Forest Restoration Guided by an Umbrella Species

Will Measures to Protect the White-backed Woodpecker Benefit Saproxylic Beetles?

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Abstract

Management shortcuts in conservation biology, like the umbrella species concept, have been debated worldwide. Umbrella species have been used to identify and delineate protective areas, but habitat requirements of umbrella species can also provide tangible targets in ecological restoration. In Sweden, forest habitats have been restored for the white-backed woodpecker (WBW, *Dendrocopos leucotos*) under the assumption that it will benefit other habitat-associated (background) species. In this thesis, the umbrella species concept was evaluated based on the response of wood-inhabiting (saproxylic) beetles to forest restoration for the WBW. The WBW is a top-predator in saproxylic food webs associated with broadleaved trees, but it is also critically endangered in Sweden because of commercial forestry practices that disadvantage broadleaved trees and reduce dead wood availability.

Spruce trees (Norway spruce, *Picea abies*) were selectively harvested during forest restoration to make way for broadleaved trees like birch (*Betula* spp.) and European aspen (*Populus tremula*). Some broadleaved trees were also killed to create high-stumps (snags) and downed logs. Commercially managed forests were compared with restored forests; either directly in comparative studies, or before and after forest restoration. Two types of flight-intercept traps were used to catch saproxylic beetles: IBL2-traps and trunk-window traps.

Results presented in this thesis show that habitat requirements of an umbrella species can be used to guide forest restoration. There were many beneficiary species at the stand-level. Commercially managed and restored forests were inhabited by different communities of saproxylic beetles, and species positively associated with broadleaved trees and sun-exposed substrates were particularly responsive. This was reflected by an increased species richness and abundance. Several near-threatened and vulnerable species were also attracted to substrates created for the WBW. This shows that efforts to bring back the WBW can benefit other resource-limited groups of conservation concern. Saproxylic beetles might even facilitate restoration efforts since many important prey species for the WBW were attracted to restored sites.

Umbrella species, like the WBW, will require landscape-level efforts to recover. This is a strength of the umbrella species concept, but also a weakness since landscape-level efforts are time consuming. The WBW is still struggling in Sweden, and failed attempts to re-establish viable populations might undermine conservation incentives. Early signs of progress, however, are sometimes provided by less demanding species, like many saproxylic beetles in this thesis. Background species can also provide much needed examples of restoration success at the stand-level.

Keywords: Broadleaved trees, Forest, Management, Restoration, Saproxylic beetles, Sweden, Umbrella species, White-backed Woodpecker

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Dedication

To my family and Kajsa

There is new life in the soil for every man. There is healing in the trees for tired minds and for our overburdened spirits, there is strength in the hills, if only we will lift up our eyes. Remember that nature is your great restorer.

Calvin Coolidge

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 Bell, D., Hjältén, J., Nilsson, C., Jørgensen, D., Johansson, T. (submitted). Forest restoration guided by an umbrella species benefits other habitat-associated organisms.

II Bell, D., Hjältén, J., Jørgensen, D., Nilsson, C., Johansson, T. (submitted). Saproxylic beetles benefit from forest restoration for the white-backed woodpecker (*Dendrocopos leucotos*).

1 Introduction

Ecological restoration has become increasingly important in areas where habitat protection and environmental guidelines fail to safeguard biodiversity (Brudvig, 2011). In fact, ecological restoration is nowadays recognized as a global priority. Global targets were recently negotiated at the COP 10 Convention on Biological Diversity in Nagaya, Japan (CBD, 2010), but strategic plans have also been developed by the European Union (EU, 2011). In both agreements, the stated goal was to restore 15 percent of the degraded land cover.

It can be difficult to quantify restoration needs at the landscape-level. Habitat threshold values are unknown for most species, and extinction debts can be extensive (Kuussaari et al., 2009). Baselines (reference points) might also have shifted in areas where anthropogenic impacts date back several generations (Pauly, 1995). Knowledge gaps, time constraints, and funding difficulties can complicate ecological restoration, but habitat requirements of umbrella species might provide tangible, landscape-level, targets (Angelstam and Andersson, 2001).

Typical umbrella species inhabit areas large enough to support viable populations of other habitat-associated (background) species (Groom et al., 2006; Seddon and Leech, 2007). Results have been presented both for (Fleishman et al., 2000, 2001; Suter et al., 2002; Caro, 2003; Kerley et al., 2003) and against (Andelman and Fagan, 2000; Caro, 2001; Rubinoff, 2001) the umbrella species concept, but rarely in a context of ecological restoration. Instead, most studies have focused on its usefulness in habitat protection. Umbrella species have, for instance, been used to identify and delineate protective areas (Seddon and Leech, 2007).

Ecological restoration is not easily defined. A widely cited definition by SERI (2004) states that “ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed". Ecological restoration has also been described as "an effort to move a degraded ecosystem or community toward the greater structural and functional complexity that characterize intact ecosystems" (A. D. Bradshaw rephrased by Groom et al., 2006). An alternative definition by Groom et al. (2006), describes ecological restoration as an inherently subjective process, and ultimately a form of human land use. Ecological restoration is undoubtedly a human endeavor, but if there is merit to the umbrella species concept, objectively chosen surrogates might benefit biodiversity at the landscape-level.

Recently, researchers have used study designs in ecological restoration to unravel spillover effects of single-species conservation. Management efforts guided by umbrella species can cause spillover effects in both terrestrial (Sheehan et al., 2014) and aquatic (Branton and Richardson, 2014) environments. Birds are often targeted in terrestrial studies, and subsequent effects are normally described for a subset of avian species. Management efforts guided by the red-cockaded woodpecker (*Picoides borealis*) and the cerulean warbler (*Setophaga cerulean*) have, for instance, been shown to benefit other disturbance-dependent bird species (Wilson et al., 1995; Sheehan et al., 2014).

Many aquatic studies have focused on salmonids in restored streams. Salmon and trout are often described as umbrella species (Törnblom et al., 2007; Branton and Richardson, 2014), but targeted organisms are rarely evaluated in terms their spillover effects. Subsidiary impacts might be described for closely related species, but cross-taxon studies are uncommon (Caro, 2010). One exception, published by Branton and Richardson (2014), showed that benthic invertebrates were negatively affected by floodplain restoration for the Coho salmon (*Oncorhynchus kisutch*), in contrast to positively affected vertebrates.

The umbrella species concept rests in the assumption that spatially demanding species, if protected, will ensure the subsistence of many naturally co-occurring species (Roberge and Angelstam, 2004). As already mentioned, many researchers have criticized the concept, namely because it can be difficult to balance its selection criteria (Roberge and Angelstam, 2004; Fleischman et al., 2000, 2001). Umbrella species are, for instance, expected to be fairly common, but also restricted to species-rich environments threatened by humans. Sometimes it is also assumed that umbrella species must be intrinsically linked to other taxonomic groups. In reality, designated species rarely fulfill all selection criteria. Even species with similar habitat requirements will sometimes be constrained by different factors. Resource-, process- and dispersal-limited species will, for instance, co-occur at different spatial and temporal scales (Lambeck, 1997).

A meta-analysis by Branton and Richardson (2010) showed that birds can provide valuable management shortcuts, and that omnivores might be particularly useful umbrella species. Omnivorous species are often widespread, and this might explain why opportunistic birds are associated with so many background species. In ecological restoration, however, it might be more important to identify specialized species that have been negatively affected by human land use (Fleischman et al., 2000; Mikusiński and Angelstam, 2004; Seddon and Leech, 2007). In fact, management shortcuts, like the umbrella species concept, might be particularly useful if there is congruence in the response of co-occurring species to manipulated environmental features (Branton and Richardson, 2014).

Forest resources have been exploited throughout human history, but never to the extent made possible by mechanized harvesting in the 1950s. Early in the 19th century, Sweden began the process of industrialization by rapidly expanding its sawmill industry, and since then many structurally complex forests have been replaced by uniform, and commercially managed, plantations (Bernes, 2011). Most broadleaved trees are eliminated during pre-commercial thinning (Östlund et al., 1997) to benefit more profitable coniferous species like Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Broadleaved trees are also disadvantaged when natural disturbance regimes, such as recurrent wildfires in forest interiors and seasonal floods in riparian habitats, are suppressed or altered (Hellberg, 2004; Johansson and Nilsson, 2002). Humans manipulate natural disturbance regimes for many reasons; water levels have been lowered to increase forest productivity (Fahlvik et al., 2009), rivers have been regulated to produce electricity (Nilsson and Berggren, 2000), wind-felled trees have been extracted to prevent pest outbreaks (Thorn et al., 2014), and wildfires have been extinguished to protect timber, property, and people (Granström, 2001). Broadleaved trees are, generally, highly competitive in frequently disturbed environments, such as periodically flooded forests and post-fire sites.

Afforested areas might be perceived as near-natural environments, but pristine and commercially managed forests are often very different. Commercially managed forests are, for instance, harvested before dead wood accumulates, and thereby deprived of dead wood (SEPA and SCB, 2011; SLU, 2012). Another problem is that stand-level volumes of timber have increased with 40-80 % since the 1950s (SLU, 2012). Plantations are generally darker than naturally disturbed environments, and this can affect warmth-demanding species negatively (Gärdenfors, 2010). Many wood-inhabiting (saproxylic) species are adapted to natural disturbance, and positively associated with broadleaved trees and sun-exposed substrates (Dahlberg and Stokland, 2004). Even formerly widespread species, and top-predators in saproxylic food webs, like the white-backed woodpecker (WBW, *Dendrocopos leucotos*), are nowadays critically endangered by forestry (Aulén et al., 2010).

Habitat protection cannot prevent detrimental effects of human land use elsewhere. If natural disturbance regimes are suppressed outside protected areas, it might still affect fire frequencies, and thereby tree assemblages in forest reserves (Kuuluvainen, 2002). In Sweden, forest owners are assigned "freedom under responsibility", and Swedish law states that production and conservation goals are equally important (Bernes, 2011). Certification systems have also been developed by, e.g., FSC and PEFC, as marketing tools for sustainably grown forest products. Forestry companies join FSC and PEFC voluntarily, and have done so since 1993, but stated environmental objectives are not always fulfilled (Angelstam and Andersson, 2001; Andersson, 2009). It is also clear that retained high-stumps on clear-cuts constitute a minor part of what is considered available habitat for most saproxylic species (Schroeder et al., 2006). Environmental considerations in forestry might also be insufficient, particularly in the short-term, if extinction debts are extensive, and if silvicultural precautions are limited to the patch scale. Large volumes of dead wood will, for instance, accumulate very slowly without human assistance (Fridman and Walheim, 2000). Ecological restoration might therefore be the only way to alleviate extinction debts.

In Sweden, habitats have been restored for the WBW based on such premises, and the underlying assumption that requirements of demanding species will ensure the subsistence of background species (Mild and Stighäll, 2005; Blicharska et al., 2014). Breeding WBW pairs require 150-650 hectares hectares of functionally intact habitat, with CWD volumes around 10-20 m^3/ha (Angelstam et al., 2003; Aulén et al., 2010). The WBW is generally considered an umbrella species, and it has been positively associated with other bird species (Törnblom et al., 2007; Roberge et al., 2008), but also beetles and cryptogams of conservation concern (Martikainen et al., 1998; Roberge et al., 2008). It is known for foraging in edge habitats (Stighäll et al., 2011), post-fire sites (Mild and Stighäll, 2005), and areas of intermediate forest cover (Mikusiński and Angelstam, 2004); where it targets wood-inhabiting invertebrates, primarily saproxylic beetles in broadleaved trees (Aulén, 1988). Habitats frequented by the WBW are also likely to be inhabited by different communities of saproxylic beetles than commercially managed forests. Several studies show that clear-felled forests, with retained dead wood from broadleaved trees, attract different saproxylic beetles than mature forests with similar substrates (Kaila et al., 1997; Martikainen, 2000; Svedrup-Thygeson and Ims, 2002).

In habitats restored for the WBW (best-praxis areas), high-stumps and downed logs are left in much larger quantities than in areas affected by forestry (*personal observation*). Spruce trees (Norway spruce, *Picea abies*) are also selectively harvested to open-up the forest canopy, and to make broadleaved trees more competitive (Mild and Stighäll, 2005). Spruce extraction provides revenues for forestry companies and private landowners involved in forest restoration. Spruce removal might also prevent pest outbreaks in adjacent forests with commercial values. These are all incentives crucial to stakeholders, and might explain why forestry companies, and other private land owners, have agreed to restore more than 10,000 hectares in Sweden. There are also future plans to restore even larger areas (Kristoffer Stighäll, *pers. comm.*).

The WBW is demanding both in terms of its diet, but also in terms of its spatial requirements. Only extensive efforts to restore its former habitats are likely to bring it back (Hof et al., unpublished). This is easily forgotten when stakeholders eagerly await immediate results. Several studies show that avian top-predators can be efficient umbrella species (Martikainen et al., 1998; Sergio et al., 2003, 2004, 2005, 2006; Roberge et al., 2008), but the evidence is not conclusive (Roth and Weber, 2008). The WBW is still struggling in Sweden, but spatially demanding (umbrella) species will not necessarily substantiate successful restoration efforts at the stand-level. Many background species, however, could provide alternative solutions in agreement with the umbrella species concept.

2 Objectives

In Sweden, forest habitats have been restored for the WBW under the assumption that it will benefit other saproxylic species. In this thesis, spillover effects of forest restoration for the WBW were evaluated based on the response of saproxylic beetles. The overall aim of the thesis was to compare commercially managed forests with restored forests in terms of (1) species richness and abundance, (2) community structure, and (3) species of conservation concern. Commercially managed forests were compared with restored forests; either directly in comparative studies, or before and after forest restoration. Saproxylic beetles with particular substrate (broadleaved or coniferous trees) and microclimatic (sun or shade) preferences were given special attention. It was hypothesized that forest restoration for the WBW would benefit (1) species positively associated with broadleaved trees, (2) species positively associated with sun-exposed substrates, (3) resource- and process-limited species of conservation concern, and (4) prey species consumed by the WBW. By examining these hypotheses, the study investigated the usefulness of umbrella species, like the WBW, in ecological restoration.

3 Methods

3. 1 Study organisms

Saproxylic beetles “are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics” (Speight, 1989). In previous studies (e.g., Gibb et al., 2006; Toivanen and Kotiaho, 2007), wood-inhabiting beetles have been categorized as either obligate (dependent on dead wood during at least part of their lifecycle) or facultative (associated with but not dependent on dead wood). In paper I and II, both groups were included in the analyses.

The Swedish red-list (Gärdenfors, 2010) was used to identify species of conservation concern. Empirical data provided by Aulén (1988) was used to uncover prey species consumed by the WBW. Substrate and microclimatic preferences were determined from previous research or large unpublished datasets (Koch, 1989; Ehnström and Axelsson, 2002; Dahlberg and Stokland, 2004; Lindhe et al., 2005; Hjältén et al., unpublished; www.beetlebase.com).

3. 2 Study area and data collection

All study sites in paper I were located within the county of Värmland in south-western Sweden (Figure 1). In paper II, study sites belonged to either Värmland or Västra Götaland County (Figure 1). In paper I, invertebrate traps were positioned in restored and commercially managed (control) forests, and all analyses were based on pair-wise comparisons. In paper II, forest stands were sampled before and two consecutive years after forest restoration.

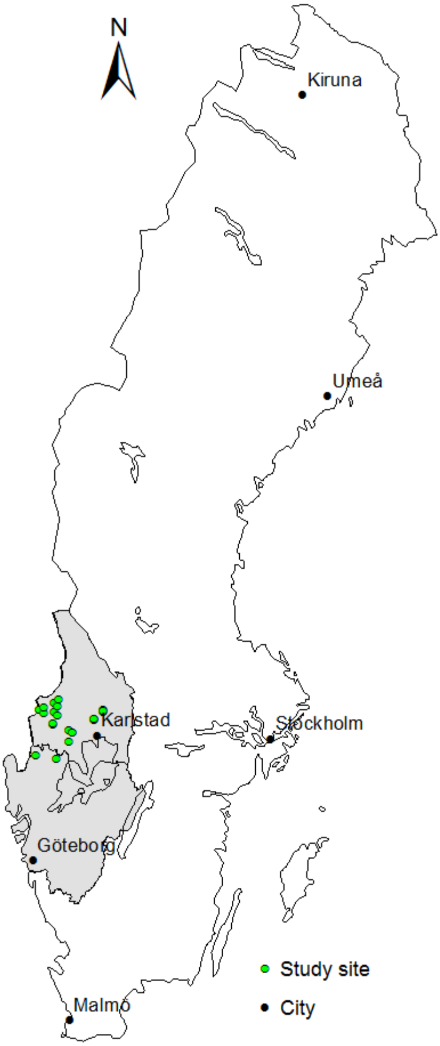

Figure 1. Map of Sweden. Study sites (in green) belonged to either Värmland or Västra Götaland County (delineated grey area).

In both papers, we used flight-intercept traps to capture saproxylic beetles throughout the entire summer, but the traps were of different designs (Figure 2). In paper I, we used Polish IBL2-traps (CHEMIPAN, Warszawa, Poland). Three IBL2-traps were positioned at breast height between two trees in every study site, i.e., 9 control sites and 9 restored sites. Semi-transparent plastic was used to construct the triangular IBL2-traps (height: 1 m, width: 1 m), and funnels were attached to the bottom of each trap to catch colliding beetles, and to lead them into bottles filled with glycol and detergent. In paper II, we used small, outward-facing windows (0.3 × 0.4 m) on tree trunks to obstruct flying beetles. Colliding insects ended up in metal containers, filled with glycol and detergent, placed underneath the windows. Five forest stands were selected for paper II, and “trunk-window traps” were positioned on 3-5 birch (*Betula* spp.) trees per study site.

Figure 2. To the left: IBL2-trap. To the right: trunk-window trap.

All saproxylic beetles in paper I and II were identified by expert taxonomists. Most specimens were identified to the species-level, but there were a few exceptions (see Methods in paper I and II for more detailed information).

Commercially managed forests were generally overgrown by Norway spruce (Figure 3), but also comprised of broadleaved trees, namely birch (*Betula* spp.) and European aspen (*Populus tremula*). Restored forests were selectively harvested to eradicate Norway spruce (*Picea abies*), and to create downed logs and high-stumps from broadleaved trees. In paper II, spruce trees were felled and retained locally (Figure 4). In paper I, all spruce trees were removed from the study locations (Figure 5). In paper I, environmental data was collected to describe stand-level characteristics such as forest age, stand basal area, canopy cover, volume of dead wood, tilt, aspect, and forest productivity. No such measurements were gathered for paper II.

Figure 3. Commercially managed forest overgrown by Norway spruce (Paper I and II).

Figure 4. Selectively harvested and retained spruce trees in a restored site (Paper II).

Figure 5. High-stumps and downed logs created from birch during forest restoration (Paper I and II). All spruce trees have been removed (Paper I).

3. 3 Statistical analyses

In paper I, we used a Student's *t*-test, or alternatively an unequal variance *t*-test (Ruxton 2006), to evaluate differences in species richness and abundance for saproxylic beetles of different substrate and microclimatic preferences. The same goes for species of conservation concern, i.e., red-listed species. The approach was also used for pair-wise comparisons of stand-level characteristics. All analyses of this sort were carried out in IBM SPSS Statistics (Version 21).

To illustrate differences in dominance structure and species composition we created non-metric multidimensional scaling (nMDS) plots. For conclusive statistical tests, however, we used PERMANOVA in PRIMER 6 (version 6.1.12) and PERMANOVA+ (version 1.0.2) by PRIMER-E Ltd. Species contributions to the observed dissimilarity between treatments were calculated in PRIMER with SIMPER.

Distance-based linear modeling (DistLM) in PRIMER showed to what extent stand-level characteristics affected saproxylic beetle communities. To explore relationships for individual variables, marginal tests were performed. All variables were afterwards subjected to a step-wise selection procedure (selection criterion: AICc) in order to develop models. Prior to analysis, environmental variables were plotted against each other in a Draftsman plot to control for co-linearity. Pearson correlation analysis was used to quantify the relationships. In all step-wise procedures and marginal tests, *P*-values were obtained with 999 permutations.

In paper II, we used a similar approach, but to account for repeated sampling between years, we performed analyses of variance (ANOVAs) with repeated measures in SPSS (IBM SPSS Statistics, version 21). For pair-wise comparisons we used a Bonferroni-Holm post hoc test (Holm, 1979). In agreement with paper I, all community analyses were performed in PRIMER 6 (version 6.1.12) and PERMANOVA+ (version 1.0.2) by PRIMER-E Ltd. Two factors, i.e., treatment (fixed) and study site (random), were included in the PERMANOVA design, and *P*-values were obtained with 999 permutations. Influential species in the community analyses were singled-out in subsequent SIMPER-analyses, and differences in dominance structure and species composition were illustrated in two nMDS-plots.

4 Results and discussion

4. 1 Summary of Paper I

Forest restoration guided by the WBW created habitats significantly different from commercially managed forests. Volumes of dead wood (coarse woody debris, CWD) were almost five times higher in restored forests, and the canopy cover was 1.5 times less extensive. Most of the dead wood was created from birch trees, and birch volumes were higher for both lying and standing CWD. As predicted, many saproxylic beetles were positively affected by forest restoration, particularly those associated with dead wood from broadleaved trees and sun-exposed substrates (Figure 6). Taxonomic groups with such preferences were more species-rich in restored sites. Saproxylic beetles favored by sun-exposure were also more abundant in restored forests. The abundance of shade-tolerant species, however, was negatively affected by forest restoration. Red-listed groups were, nonetheless, positively affected by forest restoration, both in terms of species richness and abundance.

Species assemblages in commercially managed forests were significantly different from species assemblages in restored forests. In fact, fifty percent of all species were unique to either treatment. Distance-based linear modeling showed that canopy cover was a good explanatory variable. Saproxylic beetles are intrinsically linked to dead wood, but saproxylic beetles might also respond differently to microclimatic conditions. Many saproxylic beetles have developed adaptations to natural disturbance and prefer sun-exposed substrates (Dahlberg and Stokland, 2004). In restored sites, forest features were manipulated to mimic natural disturbance. This might also explain why many red-listed species were attracted to restored sites. Natural disturbance regimes are generally suppressed in commercially managed forests, and stand-level volumes of timber have increased with 40-80 percent since the 1950s (SLU, 2012). Overgrown forests are less permeable to sun-light, and thereby less favorable for warmth-demanding species (Gärdenfors, 2010).

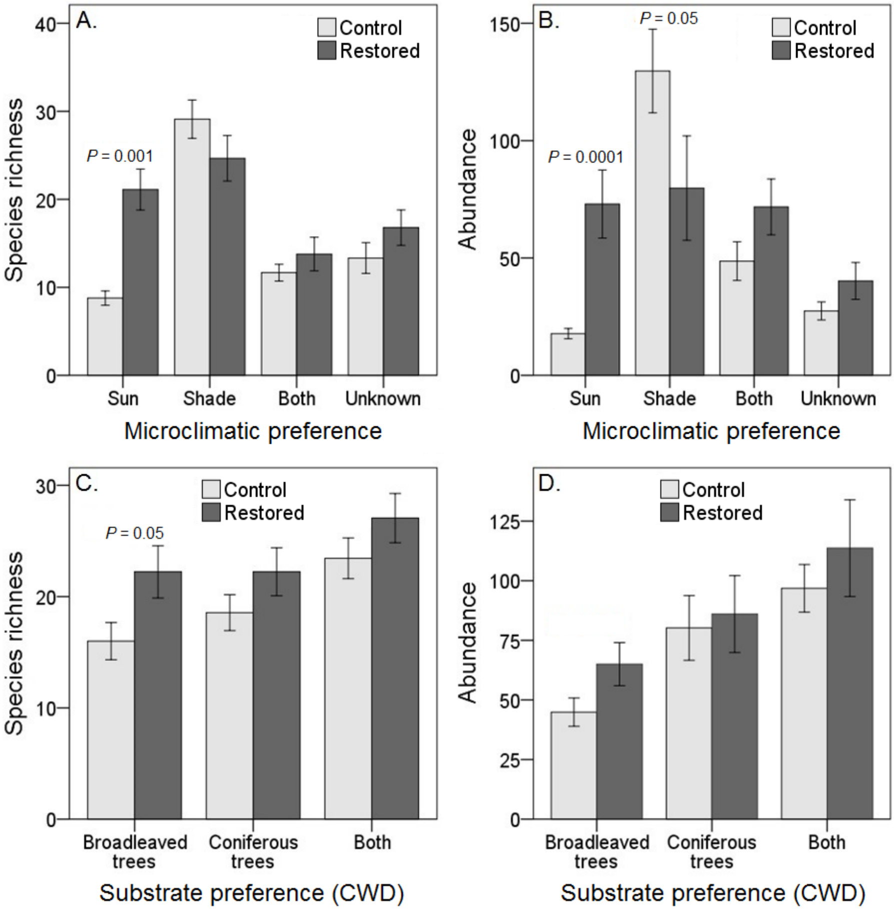

Figure 6. Species richness (A and C) and abundance (B and D) of saproxylic beetles (mean +/- SE) of different microclimatic (sun, shade, both, unknown) and substrate (broadleaved trees, coniferous trees, both) preferences. *P*-values denote significant ($P \leq 0.05$) differences between restored and commercially managed (control) forests.

4. 2 Summary of Paper II

Different assemblages of saproxylic beetles were attracted to restored sites than to non-restored sites over two consecutive sampling years. Dissimilarities between treatments were generally explained by species with coniferous preferences, but some influential species were also linked to broadleaved trees, e.g., *Diaperis boleti*, *Scolytus ratzeburgii*, *Triplax russica*, *Endomyccus coccineus*, and *Triplax aenea*. *E. coccineus* and *S. ratzeburgii* were the largest contributors to the observed dissimilarity between restored and non-restored sites two years after forest restoration. *S. ratzeburgii* has been described as an important prey species for the WBW along with 43 other saproxylic beetles (Aulén, 1988).

The overall species richness and abundance of prey species targeted by the WBW increased after forest restoration (Figure 7). In fact, forest restoration caused a 13-fold increase in prey abundance in the first year, and an 11-fold increase in the second year. Taxonomic groups associated with broadleaved trees were more species-rich both years after forest restoration, but there were no significant increases in abundance (Figure 7). Significantly more prey species positively associated with coniferous trees were also captured both years after forest restoration, and results on their abundance showed a significant (35-fold) increase in the first summer after forest restoration, but not in the following year (Figure 7).

Species of conservation concern were also more numerous in trunk-window traps positioned in post-treatment sites, and a majority were linked to dead wood from broadleaved trees. This shows that efforts to bring back the WBW can benefit other resource-limited groups threatened by commercial forestry.

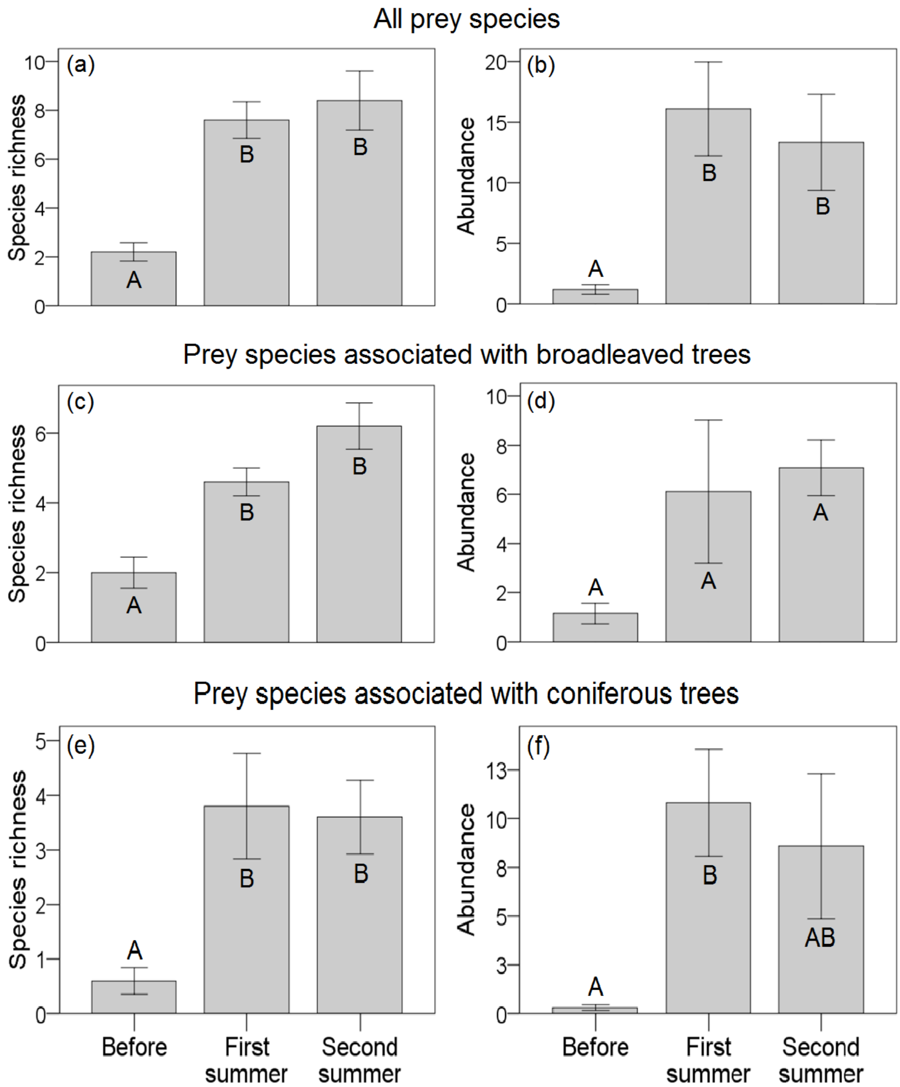

Figure 7. Species richness and abundance, before and after (first and second summer) forest restoration for confirmed prey species (saproxylic beetles). Yearly average values (mean +/- SE) were based on the mean catch size per window trap and study site. Years with different capital letters were significantly different (Bonferroni-Holm, $P \leq 0.05$). In figure (a) and (b): confirmed prey species associated with broadleaved and coniferous trees. In figure (c) and (d): confirmed prey species associated with broadleaved trees (*Betula* spp.). In figure (e) and (f): confirmed prey species associated with coniferous trees.

4. 3 Concluding remarks

This thesis shows that there is merit to the umbrella species concept. Results presented in paper I and II, showed that management efforts guided by an umbrella species can cause extensive spillover effects, in agreement with previous findings (Wilson et al., 1995; Branton and Richardson, 2014; Sheehan et al., 2014). Habitats were restored for the WBW, but there were many beneficiary species at the stand-level. Many resource- and process-limited (Lambeck, 1997) species were positively affected by the creation of dead wood, but microclimatic effects were also important. The effects of sun-exposure (canopy cover) were anticipated thanks to earlier assessments of forestry impacts. Several studies show that clear-felled forests, with retained dead wood from broadleaved trees, attract different saproxylic beetles than mature forests with similar substrates (Kaila et al., 1997; Martikainen, 2000; Svedrup-Thygeson and Ims, 2002).

Local habitat improvements will sometimes benefit lower trophic levels, but interdependent top-predators will only recover if prey species proliferate at the landscape-level. This is a strength of the umbrella species concept, but also a weakness if slowly recovering umbrella populations undermine conservation incentives. Less demanding species, however, might provide early signs of restoration progress and success at the stand-level, if there is congruence in the response to manipulated environmental features. The recovery of background species might even influence public opinion and the direction of management decisions.

Conservation shortcuts provided by umbrella species are often questioned (Andelman and Fagan, 2000; Caro, 2001; Rubinoff, 2001), but organisms of different taxonomic groups will not always overlap at scales that concern managers. Many saproxylic beetles were positively affected by forest restoration in this thesis, but the WBW is still struggling in Sweden. Forest restoration created habitats with CWD volumes similar to those found in typical WBW habitats (10-20 m^3/ha, Angelstam et al., 2003; Aulén et al., 2010), but restored sites are generally much smaller than typical WBW territories (150-650 ha, Aulén et al., 2010). If spatial requirements are fulfilled at the landscape-level, important prey species are likely to facilitate the recovery of top-predators in saproxylic food webs like the WBW. Under such circumstances, umbrella species become testimonies of ecosystem recovery rather than the management shortcuts.

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