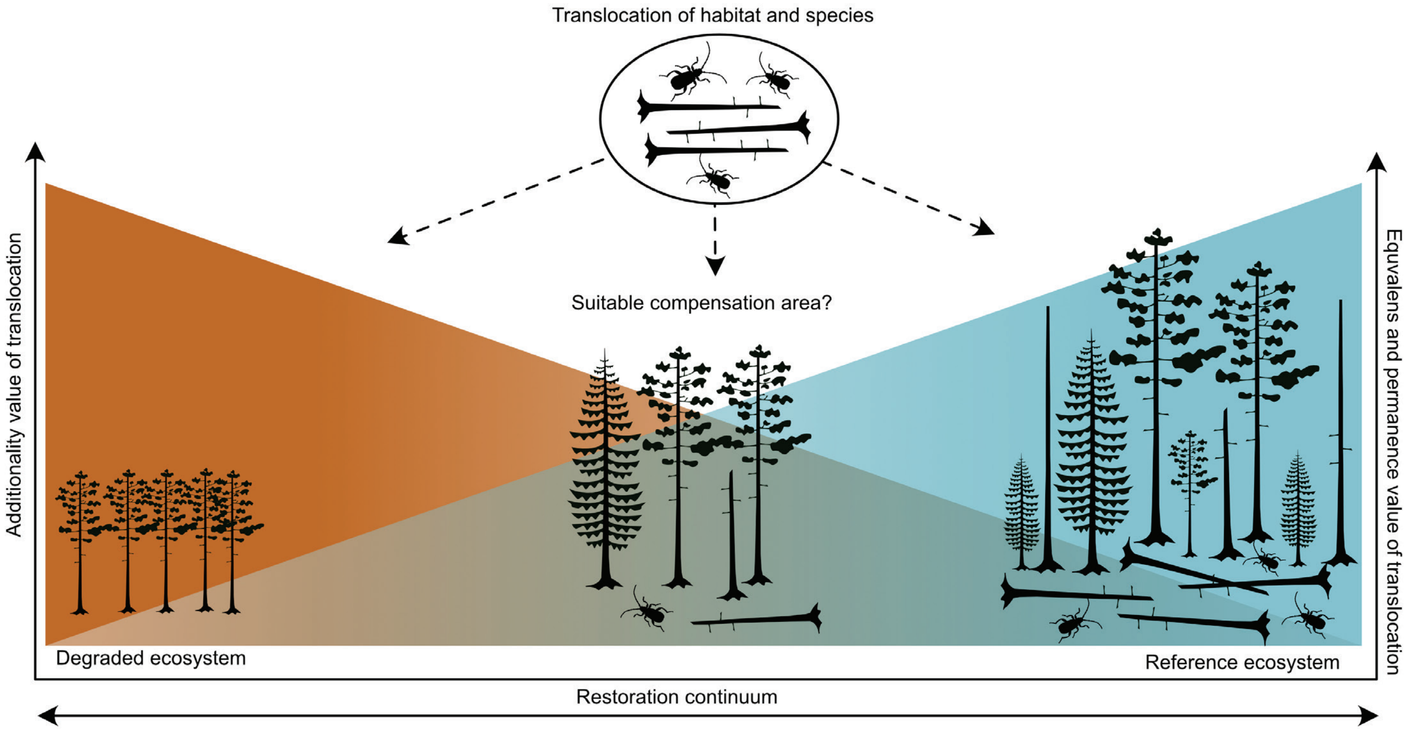

Figure 18. Selection of suitable compensation areas for translocated habitats and species along a restoration continuum (x-axis) from degraded to a reference ecosystem. Two key mechanisms must be accounted for, shown on first and second y-axis; left) the additionality value, refers to the biodiversity benefits achieved through translocation, e.g., number of new species introduced, and right) the equivalence and permanence value, refers to similarity of biodiversity added through translocation and their sustainability over time. Translocating habitat and species to similar ecosystems yields lower additionality value, as these areas already contains same species and structures, yet yields higher equivalence and permanence value, through comparable metrics and lower risk of local extinctions due to enhanced populations sizes. Illustration: Olov Tranberg.

and the gain in biodiversity would be higher. For example, translocation of species with specific habitat demands, like certain lichen species and their association to kelo wood, to compensation areas that does not hold, or has the possibility of holding, these certain deadwood types, simply creates ecological traps and extinction debts (Larsson Ekström et al., 2023).

Second mechanism to consider is the additionality value of translocations that refers to the additive value, or gains in biodiversity, that the addition of species and habitat through translocation generates that would not occur without the translocation effort (Souza et al., 2023). Enriching compensation areas with new or greater number of species or individuals, or other types of habitat, can significantly enhance the biodiversity in highly degraded ecosystems, resulting in a high additionality value. In contrast, translocating the same species or habitats to ecosystems already closer to a reference state in a restoration continuum, where these species or structures are already present, results in a lower additionality value.

Overall, deadwood translocation is an effective and cost-efficient tool for rapidly increasing habitat availability and supporting deadwood dependent species. Translocating entire species communities along with their deadwood habitats presents a more holistic approach compared to single-species translocations, supported by my findings that translocations can support complex ecological networks, particularly when diverse deadwood substrates are included. Further, a balanced approach that combines habitat preservation, targeted translocations, restoration and broader landscape management is necessary to achieve sustainable conservation outcome.

6. Future perspectives

To design effective compensation measures, it is essential to quantify both the extent of ecological impacts and the benefits of planned actions. This allows for the appropriate selection of target species and the specific objectives of translocation efforts, ensuring they are well-suited to achieve the intended conservation outcomes. The choice of metrics should be based on the ecological function of both the impact and compensation areas and focus on the natural values, functions, and/or conditions.

Effective conservation requires maintaining a variety of deadwood types to support diverse saproxylic communities. Future research should aim to develop and evaluate techniques to translocate a broader range of deadwood types, including standing deadwood, broadleaf deadwood and highly decomposed stages, to better support diverse species assemblages. Especially important to consider is that microclimatic conditions are preserved or replicated during translocation to support species with high habitat requirements, for example lichens.

Combining translocation with in situ deadwood creation or veteranization can help achieve a comprehensive range of deadwood substrates. Even so, translocation has a benefit of adding deadwood without reducing living tree volumes, allowing trees to mature and contribute to future deadwood availability. Future efforts should therefore explore combined strategies that integrate deadwood translocation with in situ creation or veteranization to achieve a more complete range of habitat conditions.

Studies of future colonizations of species originating from translocated deadwood could potentially provide more insights into their ability to establish, survive, and thrive in new locations and translocated deadwood's function as population sources in restoration areas a metapopulational perspective. Such knowledge would further develop conservation translocations as method in ecological restoration. The potential use of genetic markers to study species movements, colonization and connectivity between both translocated substrates and naturally occurring deadwood could potentially contribute to the important comprehensive monitoring necessary to follow the success of translocated species communities, ensuring long-term survival of translocated species and habitat.


Photo: Olov Tranberg


Photo: Susanna Bergström

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Popular science summary

Restoring damaged habitats is often used to help nature recover after damages, but it can take a long time for important features like large dead trees to form. These dead trees are important for many species, including insects, mosses, lichens and fungi, some of them dependent on deadwood for their survival. A novel method, called conservation translocation, involves moving not just the deadwood but also the species of mosses, lichens and beetles living in the dead trees. This method has, to my knowledge previously not been tested scientifically before. In a boreal forests in Sweden, I conducted a large field experiment to test this new way to speed up the slow process in restoring forest by moving deadwood, such as recently dead or fallen trees and older dead trees, from an old forest that was planned to be cut down to become a mine, to a selected compensation area.

My research focused on how this deadwood translocation affects beetles, mosses and lichens. I studied the number of species, their abundance, and the different types of species present after moving deadwood to a compensation area set up to offset the environmental effects of a mine expansion.

Moving deadwood quickly provided habitats for many species, especially in areas where a lot of translocated wood was added. I saw an increase in the number of species and a greater variety of wood-dependent beetles. Mosses also thrived, with more species after the translocation. However, lichens showed little change, indicating that some species may respond negatively.

The translocated deadwood had a significant different composition compared to the naturally occurring deadwood in both the compensation area and the impact area affected by the mine construction. This suggests that while deadwood translocation could be a cost-effective tool for restoring habitats, it needs to be carefully planned and continuously improved to maximize its benefits for biodiversity.

Overall, I show that translocating deadwood can help restore habitats faster, but it’s not a one-size-fits-all solution. Further research and refinement are needed to make this method as effective as possible for different species and ecosystems.

Populärvetenskaplig sammanfattning

Att restaurera eller återskapa naturmiljöer används ofta som metod för att hjälpa naturen att återhämta sig efter störningar eller skador. Det kan dock ta lång tid att återskapa till exempel grova döda träd, så kallad död ved, som är viktiga habitat för många arter, inklusive insekter, mossor, lavar och svampar, varav vissa är beroende av död ved för sin överlevnad. En ny metod, som kallas translokering, innebär att man inte bara skapar färsk död ved, utan att man flyttar redan befintlig död ved tillsammans med de arter av mossor, lavar och skalbaggar som lever i de döda träden. Denna metod har dock inte utvärderats vetenskapligt tidigare.

I ett storskaligt fältexperiment i boreal skog i Sverige utvärderade jag denna metod för att påskynda den långsamma processen med att restaurera skogar genom att flytta död ved. I experimentet flyttades nyligen döda, fallna träd och äldre döda träd, från en gammal skog som planerades att avverkas för att ge plats för en gruva, till ett utvalt kompensationsområde. Min forskning fokuserar på hur translokering av död ved påverkar skalbaggar, mossor och lavar. Jag studerar antalet arter, deras förekomst och vilka olika typer av arter som fanns efter att ha flyttat död ved till ett kompensationsområde.

Flytt av död ved skapade snabbt livsmiljöer för många arter, särskilt i områden dit mycket död ved hade tillförts. Jag såg en ökning i antalet arter och en större variation i samhällen av vedlevande skalbaggar. Mossor ökade också och fler arter hittades efter translokeringen. Däremot visade lavar små förändringar, och en del av resultaten tyder på att vissa arter reagerar negativt på flytten. Den flyttade döda veden bestod av olika typer jämfört med både naturlig död ved på plats i kompensationsområdet och det område som gick förlorat på grund av gruvbygget. Detta tyder på att även om translokering av död ved kan vara ett kostnadseffektivt verktyg för att återställa livsmiljöer, måste det planeras noggrant och förbättras för att maximera dess fördelar för biologisk mångfald.

Sammanfattningsvis visar denna studie att translokering av död ved kan hjälpa till att återställa livsmiljöer snabbare, men det är ingen universallösning. Ytterligare forskning och förbättringar av metoden behövs för att göra den så effektiv som möjligt för olika arter och ekosystem.

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Finally, I extend a future-looking thanks to all the bookshelves where my thesis will rest until end of time.


Photo: Olov Tranberg

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RESEARCH ARTICLE

Translocation of deadwood in ecological compensation: A novel way to compensate for habitat loss

Olov Tranberg, Anne-Maarit Hekkala, Ola Lindroos, Therese Löfroth, Mari Jönsson, Jörgen Sjögren, Joakim Hjältén

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Abstract Restoration of degraded habitat is frequently used in ecological compensation. However, ecological restoration suffers from innate problems of long delivery times of features shown to be good proxies for biodiversity, e.g., large dead trees. We tested a possible way to circumvent this problem; the translocation of hard-to-come deadwood substrates from an impact area to a compensation area. Following translocation, deadwood density in the compensation area was locally equivalent to the impact area, around 20 m^3 ha^{-1}, a threshold for supporting high biodiversity of rare and red-listed species. However, deadwood composition differed between the impact and compensation area, showing a need to include more deadwood types, e.g., late decomposition deadwood, in the translocation scheme. To guide future compensation efforts, the cost for translocation at different spatial scales was calculated. We conclude that translocation of deadwood could provide a cost-efficient new tool for ecological compensation/restoration but that the method needs refinement.

Keywords Biodiversity offset · Boreal forest · Conservation · Cost-efficiency · Deadwood · Restoration

INTRODUCTION

Exploitation of forest ecosystem has led to changes in ecosystem structures and processes, and to biodiversity loss (FAO 2010; Ceballos et al. 2015). To simultaneously conserve biodiversity and continue economic development is a major challenge for human society (Lubchenco 1998). While sustainable development depends on functional ecosystems in numerous ways, economic growth and biodiversity conservation are often perceived to be incompatible.

Within this context there is an increasing pressure on corporations by consumers and stakeholders to be environmentally conscious and more focus is directed towards alternative approaches in adapting to this demand (Sjåfjell 2012; Verrier et al. 2014). One such approach is the relatively recent concept of ecological compensation (biodiversity offsetting) which is based on the principle that those who damage or destroy natural values are to compensate for the loss by generating or protecting natural values at a different/substitute location (polluters-pay-principle) (OECD 1992; Bull et al. 2013). Thus, ecological compensation, at least in theory, provides an approach to allow economically important human development while ensuring that 'no-net-loss', or even 'net positive gain', in biodiversity is achieved (Bull et al. 2013; Gardner et al. 2013). Although legislation mandating ecological compensation, as a final measure in mitigating negative impact by exploitations, exist in many countries, principles and methods for biodiversity offsetting are still under development (Koh et al. 2017; Blicharska et al. 2022). Methods for ecological compensation can involve protection of areas that are otherwise at risk of exploitation, ecological restoration or other positive management interventions and, in some circumstances, the recreation of habitat that has been lost.

Restoration of degraded habitat is often used in ecological compensation and our knowledge of the effects of different restoration methods on biodiversity has improved in recent years (Berglund et al. 2011; Halme et al. 2013; Hekkala et al. 2014; Hjältén et al. 2017, 2023). However, restoration often suffers from the innate problem that, even if in situ restoration provides substrates or habitat for species that we want to favor, those species may not be able to disperse to restored habitats or areas (Kouki et al. 2012; Bell et al. 2015), often referred to as "field-of-dreams" dilemma (Palmer et al. 1997; Hilderbrand et al. 2005). Furthermore, the delivery time on certain types of habitats is very long, several hundreds of years for, e.g., live and dead large-diameter trees and advanced decay classes of deadwood. Thus, the loss of these kinds of habitats are difficult to compensate for in ecological compensation. One potential approach to circumvent problems with dispersal and long delivery time is the translocation of some of these unique substrates together with associated species.

Such translocation of deadwood can potentially play an important role in ecological compensation, as it constitutes a key habitat for biodiversity in the boreal forest. Decrease in deadwood availability and diversity due to forestry and other types of land use is the main explanation for loss of biodiversity on saproxylic species (Siitonen 2001; Stokland et al. 2012; Löfroth et al. 2023). Species richness and ecological communities of deadwood dependent species (insects, wood fungi, bryophytes and lichens, and indirectly also top predators such as woodpeckers) is determined by amount (abundance and volume) and diversity of deadwood in terms of tree species, trunk size, posture, mortality factor (e.g., wind, fire) and stage of decomposition (Siitonen 2001; Similä et al. 2003; Junninen and Komonen 2011; Seibold et al. 2016; Hägglund and Hjältén 2018; Kärvemo et al. 2021). In general, high amounts of deadwood have shown to be good a proxy for biodiversity with 20 m^3 ha^{-1} serving as a threshold for maintaining high species richness of rare and red-listed saproxylic species, e.g. fungi, in boreal forests (Penttilä et al. 2004; Hekkala et al. 2023). In addition, the volume of deadwood has been identified as one of the EU-level indicators used to quantify the state of forests' biological diversity (Bozzano and Oggioni 2020). Maintaining high volumes and diversity of deadwood is therefore crucial for saproxylic biodiversity.

Still, translocation of deadwood has rarely been conducted at large scale and the method has to the best of our knowledge never been scientifically evaluated. In theory, translocation of deadwood offers a rapid establishment of high-quality habitat and assisted migration of various deadwood dependent species, communities that might take long time to colonize through natural processes (Morris et al. 2006; Fenton and Bergeron 2008; Toivanen and Kotiaho 2010). In contrast creating deadwood in situ, although a slow process, result in a more gradual establishment of habitats and communities (Toivanen and Kotiaho 2007; Djupström et al. 2012). In situ creation of deadwood also generally requires less resources compared to translocation. Therefore, there is a need to assess if, in practice, the translocation can result in similar densities and compositions of deadwood between the area they were translocated from and the area they were moved to. We are also lacking knowledge of what constitutes feasible scales for translocation of deadwood, in terms of the costs incurred and deadwood amounts needed when translocating to plots, forest stands and landscapes (Lindroos et al. 2021). This information is needed even for the assessment of the value of deadwood translocation compensation for related associated biodiversity.

There is also a need to assess the cost of compensation measures as this will impact if they will be implemented or not. When costs for ecological compensation projects have been investigated, it has often been in terms of the total costs for compensation projects carried out. However, there are also some research focusing on making it possible to compare alternatives to find and develop cost-efficient practices (e.g., Cuperus et al. 2001; Lindroos et al. 2021). However, the costs of deadwood translocation to different spatial scales have never been investigated. Even when the ecological compensation constitutes a minor part of large-scale projects, such as the construction of roads and establishment of mines, cost-efficiency is, nevertheless, instrumental for increasing both the use of ecological compensation and increasing the benefits from a given economic input.

A large-scale experiment, using a before-after-control-impact approach, was initiated in 2016 to assess the effects of translocating deadwood from a high conservation value forest (impact area, subjected to exploitation due to expansion of the Aitik mine) to a compensation area with lower conservation value on important habitat characteristics and the costs of translocation. This experiment is exceptional in its magnitude and standard, as 637 deadwood substrates, including various qualities of deadwood such as very old and uncommon types and different tree species, were relocated to a nearby compensation area.

The main objective of this study was to assess if translocation of dead trees to a lower quality forest landscape assigned as compensation area can be used to re-create the deadwood amount, diversity and composition found in the impact area and thus above suggested thresholds for maintaining species richness of rare and red-listed saproxylic species at different scales. Furthermore, to guide future compensation efforts we calculated costs for translocation at different spatial scales.

MATERIALS AND METHODS

Study area and design

The study area belong to the north boreal vegetation zone (Ahti et al. 1968) and all sites included in the study have previously been under management, predominantly subjected to selective felling, but have not been managed during the latest decades. The forests are conifer dominated bilberry type or mixed forests (conifers + broadleaves) dominated by Norway spruce [*Picea abies* (L.) Karst.] and Scots pine (*Pinus sylvestris* L.) with scattered occurrence of mainly Downy birch (*Betula pubescens* Ehrh.) and Goat willow (*Salix caprea* L.).

The study includes two sites; an impact area and a compensation area. The impact area encompassed 376 ha out of which 167 ha consisted of forests of high or very high conservation values (by definition of assessment by Swedish Standards Institute (2014), including high volumes of deadwood (mean 21.1 $m^3 ha^{-1}$) and occurrence of 16 red-listed species of wood fungi and lichens (Forsgren et al. 2016). Remaining 209 ha in the impact area consisted of forest of lower conservation values (144 ha) and non-productive forest, mires or open water. The compensation area encompassed 397 ha, out of which 192 ha had high conservation values (no forest of very high conservation value), with moderate volumes of deadwood (mean 9.3 $m^3 ha^{-1}$) and occurrence of 11 red-listed species of wood fungi and lichens. Remaining 205 ha of the compensation area consisted of forests of low conservation value (113 ha) and non-productive forest, mires or open water (Forsgren et al. 2016) (Fig. 1).

In 2016, prior to translocation, 10 experimental plots were established in the impact area, each with a radius of 25 m, distributed randomly across productive forestland of higher conservation value. In the compensation area, 30 equally sized plots were created and randomly assigned to one of three groups: no translocation (NTP, n = 10), medium density translocation (MDP, n = 10), and high density translocation (HDP, n = 10). All plots were situated at least 150 m apart from one another. This design was implemented to evaluate the response of wood-living organisms to translocation of different densities of deadwood. Translocation was performed in autumn 2017 and post-translocation measurement was performed in spring 2018.

Translocation method

The translocation of deadwood followed a seven-step scheme: (1) identification of suitable compensation area, (2) identification of suitable deadwood objects (large-end diameter ≥ 25 cm) logs and living trees of high conservation

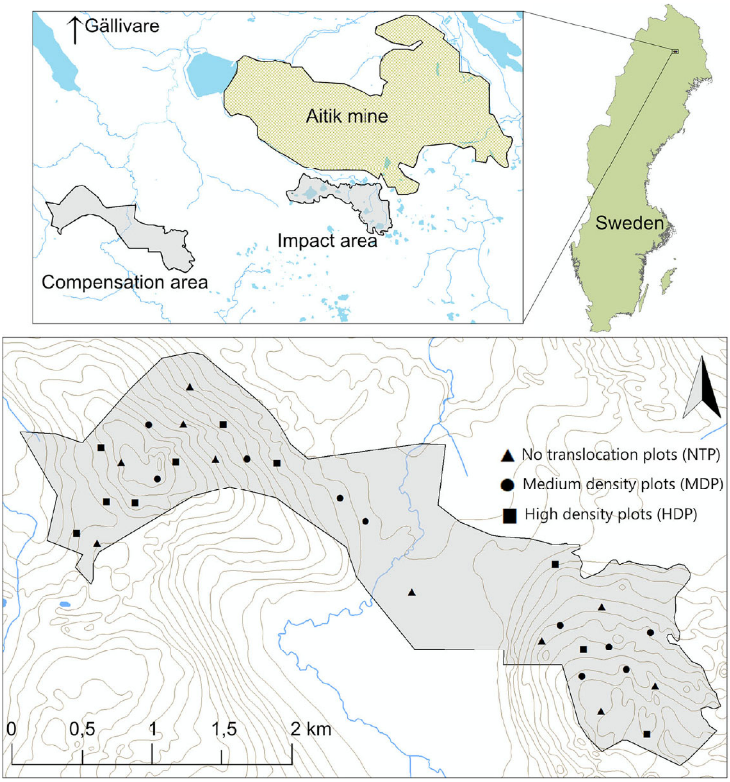

Fig. 1 Map of Sweden showing the two sites in the study: impact and compensation area, denoted in grey. The impact area includes forest of high or very high conservation values. Symbols in lower figure indicate plot type in the compensation area

value to be translocated, (3) cutting and bucking of selected logs and trees, (4) ID marking of the selected substrates, (5) extraction of the substrates from impact forest to road, (6) road transport from impact area to compensation area and (7) insertion from road into compensation forest (Fig. 2). More details about the translocation work can be found in Lindroos et al. (2021).

Eight types of suitable deadwood substrates, of Norway spruce and Scots pine, were identified and used for selection (Table 1) from the entire impact area. Only deadwood

Fig. 2 Steps in the translocation process; **a** selection of substrates, **b** marking and storing of substrates, **c** transport to the compensation area, and **d** forwarding to compensation/experimental plots. *Photo* Maria Nordlund (**a**–**b**) and Joakim Hjältén (**c**–**d**)

Table 1 Translocated substrates from the impact area were categorized into eight groups based on two tree species, three posture types, decomposition classes, and length. The table presents the distribution of substrates in the impact area, which were translocated to the compensation area and divided into 30 experimental plots; No Translocation Plot (NTP), Medium Density Plots (MDP), and High Density Plots (HDP). A total of 637 substrates were identified, cut, permanently marked, and translocated. DC-class stands for Decomposition Class according to Thomas and Parker (1979)

Substrate type	Tree species	Posture, before translocation	DC-class	Allowed substrate length (m)	Number of received translocated substrates/plot in compensation area			Total (n = 30 plots)
					NTP (n = 10)	MDP (n = 10)	HDP (n = 10)	
Translocated substrates	Pine	Downed	1	4 ± 1	–	1 ± 1	1 ± 1	18
	Pine	Downed	2–3	3	–	1 ± 1	4 ± 2	65
	Pine	Standing dead	3–7	4 ± 1	–	3 ± 1	5 ± 2	97
	Pine	Living	1	4 ± 1	–	3 ± 1	8 ± 3	133
	Spruce	Downed	1	4 ± 1	–	2	6 ± 2	80
	Spruce	Downed	2–3	3	–	2 ± 1	6 ± 1	79
	Spruce	Standing dead	3–7	4 ± 1	–	2 ± 1	6 ± 1	81
	Spruce	Living	1	4 ± 1	–	2 ± 1	6 ± 1	84
Total					0	16 ± 1	48 ± 1	637
Trees cut on site					2	2	2	60

substrates that were feasible to move without breaking were selected, which includes only downed deadwood in decomposition classes 1–3 and standing dead trees in decomposition classes 3–7 (classes according to Thomas and Parker 1979). The upward-facing part of the selected downed deadwood was marked with color to be able to reset the substrate in the same posture after translocation. A total of 637 deadwood substrates were selected (mean volume 0.292 m^3), cut and bucked to a length of 3–5 m. The goal was to translocate 80 substrates from each of the eight substrate groups, but due to insufficient numbers of substrates of pine logs, additional substrates were supplemented from standing dead trees and living trees of pine (Table 1). All translocated substrates ended up as downed deadwood in the compensation area.

Within the compensation area, each plot assigned to the medium density translocation group (MDP) received 16 translocated deadwood substrates, approximately two of each substrate type (Table 1), while each plot assigned to HDP received 48 translocated deadwood substrates, approximately 6 of each substrate type. No deadwood substrates were translocated to the NTPs. Additionally, in all compensation area plots, one living pine and one living spruce tree were cut and left unbucked to allow for evaluating future colonization of saproxylic species on the deadwood.

Field measurements of deadwood

In 2016, prior to exploitation and translocation, measurements of deadwood were conducted in the impact area and the compensation area. Deadwood characteristics were measured (Table 2) from the 25 m radius plot for all naturally occurring dead trees with minimum large-end diameter $\geq$ 5 cm, including base and top diameter, tree species and trunk length. Posture of each tree was determined into two classes, standing dead trees or downed logs. Trees originated from outside the plots were not measured. Height and DBH of standing dead trees and snags were measured. Decomposition class (DC) for coniferous deadwood was determined by the classification system derived from Thomas and Parker (1979), including classes DC1–5 for downed and DC1–7 for standing deadwood. For broadleaves decomposition class was determined by the classification system from Gibb et al. (2005) into deadwood softness ("hard" or "soft"). The deadwood inventories were repeated in 2018 after translocation, thus including measures of both naturally occurring and translocated deadwood.

Data processing and analysis

Deadwood volume for logs were calculated using the formula for a truncated cone (V_t) where L is the length, r_{max} the maximum radius and r_{min} the minimum radius.

$$V_t = \left(L * \frac{\pi}{3}\right) * \left({r_{max}}^2 + r_{max} * r_{min} + {r_{min}}^2\right).$$

The deadwood volume for whole standing dead trees (snags) was calculated using functions from Näslund (1940) with specific functions for pine, spruce and birch. Deadwood volume for high stumps or broken trees was calculated using the formula for a cylinder (V_c) where h marks height of the high stump and r the DBH divided in two.

$$V_c = \pi r^2 * h.$$

Using the conversion method by Thomas and Parker (1979) we converted decomposition class for standing deadwood (DC1–7) into corresponding class of downed deadwood (DC1–5) to make one consistent decomposition class system. For the same reason, the decay class for birch and willow was converted from softness of deadwood into

Table 2 PERMANOVA analyses (ADONIS) results for the effects and significance of differences in the deadwood composition in the five studied translocation groups/treatments. Response categories represent the different plot types in comparison

Response category 1	Response category 2	R^2	p-value
Impact area			
	Compensation area before	0.161	< 0.001
	No translocation plots	0.127	0.003
	Medium density plots	0.407	< 0.001
	High density plots	0.532	< 0.001
No translocation plots			
	Medium density plots	0.436	< 0.001
	High density plots	0.567	< 0.001
Medium density plots			
	High density plots	0.573	< 0.001

corresponding decay classes (DC3–4) derived from Thomas and Parker (1979).

Using linear regression, we tested for differences in deadwood volumes between the plots in the impact area and the different translocation plots, followed by Tukey pairwise post hoc multiple comparisons of means on a 95% family wise confidence level. We calculated volume of deadwood on plot (radius of 25 m), stand (1 ha) and landscape scale (up to 500 ha) to assess the cost and effort needed for compensation at different spatial scales. To determine deadwood volume on plot scale we measured both the initial deadwood volume before translocation and the translocated deadwood. To estimate deadwood volume on stand scale, we multiplied the initial volume before translocation for each plot and treatment (NTP, HDP, and MDP) by the area of one hectare, followed by addition of the translocated deadwood volumes to each treatment. To evaluate the effect of deadwood addition on larger scales we calculated how much deadwood would be needed to enrich a landscape up to 500 ha. The needed deadwood enrichment was calculated as the difference between the deadwood volume in the impact area minus the background level in the compensation area before translocation.

In order to compute the costs of alternative intensities and sizes of areas for compensation measures, data from the executed translocation work and derived models reported in Lindroos et al. (2021) were used. The costs were set to fixed values for area identification (33.4 SEK/log), for substrate identification (73.8 SEK/log) and for felling (164.1 SEK/log). For the transport related work, the cost was a function of the hourly cost for the work, the load size and the transport distance. For extraction, the hourly cost was set to 900 SEK, to 750 SEK for road transport and to 900 SEK for insertion. Load size was set to 18 logs in extraction, 105 logs in road transport and 10 logs in insertion. The road transport distance was set to 24 km, whereas the extraction and insertion distances depended on the area of the assumed impact and compensation areas. For simplicity, it was assumed that the impact and compensation areas were of the same sizes, circular and located right next to roads. Extraction and insertion distances were therefore identical, and equivalent to the radius of a circle with the given area.

We examined the diversity of deadwood substrates, including both translocated and natural occurring deadwood, in the impact area compared with the two different types of translocation plots (MPD and HDP). We generated specific deadwood substrate groups using all possible combinations of four selected deadwood variables including *tree species*, *decomposition class*, *diameter class* (10 cm intervals) and *type* (snag or downed), resulting in 240 possible unique deadwood types. The count of unique deadwood types per plot was considered as deadwood diversity on the plot. Diversity patterns were furthermore visualized with NMDS using unique deadwood types as species, followed by PERMANOVA, using the function *adonis* in the R-package Vegan (Oksanen et al. 2020). To examine specific deadwood types with significant higher occurrence (presence/absence) in any of the translocation plots or study areas, we used indicator species analysis from the *indicspecies*-package (De Cáceres et al. 2022). All statistical calculations and analyses were performed with R software (R Core Team 2021).

RESULTS

Deadwood volume

On average, the compensation area plots had half the volume of deadwood prior to translocation when compared to the impact area plots (1.8 and 4.1 m^3 $plot^{-1}$, respectively). Following translocation, HDP had significantly higher volumes ($p < 0.001$) than the other plot types, while MDP had higher volumes than NTP ($p < 0.001$), as illustrated in Fig. 3. After translocation, both HDPs and MDPs had higher total deadwood volumes than the impact area ($p < 0.001$ for both). Translocated deadwood accounted for 89%, 76%, and 0% of the total volume of deadwood in HDP, MDP, and NTP, respectively.

Neither of the two translocation plot types, MDP and HDP, had significantly different volume compared to the impact area at the stand level (MDP = 15.4 ± 1.8, HDP = 24.3 ± 2.0 and impact = 21.1 ± 4.8 m^3 ha^{-1}, respectively, and $p = 0.21$ for MDP and $p = 0.12$ for HDP, respectively). Translocated deadwood accounted for 61%, 39%, and 0% of the total volume of deadwood in HDP, MDP, and NTP, respectively, as shown in Fig. 3.

On smaller spatial scales, such as plot and stand level, the executed compensations resulted in similar deadwood volumes as those found in the impact area (Fig. 3). However, when accounting for the full impact area, the executed compensations resulted in a considerable deadwood shortage compared to the amount of deadwood in the impact area. In total 637 logs were translocated to the compensation area of 310 ha (excluding mires and open water), which equals a deadwood addition of on average 2.1 logs ha^{-1}, or 0.58 m^3 ha^{-1} to the 9.3 m^3 ha^{-1} already present in the compensation area. This should be contrasted to 21.1 ± 4.8 m^3 ha^{-1} of deadwood found in the impact area, which is equal to 72.2 ± 16.4 logs ha^{-1}. To fully reach levels similar to those in the entire impact area, an additional 7.0–16.6 m^3 ha^{-1}, equivalent to 23.9–56.8 logs ha^{-1}, of deadwood would be needed when taking the entire compensation area in consideration.

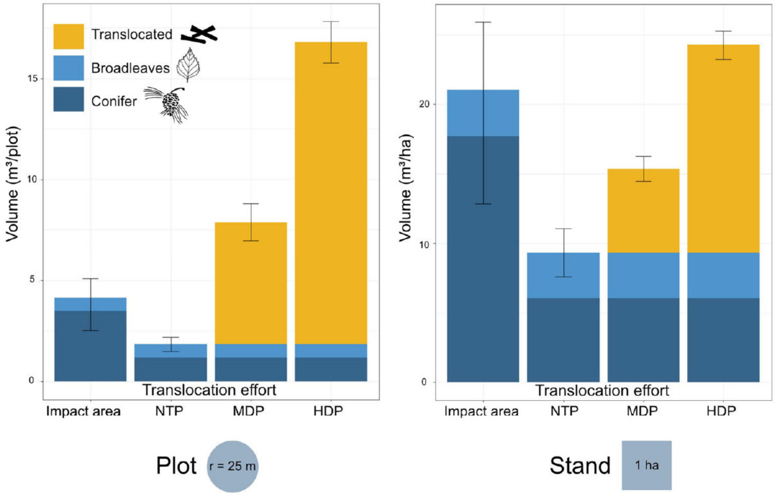

Fig. 3 Deadwood volumes in the impact area (far left) and compensation area, the later divided into NTP, no translocation plots (no deadwood addition); MDP, medium density plots (addition of 16 substrates/plot) and HDP, high density plots (addition of 48 substrates/plot). Translocated deadwood (yellow) consist only of conifers

The total cost of translocating deadwood to compensate for deadwood loss increases with the size of both impact and compensation areas, as visualized by the theoretical example in Fig. 4. To compensate deadwood loss in a landscape context to the levels found in the impact area would require an addition of approximately 12 500 logs at a total cost of 5.8 million SEK, compared to the actually performed compensation measure in which 640 logs were translocated at a cost of 0.3 million SEK. To fully compensate on landscape level, it would, hence, require a 20 times higher effort in both number of logs and costs.

Deadwood composition

In total, 2086 individual deadwood substrates were identified across all examined plots, including both existing and translocated substrates. These were further categorized into 92 unique deadwood types out of a possible 240. Prior to translocation, the composition of unique deadwood types in the compensation area differed significantly from that in the impact area. Following translocation, we observed significant differences not only between the impact area and compensation treatment plots but also among the different translocation plots, as presented in Table 2 and Fig. 5.

Indicator species analysis

Four specific deadwood substrate groups, pine snags in DC3 and with a diameter class of 20–30 cm (Kelo trees;

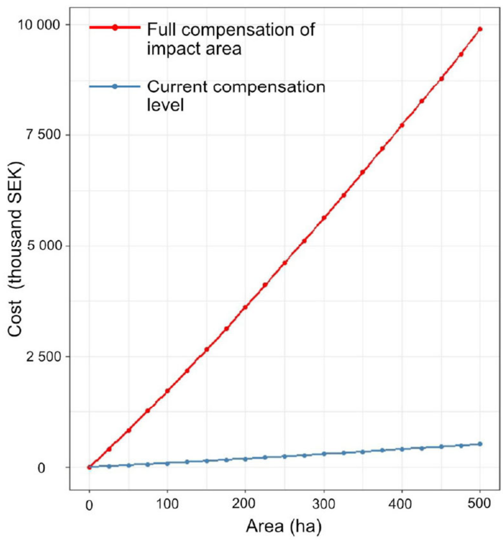

Fig. 4 Relationship between size of area to compensate and the total costs of translocation, derived from functions in Lindroos et al. (2021). Current compensation level (blue line) of MDP and HDP pooled (equivalent to addition of 2.1 logs ha^{-1} in entire compensation area) and theoretical compensation level needed to reach full compensation, or deadwood volumes similar to those found in impact area (red line, equivalent to addition of 40.4 logs ha^{-1} in entire compensation area)

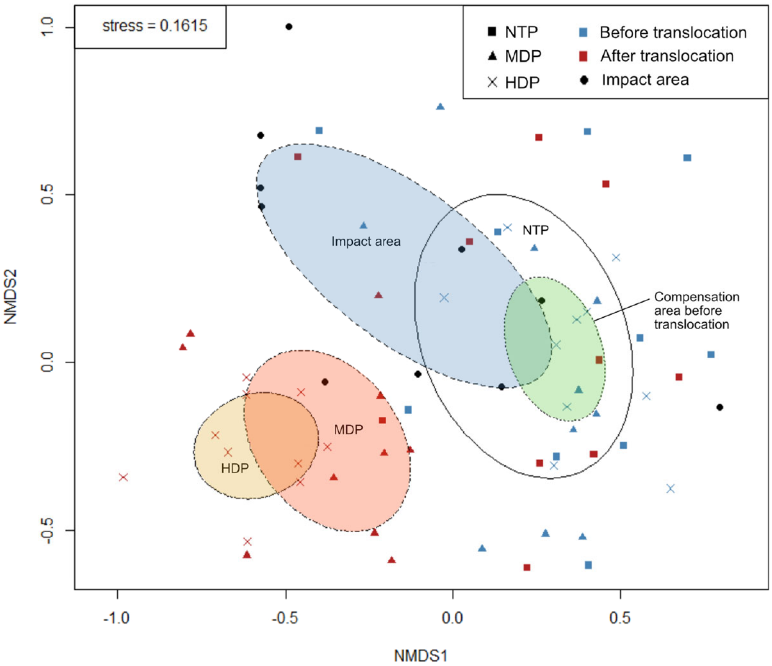

Fig. 5 NMDS ordination results for the composition of deadwood substrates on plot level for the four studied treatment groups; impact area, no translocation plots (NTP), medium density plots (MDP) and high density plots (HDP). Color labels the temporal scale; blue symbols indicate plots before translocation, red symbols after translocation and black symbols the impact area that was cut down. Ellipses display the standard errors for the five groups

decorticated and resin-impregnated long ago deceased pines), spruce snags in DC1 + DC2 with a diameter class of 30–40 cm, and downed willow in DC3 (hard) with a diameter class of 10–20 cm, were shown to be significant indicators of the impact area (Table 3). Willows were not translocated but they were frequent in the plots prior to translocation.

In the compensation area, MDPs had only downed pine in DC2 and with a diameter class of + 50 cm as a significant indicator, while the HDPs had the highest number of indicators. Among the 14 significant indicators, all except one were substrate groups that had been translocated. The remaining significant indicator was birch snags in DC3 with a diameter class of 10–20 cm, which had not been translocated but were frequent in the compensation plots prior to translocation.

The decomposition class distribution changed due to translocation. The relative volume of early decomposition class (classes 1 and 2) deadwood increased in the MDP and HDP (Fig. 6).

DISCUSSION

We assessed if this novel method for ecological compensation, translocation of high-quality deadwood, potentially could help solve long delivery time of certain substrates and structures, in our case large-diameter deadwood of unusual qualities. Translocation of deadwood and associated organisms is a method that has rarely been used and that has, to our knowledge, never been scientifically evaluated. This despite the fact that it is a potentially very useful method for advancing ecological compensation and restoration.

Deadwood density at plot and stand scale

We found that translocation clearly increased the deadwood volumes in our experimental plots to levels well above (two to four times) compared to the impact area and equivalent to volumes found in deadwood rich old growth forest (Siitonen 2001). Furthermore, when we extrapolated the deadwood volumes observed in our experimental plots to the stand level, we found that the volumes in MDP and HDP were comparable (mean of 15.4–24.3 m^3 ha^{-1}) to

Table 3 Results of indicator species analysis for unique deadwood types consisting of tree species, decay class, diameter class and position. The table only includes substrate groups showing significant ($p > 0.05$) indicator value. Number of translocated substrates within parentheses marks the number of substrates belonging to a specific substrate group which was reclassified to another group after translocation, e.g., snags that after translocation were classified as downed deadwood

Area	Tree species	DC-class	Diameter class (cm)	Deadwood position	p-value	Number of substrates in compensation plots prior to translocation	Number of translocated substrates
Impact area	Pine	3	20–30	Standing	< 0.001	0	(12)
	Spruce	2	30–40	Standing	0.008	1	(18)
	Spruce	1	30–40	Standing	0.034	0	(98)
	Willow	3	10–20	Downed	0.006	1	0
Compensation area							
MDP	Pine	2	50+	Downed	0.032	0	4
HDP	Birch	3	10–20	Standing	0.032	109	0
	Pine	1	20–30	Downed	< 0.001	1	51
	Pine	1	30–40	Downed	< 0.001	0	77
	Pine	1	40–50	Downed	< 0.001	0	71
	Pine	1	50+	Downed	< 0.001	0	39
	Pine	2	20–30	Downed	< 0.001	0	21
	Pine	2	30–40	Downed	< 0.001	0	32
	Pine	3	40–50	Downed	0.018	3	11
	Spruce	1	20–30	Downed	< 0.001	4	108
	Spruce	1	30–40	Downed	< 0.001	2	98
	Spruce	1	40–50	Downed	< 0.001	0	41
	Spruce	1	50+	Downed	0.003	0	9
	Spruce	2	20–30	Downed	< 0.001	2	42
	Spruce	2	30–40	Downed	< 0.001	1	18
	Spruce	3	40–50	Downed	0.009	0	3

those observed in the impact area (mean of 21.1 $m^3 ha^{-1}$). In comparison, Rudolphi and Gustafsson (2011), reported average deadwood volumes of 21 $m^3 ha^{-1}$ in old growth boreal forests that had not been subjected to clear-felling and contrasting to this, Jonsson et al. (2016) showed that the average deadwood volumes in production forests in northern Sweden is between 7.87 and 8.25 $m^3 ha^{-1}$, depending on region. Thus, purely based on volume, the method of deadwood translocation increased deadwood volumes in the MDP and HDP to levels equivalent or above levels found in targeted old growth forest. It is difficult to estimate volumes of deadwood needed to maintain intact communities of deadwood associated organism, however 20 $m^3 ha^{-1}$ is often used as rule of thumb for threshold volumes of deadwood, albeit rare and demanding saproxylic species might demand higher levels and specific qualities of deadwood (Müller and Bütler 2010). According to Hekkala et al. (2023), 20 $m^3 ha^{-1}$ is the threshold volume of deadwood for significantly higher richness of red-listed species in boreal coniferous forests. This indicates that purely based on volume, and not considering diversity, the levels of translocated deadwood would be sufficient to maintain population of rare and red-listed species in the compensation area at stand level.

The current translocation method with aggregation of high volumes of deadwood in experimental plots, could potentially work as “deadwood hotspots” in the landscape with high density and diversity of habitat for saproxylic species. Restoration, especially enrichment with deadwood, speeds up the development of the deadwood volumes needed to host large portions of biodiversity (Hekkala et al. 2016; Hägglund and Hjältén 2018) and potentially this method will circumvent the long delivery times for large dimension deadwood (Morris et al. 2006). These deadwood hotspots could possibly work as sources of dispersal in a metapopulational perspective (Ovaskainen and Hanski 2004) enriching the surrounding landscape. In ecological restoration, local enrichment with deadwood, attracts a large number of saproxylic insects and a high diversity of deadwood substrates that translates to a high diversity of saproxylic species (Hjältén et al. 2012; Lee et al. 2014; Hekkala et al. 2016; Seibold et al. 2017; Hägglund and Hjältén 2018).

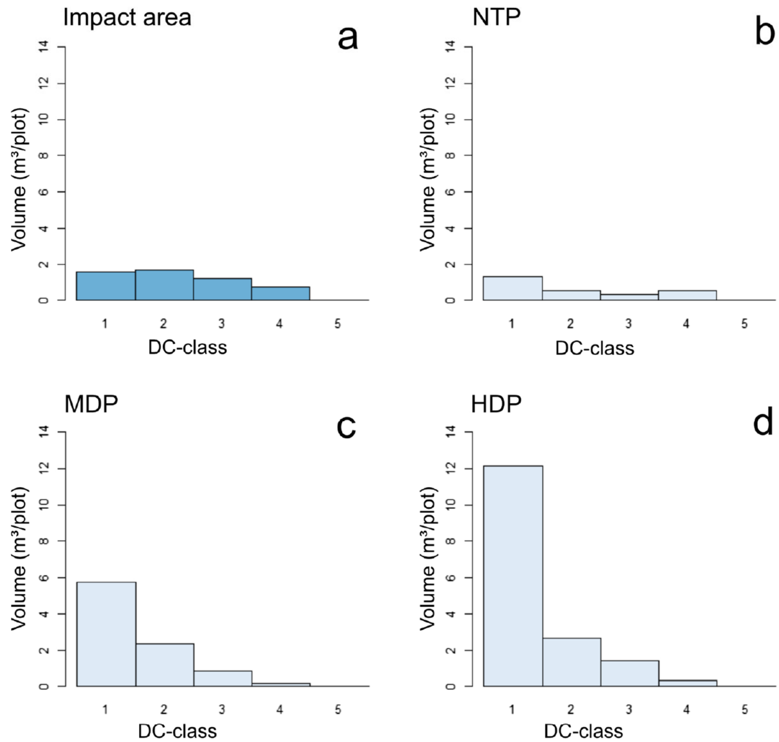

Fig. 6 Decomposition class distribution before deadwood translocation in impact area (**a**) and NTP (**b**) and after translocation in MDP (**c**) and HDP (**d**)

One of the primary benefits of translocating high-quality deadwood is the assisted migration of rare species associated to these substrates. Restoration efforts like in situ deadwood creation require long timeframes to reach similar advanced decomposition stages and deadwood dependent communities might take long time to colonize through natural processes (Morris et al. 2006). Assisted migration of species, that would otherwise have been destroyed in impact areas, offers the possibility of preserving them and potentially establishing populations in new areas. Yet, the challenges persist: can they endure the translocation and thrive in new habitats and potentially colonize from translocated to local substrates? Though not explored here, this potential advantage demands further research and consideration.

An additional advantage is that translocation increases the amount of deadwood in the compensation area without reducing the standing tree volume of living trees. This enables trees within the compensation area to mature over time, subsequently contributing with higher amount of quality deadwood in the future.

Costs for full landscape scale compensation and cost efficiency

Our calculations of the translocation effort needed to compensate for deadwood loss at larger spatial scales or landscape level, and the costs associated with this, revealed that a greater translocation effort is needed to fully compensate the losses of deadwood. In this respect, it should be noted that it was never the intention with this experiment to fully compensate for deadwood loss at landscape level, since this experiment was only a small part of the total compensation effort. Even so, our results show that it is possible to compensate for deadwood loss at smaller scales without extensive cost. Increasing the spatial scale also increases the difference between deadwood volumes added by the executed translocation level and deadwood volumes in the impact area. To fully compensate on landscape level, it would require a 20 times higher effort in both number of logs and costs compared to the executed compensation. Under the conditions in our theoretical example, the average additional cost for full compensation would be in the range of 16

000–20 000 SEK ha^{-1} for landscapes between 25 and 500 ha. Hence, the cost of 0.3 million SEK for the executed translocation would suffice for fully compensating an area of approximately 20 ha. To fully compensating the whole impact area of 376 ha would cost around 6 million SEK. This is of course a considerable cost, but should be seen in the perspective of the generally very high cost of these types of industrial projects. In this perspective the additional cost of increase the executed translocation level to fully compensate the habitat loss could not be considered remarkably high.

Furthermore, deadwood translocation costs can be considerably reduced by making the translocation process more efficient. The largest part of the executed compensation cost originated from the insertion of logs into the compensation area (29% of the cost), followed by log marking (24%) (Lindroos et al. 2021). If these types of work could be done more efficiently, it would substantially reduce the costs. That work is directly dependent on the volumes required to translocate, which in turn is dependent on the difference in deadwood densities between impact and compensation area. If the difference is little, deadwood from only a part of the impact area might be required. If so, deadwood close to the road could be collected, which would decrease costs. In addition to high amount of deadwood in the compensation area, it could also be selected based on its closeness to roads to decrease insertion distances and thereby costs. Since the cost for road transport was quite small per distance (5% of total cost in the executed translocation) (Lindroos et al. 2021), it would be cost-efficient to carefully select the compensation area without focusing too much on the closeness to the impact area. Additional measures would be to use a larger forwarder during insertion, and to place a larger proportion of the logs closer to the road. Aggregating deadwood into plots that are adapted to the loading capacity of the forwarder may also be more practical and cost-efficient in terms of creating higher deadwood density and diversity on a smaller number of plots.

However, as discussed in Lindroos et al. (2021), there is a trade-off between cost-efficiency and the created ecological values. Ongoing monitoring and research will reveal associated biodiversity benefits from aggregating deadwood into MDP versus HDP, revealing short- and long-term cost-efficiency of the methods. For large-scale exploitation projects, and as a last step in the mitigation hierarchy, substrate translocation can be a cost-efficient method provided that the loss of biodiversity is compensated.

Deadwood composition

Deadwood diversity is strongly connected to diversity of wood-living organism (Hjältén et al. 2012; Lee et al. 2014; Seibold et al. 2017; Hägglund and Hjältén 2018). Maintaining a high diversity of deadwood is therefore instrumental for biodiversity conservation (Ulyshen and Hanula 2009; Toivanen and Kotiaho 2010; Stokland et al. 2012). Although the translocation of deadwood resulted in increased volumes of deadwood, we found that the composition of deadwood differed between the impact area and the experimental plots also after translocation. A higher number of translocated deadwood in the HDP did not reduce the dissimilarity in deadwood composition between the impact area and compensation plots, if anything it increased the differences in deadwood composition, depending on the selection of translocation substrates. Thus, translocation of deadwood will not automatically result in a similar deadwood composition as in an impact area.

Indicator species analysis revealed that three unique deadwood types had significantly higher density in the impact area; standing kelo trees of pine in DC3, standing recently dead spruce trees (DC1 and DC2), and down deadwood of willow in DC3 (slightly softened). Several factors contribute to this difference in deadwood composition between impact and compensation area. The clearest reason is the methodology used to translocate standing dead trees. When placed in the compensation plots the posture of standing deadwood was changed, since all translocated snags were downed. This could potentially lead to insufficient amount of standing deadwood and could have negative effects for saproxylic species dependent on this type of habitat. Deadwood stature has been shown to have a strong impact on the composition of deadwood living organism such as insect, wood fungi, bryophytes and lichens (Ulyshen and Hanula 2009; Toivanen and Kotiaho 2010; Hjältén et al. 2012; Stokland et al. 2012; Santaniello et al. 2017; Hägglund and Hjältén 2018). The conversion of standing kelo trees to downed logs make them unsuitable for species associated with standing deadwood (Santaniello et al. 2017). In future ecological compensation, or restoration projects involving translocation of deadwood, should be designed to maintain standing deadwood in vertical position even after translocation, alternatively combined with in situ creation of standing dead trees. Problems related with this include increased costs, practical and safety considerations since placing and maintaining large deadwood in a standing position in a safe way is not an easy task. However, methods to move standing deadwood and keep it standing with support from living trees on sites have been tried in smaller scales so evaluation of these trials together with method development could make this possible in the future.

In the case of deadwood from willows, this type of deadwood was not translocated (only pine and spruce) and willows were rare in the compensation area, which explains the higher density in the impact area. As deciduous trees harbors saproxylic communities distinct from conifers

(Jonsell et al. 2007; Müller et al. 2015; Kärvemo et al. 2023) the lack of deadwood from willows in the compensation area could result in a lower species richness and abundance of willow-associated species. Thus, no-net-loss for this species group will not be achieved and further detailed studies are needed to assess translocation of deciduous trees. This could be an important future conservation measure, since other studies have revealed a strong positive correlation between availability of deadwood from deciduous trees and associated saproxylic species (Johansson et al. 2017).

The positive aspect of translocation was that many substrate types became more common in the compensation area than in the impact area. The indicator species analyses revealed that many of the deadwood indicators of HDPs belonged to DC1–2. This is a direct result of the fact that the selection of suitable deadwood substrates for translocation was limited to substrates that would not break during transport. In fact, many of the translocated substrates in early decomposition classes origins from cut living trees of high conservation values (very old and with large diameter). This resulted in an overrepresentation of deadwood in early decomposition stages, omitting more decomposed substrates. This means large amounts of habitats have been translocated for early successional saproxylic species. With time, these substrates in early decomposition classes will progress to more advanced decay classes and thereby serve as habitat for late successional species, even those demanding large diameter deadwood (Juutilainen et al. 2011). The transformation of living trees with high conservation value to early decay deadwood means that the rich abundance of old trees was not compensated for. One way to compensate for lack old trees, diversity in tree microhabitats (e.g., scars, resin flows, hollows), is to apply veteranisation on trees in the compensation area, e.g. by bark stripping.

Translocation increased the occurrence of a type of deadwood substrates that are becoming extremely rare in the forest landscape, large diameter deadwood (> 30 cm in diameter) (Fridman and Walheim 2000) but that are regarded as beneficial for many specialist saproxylic species (Juutilainen et al. 2011). Thus, in this case translocation not only increased deadwood volume in the compensation area but potentially also quality of deadwood compared to the surrounding forest matrix.

The indicator species analyses also revealed that deadwood of birch and large diameter downed logs were indicators of HDPs. As no birch was translocated this result is explained by a higher occurrence of birch deadwood in the compensation area than in the impact area. As deadwood of birch harbor a large variety of saproxylic organisms and a different species community than conifers (Stokland et al. 2012; Bell et al. 2015; Hägglund and Hjältén 2018), this also potentially contributes to the overall biodiversity in the compensation area.

CONCLUSIONS AND PRACTICAL IMPLICATIONS

Translocation of deadwood in ecological compensation areas could be viewed as a new tool for forest restoration and ecological compensation, reducing long delivery times of high-quality substrates, as well as providing means to improve colonization of deadwood associated species to a new area. Our results show that using this method, deadwood volumes at stand level would reach levels around or above the 20 m^3 ha^{-1}, suggested as a threshold for maintaining high species richness of rare and threatened saproxylic species. However, as translocation of deadwood is a novel method rarely used and very poorly evaluated, it requires improvements. Based on experiences from this case study we stress the importance of increasing the selection of suitable translocation substrates, but also to evaluate compensation strategies that combines translocation with in situ creation or veteranization of deadwood, to include the full range of deadwood decomposition classes and tree species, as far as possible. New translocating methods for late decay downed deadwood and standing deadwood need to be developed and evaluated. Further, it is important to try to maintain standing deadwood standing also after translocation, so this type of substrate does not become unsuitable (i.e., an ecological trap in connection with translocation) for associated organisms following translocation.

Full compensation of deadwood volumes on scales similar to the impact area is resource demanding but our calculations show that even without methodological improvements the costs are low in comparisons to the budgets of large-scale exploitation projects such as a mine expansion. Provided that the desired biodiversity benefits are achieved, such compensation methods can be considered efficient. However, provided the novelty of the methods, cost-related improvements could most likely be made. Hence, there is a need to investigate how the cost-efficiency could be increased, while maintaining the desired biodiversity benefits.

To gain further essential knowledge of this novel compensation method it is of outmost importance to conduct monitoring of the fate of the species communities moved with the translocated high-quality logs, e.g., their ability to colonize available substrates in the compensation area. Such monitoring programs should be given high priority as they are essential for assessing the potential biodiversity benefits with translocation. Finally, our findings emphasizes a broader principle of ecological compensation, applicable to all comparable impacts, such as urban and infrastructure development. The optimal strategy should be to preserve the most valuable habitats from irreversible harm. Only when preservation is impossible due to societal justifications for the impact outweigh conservation concerns should compensatory actions, including translocation, be pursued.

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Declarations

Conflict of interest No potential conflict of interest was reported by the author(s).

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AUTHOR BIOGRAPHIES

Olov Tranberg (✉) is a Doctoral Student at the Swedish University of Agricultural Sciences. His research focuses on ecological consequences of translocation of deadwood and associated species as a novel method within restoration ecology.
Address: Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.
e-mail: olov.tranberg@slu.se

Anne-Maarit Hekkala is an Associate Professor at the Swedish University of Agricultural Sciences. Her research interests cover restoration and other active measures to benefit forest biodiversity and resilience.
Address: Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.
e-mail: anne.maarit.hekkala@slu.se

Ola Lindroos is a Professor in Forest Operations with the Swedish University of Agricultural Sciences. His research focus on work operations in forests, and how they can be performed efficiently to achieve economical, ecological and social objectives.
Address: Department of Forest Biomaterials and Technology, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.
e-mail: ola.lindroos@slu.se

Therese Löfroth is an Associate Professor at the Swedish University of Agricultural Sciences. Her research interests include restoration ecology including the effects of wildfire and prescribed burning on ecological communities and responses of biodiversity to present and historical land use.
Address: Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.
e-mail: therese.lofroth@slu.se

Mari Jönsson is an Associate Professor at the Swedish University of Agricultural Sciences. Her research interests include citizen science, biodiversity, forest ecology and conservation.
Address: SLU Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden.
e-mail: mari.jonsson@slu.se

Jörgen Sjögren is an Associate Professor at the Swedish University of Agricultural Sciences, responsible for the competence area Restoration Ecology. In his research he investigates patterns and processes in multi-taxon responses to land use and biodiversity restoration efforts.
Address: Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.
e-mail: jorgen.sjogren@slu.se

Joakim Hjältén is a Professor Emeritus at the Swedish University of Agricultural Sciences. His research interests includes, restoration ecology, ecological compensation, conservation biology, community ecology and plant–herbivore interactions in forest ecosystems.
Address: Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden.
e-mail: joakim.hjalten@slu.se

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Restoration and ecological compensation faces challenges in delivering important biodiversity features, like large and decayed deadwood substrates. I tested a novel method in ecological compensation; translocation of deadwood and associated species from an impact area to a compensation area. Focusing on saproxylic beetles, bryophytes, and lichens, the results show that deadwood translocation provided an effective and cost-efficient tool to rapidly increase habitat availability and beetle species richness. For sessile species, both colonisations and local extinctions was shown.

Olov Tranberg received his doctoral education at the Department of Wildlife, Fish, and Environmental Studies, SLU, Umeå. He obtained his MSc and BSc in Biology and Forest Science at SLU, Alnarp and Umeå.

Acta Universitatis Agriculturae Sueciae presents doctoral theses from the Swedish University of Agricultural Sciences (SLU).

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