How α- and β-Diversity of Carabids and Ground Dwelling Spiders differ in Clear-Cuts and Retention Patches, 3 Decades Post-Implementation

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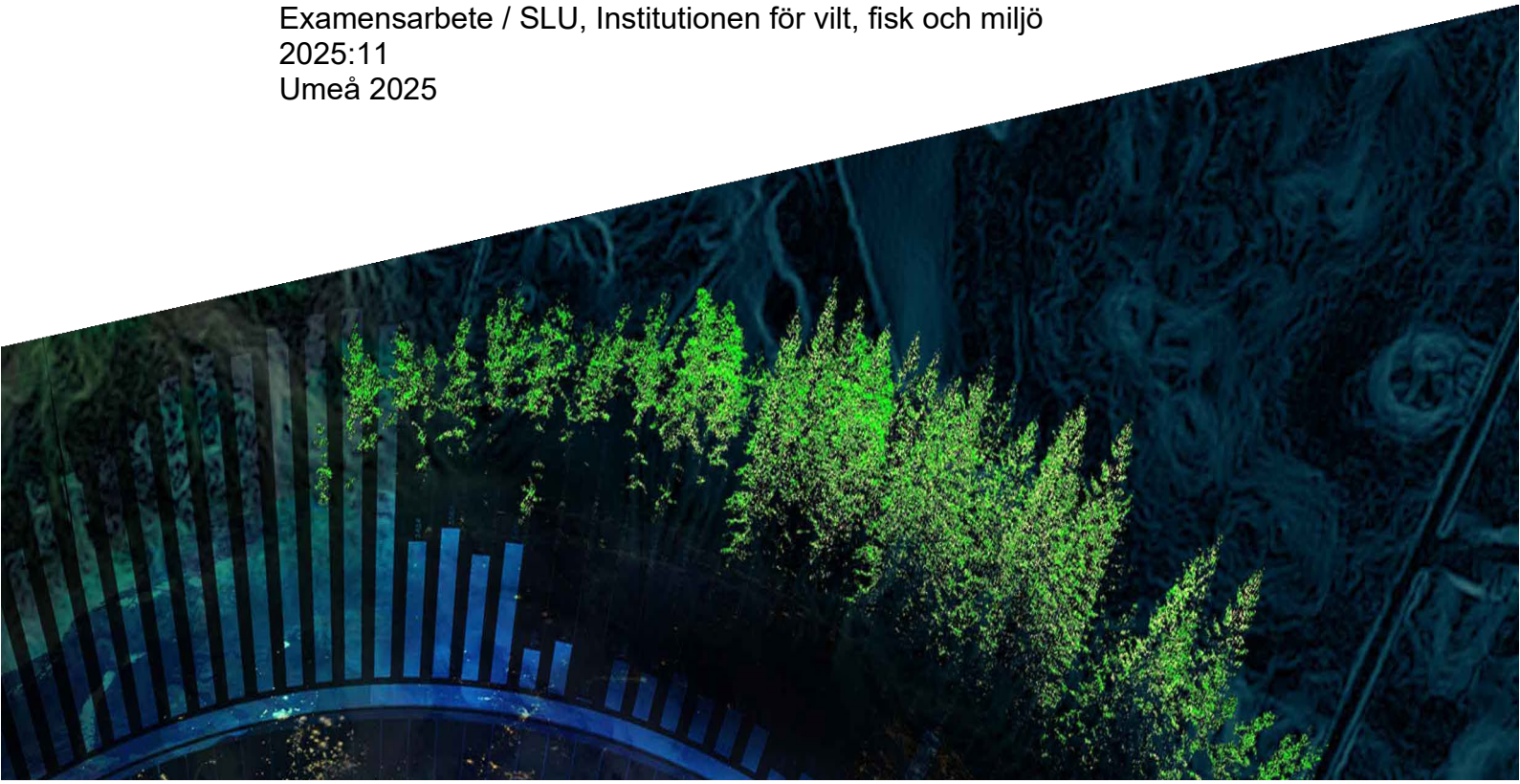

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Abstract

Clear-cutting and retention forestry practices have long-lasting ecological impacts, yet their consequences on biodiversity and more specifically on arthropod communities decades after implementation remain poorly understood. This study investigates the differences in ground-dwelling carabid beetle and spider diversity and communities in a Swedish boreal forest, 30 years post-implementation.

Both taxa were sampled using standardized pitfall trapping with an equal division of traps among clear-cuts, retention patches and set asides in the Hälsingland area in central Sweden.

The analysis of alpha-diversity revealed that only abundance patterns and not species richness nor evenness differed significantly with forest treatments. Carabid abundance was highest in set asides, suggesting sensitivity to structural simplification in highly disturbed sites while spider abundance peaked in clear-cuts, likely driven by the dominance of disturbance-tolerant wolf-spiders (*Lycosidae*).

Beta-diversity analysis showed only minor abundance-based compositional differences and no shift in species presence/absence for carabids, reflecting greater resilience or generalist behaviour. In contrast, spider communities exhibited significant compositional shifts, indicating lasting legacy effects of clear-cutting. Retention patches partially mitigated biodiversity loss, particularly for carabids but failed to restore pre-disturbance community structures when compared to the set asides.

These findings highlight taxon-specific resilience and suggest that while retention forestry offers benefits, it is not a replacement for conservation measures such as set asides. Future research needs to incorporate multi-factorial analysis and long-term monitoring to better inform sustainable forest management strategies.

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Introduction

Growing global demand for natural resources, coupled with the accelerating negative impacts of climate change, has underlined the need for sustainable ecosystem management. Using renewable energy comes with a wide array of challenges, one being the sustainable use of resources while at the same time guaranteeing environmental resilience. Biological and ecological resources, particularly the diversity of species, genetic variability within species, the regional species- and ecosystem pool, the size of the forest and the condition and character of the adjacent landscape define resilience of natural ecosystems (Thompson, 2009, p.8) and allow perseverance and adaptation in the face of natural and anthropogenic disturbances.

In this regard, a key element to understand the development of a natural ecosystem, is biodiversity. The latter can be measured at multiple levels, alpha-diversity representing the species richness at a local scale while beta-diversity is focusing on the differences in species composition between sites (Anderson et al., 2011). Understanding how forest management and particularly the choice of practices affects both aspects is key to assessing long-term ecological outcomes.

Forestry has a well-documented and ongoing history of nature degradation (Fedrowitz et al., 2014) due to practices such as clear-cutting. In the Swedish context, this method can be retraced to the late 19th century when clear-cutting was thought to be more advantageous than the various prevailing forms of silviculture of that time. Among other sources, the expansion of the Swedish pulp industry as well as an increased demand of timber from industrially developed countries in Europe explain the change to this forestry approach (Lundmark et al., 2013). The practice of clear-cutting involves the removal of all trees, vegetation and woody remains followed by ploughing of the surface (Hamřík et al., 2024). Consequently, this management approach alters natural ecosystem dynamics due to the simplification of the environment, increasing landscape homogeneity and reducing structural complexity on different scales by replacing multiple successional stages with even-aged stands. Moreover, it leads to more extreme microclimates and, in contrast to natural disturbances, extracts most of the biota, leaving little biological legacies such as live or dead trees or fallen woody debris which are essential to a wide range of species (Tews et al., 2004).

It is only in the 1970s that a modification was introduced as a reaction to clear-cutting, namely the use of retention patches. According to Simonsson et al. (2015) there are six key factors that define said reaction: public and

international criticism against the practice of clear-cutting, the establishment of threatened species lists (i.e. Red Lists), fear of the forestry sector of harsher restrictions imposed by the government (e.g. more nature reserves), a higher demand of environmentally-friendly forestry by European consumers, the simultaneous development and implementation of retention patches in the Pacific Northwest and finally the creation and implementation of certification schemes in forestry. As the name suggests, either single standing or patches of living and dead trees are retained, harvest stand elements such as stumps, logs and woody debris are preserved and thus complex habitat structure and species richness in the harvested forests are conserved (Hamřík et al., 2024).

A counterweight to the aforementioned forest practices is the implementation of set asides. These excluded and unused forest areas fulfil the purpose of conserving key structural elements such as large trees, dead wood and cavity-bearing trees among other elements and thus conserving structural diversity, a key component of forest biodiversity (Roberge et al., 2015). Today, around 5,2% of the total forested land in Sweden, that is 1,2 million ha, are set aside and used as a complement to formally protected reserves to support conservation of forest biodiversity (Grönlund et al., 2019).

Spiders and carabid beetles are among the many species that rely on structurally diverse landscapes due to certain biological life history traits.

Carabid beetles have been the focus of a myriad of studies in the context of biodiversity and forestry due to their diversity and abundance, a well-studied taxonomy and their highly sensitive nature and fast response times to habitat changes (Niemelä et al., 1993, 2007; Rainio & Niemelä, 2003).

The reliance on habitat structure for spiders is a product of different hunting strategies including active and passive methods depending on the family they belong to. Wolf spiders (*Lycosidae*) are active generalist hunters whereas orb weavers (*Araneidae*) spin webs and wait for prey to get tangled. Both require structural complexity for their hunting method and for prey availability (Moulder & Reichle, 1972).

The aim of this paper is to understand how different forest management methods, namely clear-cutting with and without the retention of trees, differ in community structure and the diversity of spiders and carabids in Swedish boreal forests 30 years after their implementation. This will be achieved by focusing on the following questions:

- Does clear-cutting bring about a reduction in species richness, abundance and evenness in carabid and spider assemblages compared to retention patches and set asides?
- Does the retention method mitigate the possible reduction in the aforementioned alpha diversity metrics?
- Do clear-cuts and retention patches negatively affect community composition (i.e. beta-diversity) compared to the control (i.e. set asides) for both taxa?

Material and Methods

Site selection and sampling design

Sampling was conducted in the Hälsingland municipality in Sweden during June of 2022. 60 plots were designated with an equal division for each forest treatment, meaning 20 plots for old clear-cuts, 20 plots for retention patches and 20 plots in set asides. The old clear-cuts included many saplings and smaller living trees but only few nature value trees or deadwood. Nature value trees were defined as trees that had especially valuable bark structures, cavities or trees that are species of special importance for biodiversity. Comparatively, retention and set aside plots generally included larger living trees, more nature value trees and more deadwood but the type and volume of deadwood recorded differed (e.g. differences in standing and lying deadwood). By the time this study commenced, all plots had been untouched for the last 30 years, i.e. treatments had been conducted 30 years prior to this study. All sites were selected based on the following criteria:

- For each of the three forest treatments, half of the sites were dominated by Norway spruce (*Picea abies*) and the other half by Scots pine (*Pinus sylvestris*).
- Composition of trees not including the dominant species was relatively equal between all sites.
- The location of the forests was focused on mesic to moist soil types while avoiding the wettest and driest forests.

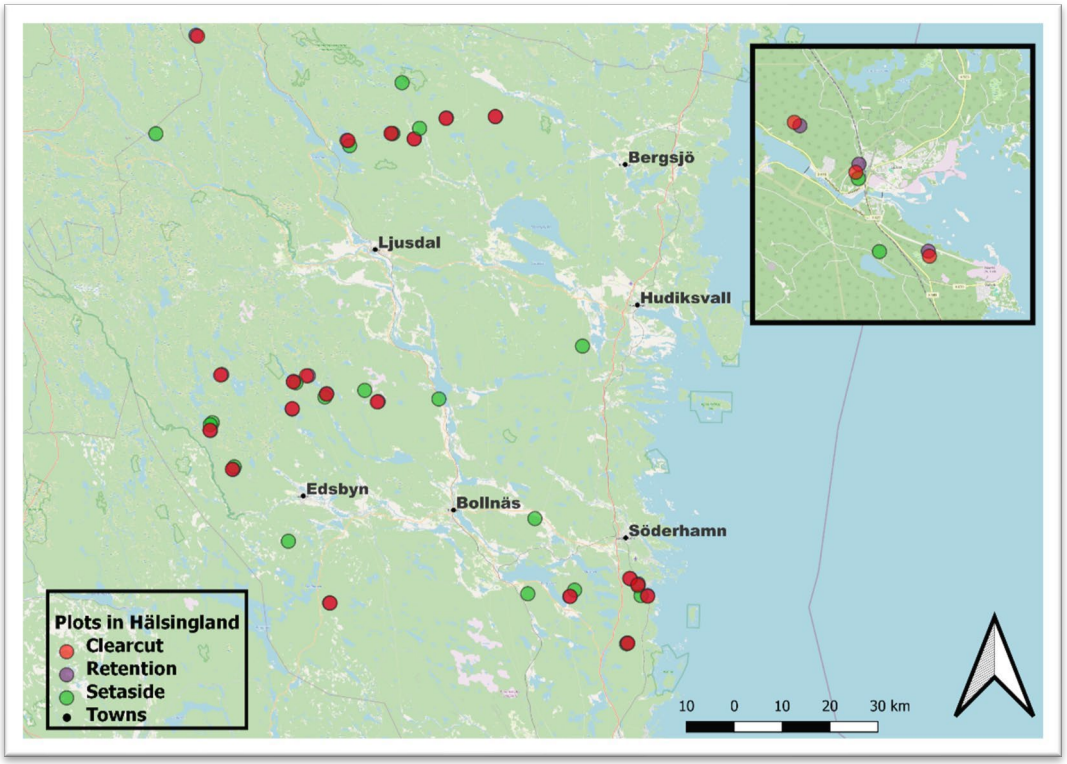

Figure 1: Map of the sampling sites in Hälsingland showing the different forest treatments (e.g. clear-cuts, retention forests and set asides). Given their proximity, most retention patches seem non-existent. A close-up in the upper right corner of the map illustrates their presence. This example represents the batch close to Söderhamn.

Spider and carabid samples were collected using standardized pitfall traps which had a mouth of 80 mm with a capacity of 2-3 dl, a cover of 10 by 10 cm to avoid accumulation of debris and water and contained a strong salt-water solution in addition to a drop of detergent to break the surface tension. Each pitfall sample was made of four cups which, during collection, were pooled (i.e., emptied into the same storage container) and labelled for later identification. Once collected, the samples were cleaned by removing debris and other non-target taxa and then identified to species level using stereomicroscopes ranging from 40x to 90x magnification. Juveniles were recorded to family level but excluded in the analysis given the impossibility of species identification in that life stage.

Plots with missing traps were excluded in both datasets. For the spider dataset, a mix-up during the storage of the *Linyphiidae*, *Theridiidae* and *Cybaeidae* of two plots led to an exclusion of these due to the uncertainty of providence of said individuals. In total, 54 samples were included for the carabids and 52 for the spiders.

Spider samples that could not be identified to species level were identified to genus and grouped as a morphospecies based on their similar physiology and distribution (see *Agyneta cauta/olivacea* and *Walckenaeria*

antica/alticeps in Appendix 1). Adult spiders missing their sexual reproduction organs (i.e. pedipalps or epigyne) were excluded because they cannot be identified with 100% certainty (n=11).

Data analysis

All statistical analysis were realized using R version 4.3.1 (R Core Team, 2023) for the carabid and spider dataset. Moreover, a coverage based rarefaction was implemented using the iNEXT.beta3D package by Chao et al. (2023) to test for any systematic biases in trap effectiveness with treatment.

Alpha diversity metrics, namely species richness, abundance and evenness, were analysed using the “Mass” package (Ripley & Venables, 2025).

In order to understand how forest treatments affect each alpha-diversity metric, generalized linear models (GLM) predicting alpha diversity values using the categorical variable forest treatment were used. A negative binomial regression (identity link) was employed to account for the overdispersion in the data. Additionally, boxplots were used to visualize the result. Pairwise comparisons between the forest treatments were handled using the “emmeans” package (Lenth, 2025) to test which forest types differ significantly in terms of abundance, species richness and evenness.

Two metrics of beta diversity were used which allowed the identification of groups of plots with similar species composition, taking into account the species’ identity and relative abundances, and Jaccard which only considers species identities. Both beta diversity metrics were calculated using the “vegedist” function of “vegan” community ecology package (Oksanen et al., 2022). This served as the basis for the test of homogeneity of group dispersion (i.e. variation among pitfall traps within forest treatments) using the “betadisper” function. The Jaccard dissimilarity was employed to see if rare species change the outcome. The Bray-Curtis metric ignores joint absences (e.g. both samples having joint absences for a given species) while focusing solely on the distribution of existing abundances. In this way, if certain species dominate a few samples, rarer species will be overshadowed. Jaccard, using incidence data, can help highlight differences in species composition per se, rather than being dominated by extremely abundant taxa. An ANOVA was used on the computed spreads (i.e. betadisper) to test the null hypothesis that all treatments have the same mean dispersion. A Tukey HSD compared each pair of groups to see which differ in dispersion.

Furthermore, a PERMANOVA test with 999 permutations was used to test whether the mean community composition differed among the forest

treatments and thus find statistical evidence on the influence of treatment in shaping carabid and spider communities. An important assumption of PERMANOVA is that the multivariate dispersion among groups is homogenous. If groups have significant differences in dispersion, the results may be partly or entirely due to different within-group variability, not different centroids. Therefore, we report results from both betadisper and PERMANOVA.

A 2-dimensional non-metric multidimensional scaling (NMDS) plot was also created based on the Bray-Curtis and Jaccard dissimilarities to illustrate beta diversity using the “vegan” package with respect to the stress value which reflects how well the ordination summarises the observed relative distances among the samples. A weaker stress, the rule of thumb being stress below 0.2, means better quality of representation and thus an adequate fit.

Results

545 carabids were sampled with 22 distinctive species (see Appendix 1). Within the *Carabidae* family, the most abundant species were *Carabus violaceus* (n=114), *Pterostichus oblongopunctatus* (n=114) *and Agonum fuliginosum* (n=81). In total 3188 adult spiders from 18 families and 128 species were collected. The most abundant families in this study were *Linyphiidae* (n=1194) followed by *Lycosidae* (n=1120) and *Gnaphosidae* (n=143). Likewise, species richness was highest in the *Linyphiidae* (n=65), followed by *Lycosidae* and *Gnaphosidae* (both n=14) and the most abundant species were *Pardosa lugubris* (n=524), *Trochosa terricola* (n=351) and *Tapinocyba pallens* (n=307).

Using the iNEXT.beta3D package (Chao et al., 2023), coverage based rarefaction has shown that current sampling ranges from 33% to 100% for carabids and 66% to around 95% for spiders. Several plots (see Appendix 3), particularly in clear-cuts, required almost double the effort to reach standard completeness (SC[2n] > 0.95) whereas others did not improve much with double the effort (see Assemblage T18R and N19C in spiders, Appendix 3).

Species richness, total abundance and evenness (i.e. alpha diversity)

Carabids

Species richness

The negative-binomial generalized linear model revealed that forest treatment did not significantly affect carabid species richness (likelihood-ratio χ^2_2 = 1.25, P = 0.54). Estimated marginal means of species per plot were highest in set asides (3.30 ± 0.41 SE), followed by clear-cuts (2.85 ± 0.55), and lowest in retention stands (2.69 ± 0.58). Tukey-adjusted pairwise contrasts confirmed the absence of differences between set asides and clear-cuts (estimate = 0.45 ± 0.56, z = 0.81, P = 0.70), set asides and retention (0.61 ± 0.58, z = 1.06, P = 0.54), and clear-cuts versus retention (0.16 ± 0.56, z = 0.29, P = 0.95).

Total abundance

In contrast, total carabid abundance per plot differed clearly among treatments. The negative-binomial GLM showed a significant overall effect (likelihood-ratio χ^2_2 = 18.65, P < 0.001). Set asides had on average 16.0 ± 2.82 SE individuals, whereas clear-cuts and retention stands supported 5.65 ± 3.02 and 7.00 ± 3.18, respectively (i.e. reductions of 10.35 and 9.00 individuals relative to set aside). Post-hoc Tukey tests confirmed that set asides had significantly greater abundance than clear-cuts (difference = 10.35 ± 3.02, z = 3.42, P = 0.0018) and retention plots (9.00 ± 3.18, z = 2.83, P = 0.0129), while clear-cuts and retention stands did not differ from one another (-1.35 ± 1.82, z = -0.74, P = 0.74).

Evenness

Pielou's evenness was analysed with a Gaussian linear model. Neither the overall F-test ($F_{2,41}$ = 0.44, P = 0.65) nor pairwise Tukey comparisons detected differences among treatments. Mean evenness was 0.820 ± 0.058 in set asides, 0.853 ± 0.085 in clear-cuts, and 0.905 ± 0.090 in retention stands; contrasts between set asides and clear-cuts (-0.033 ± 0.085, t = -0.39, P = 0.92), set asides and retention (-0.084 ± 0.090, t = -0.93, P = 0.62), and clear-cuts versus retention (-0.052 ± 0.093, t = -0.56, P = 0.84) were all non-significant.

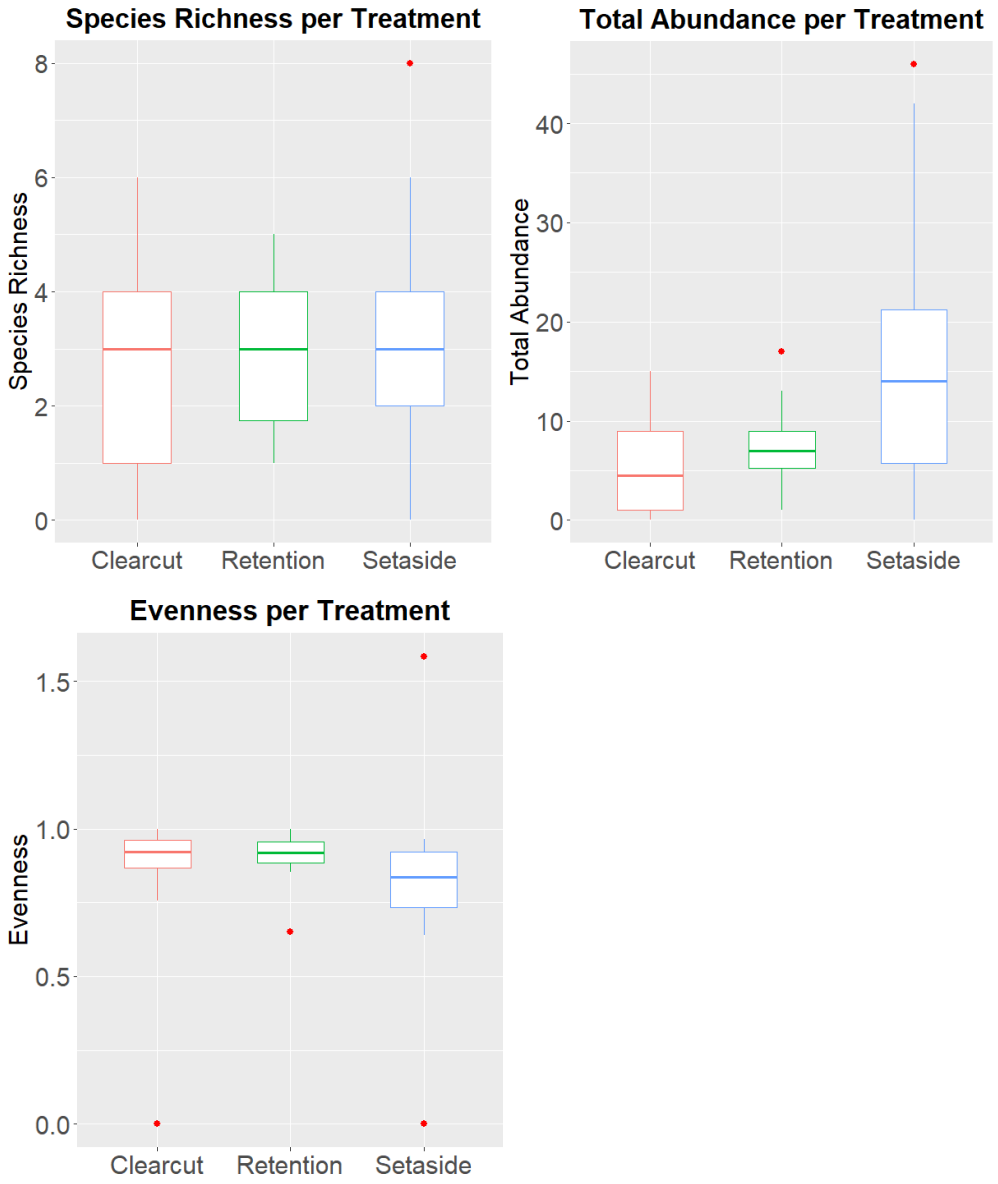

Figure 2: Effect of forest treatment on species richness, total abundance and evenness of carabids. The median values are depicted as a line in the box which represents 50% of the data distribution. The vertical lines show the extreme upper and lower 25% of data.

Spiders

Species richness

The negative-binomial GLM showed no overall effect of forest treatment on spider species richness (likelihood-ratio χ^2_2 = 1.80, P = 0.41). Estimated marginal means were highest in clear-cuts (18.94 ± 1.93 SE species per plot), intermediate in retention stands (17.69 ± 1.91), and lowest in set asides (16.37 ± 1.25). Tukey-adjusted pairwise contrasts confirmed that none of the differences reached significance (set aside vs. clear-cut: -2.57 ± 1.93, z = -1.33, P = 0.38; set aside vs. retention: -1.32 ± 1.91, z = -0.69, P = 0.77; clear-cut vs. retention: 1.25 ± 2.06, z = 0.61, P = 0.82).

Total abundance

By contrast, total spider abundance differed significantly among treatments (likelihood-ratio χ^2_2 = 9.21, *P* = 0.01). Set asides showed an average of 42.32 ± 5.19 SE individuals per plot, clear-cuts 70.47 ± 10.37, and retention stands 64.50 ± 9.95 (i.e. +28.15 and +22.18 individuals relative to set asides). Post-hoc Tukey tests showed clear-cuts held significantly more spiders than set asides (difference = -28.15 ± 10.40, *z* = -2.72, *P* = 0.018), retention stands were marginally higher (-22.18 ± 9.95, *z* = -2.23, *P* = 0.066), and clear-cuts and retention did not differ (5.97 ± 12.40, *z* = 0.48, *P* = 0.88).

Evenness

Pielou's evenness was analysed with a Gaussian linear model. Neither the overall F-test ($F_{2,49}$ = 0.97, *P* = 0.39) nor pairwise Tukey contrasts detected treatment differences. Mean evenness was 0.942 ± 0.016 in set asides, 0.925 ± 0.023 in clear-cuts, and 0.910 ± 0.023 in retention stands; contrasts between set asides and clear-cuts (0.017 ± 0.023, *t* = 0.75, *P* = 0.73), set asides and retention (0.032 ± 0.023, *t* = 1.38, *P* = 0.36), and clear-cuts versus retention (0.015 ± 0.024, *t* = 0.63, *P* = 0.81) were all non-significant.

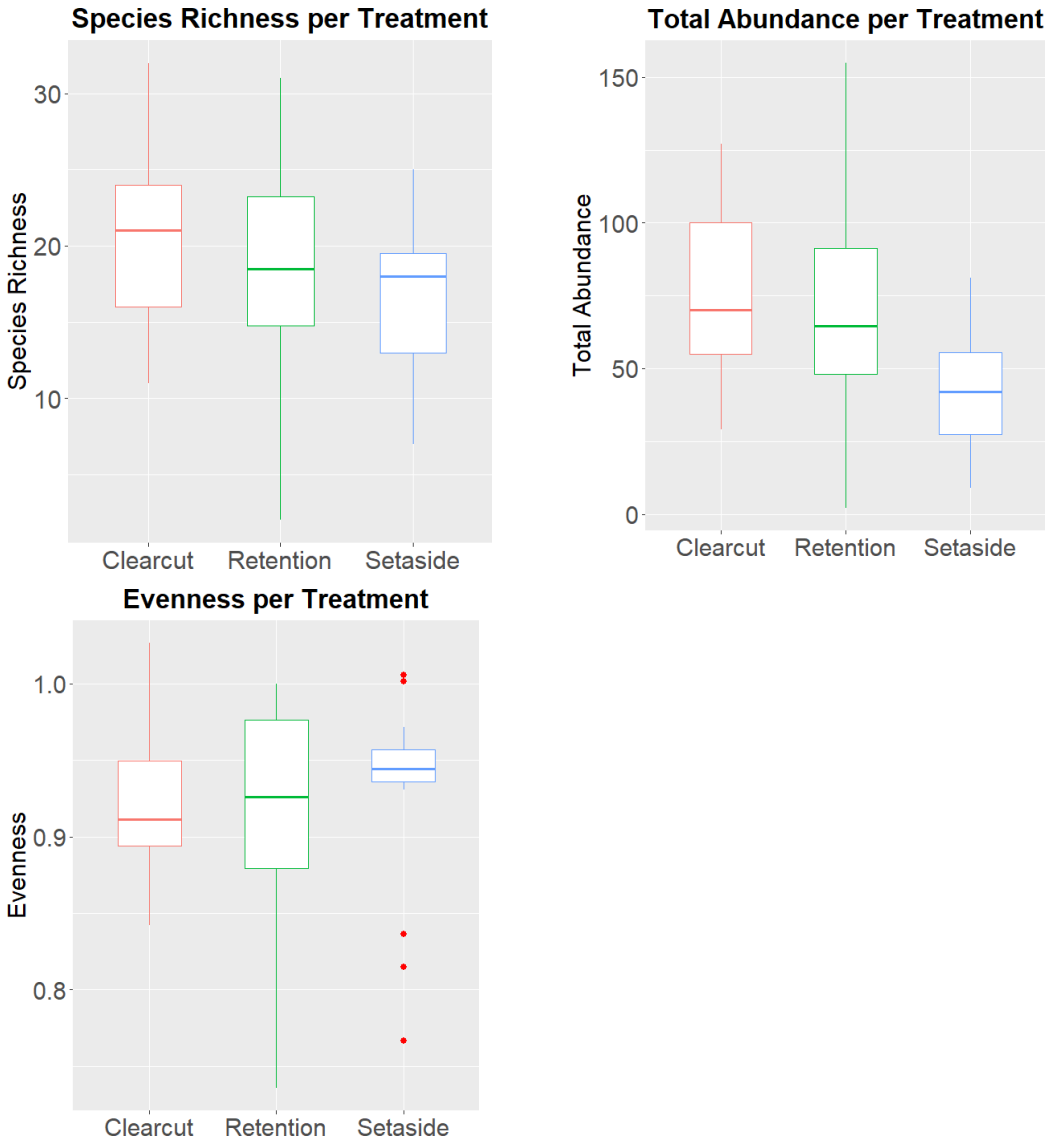

Figure 3: Effect of forest type on species richness, total abundance and evenness of spiders. The median values are depicted as a line in the box which represents 50% of the data distribution. The vertical lines show the extreme upper and lower 25% of data distribution and any outliers are figuring as red dots.

Assemblage composition (i.e. beta diversity)

Carabids

Multivariate dispersion, assessed as the average distance to the group centroid, did not show any significant difference among treatments (Table 2, ANOVA P=0.80) and Tukey adjusted pairwise contrasts were non-significant (all P >/= 0.79). Moreover, PERMANOVA analysis showed a small but statistically significant effect of forest treatment on species abundance composition for carabids (Table 1). Therefore, PERMANOVA reflects genuine shifts in community centroids rather than unequal within-group variability. These results are also reflected in the NMDS (Figure 5).

On the other hand, PERMANOVA under the Jaccard distance matrix, found no statistically significant effect of treatment. Comparatively, dispersion among groups was homogenous (Table 2) and Tukey comparisons on those distances were all non-significant (P >/= 0.31). This is again reflected in the NMDS (Figure 6).

Spiders

PERMANOVA for both Bray-Curtis and Jaccard showed high significance (Table 1), indicating differences in spider communities in both abundance and incidence composition among treatments. Multivariate dispersion was homogenous for Bray-Curtis (Table 2, ANOVA P=0.16) and Tukey adjusted pairwise contrasts were also non-significant (all P >/= 0.14).

However, even though dispersion for Jaccard (Table 2) did not show much variation, the ANOVA test showed significant variation (P=0.041) and Tukey adjusted pairwise comparison (Appendix 2) showed significant variation only between set asides and clear-cuts (Padj=0.047).

Table 1: PERMANOVA results showing the effect of forest treatment on spider and carabid assemblages.

Group	Metric	Variable	Sum of Sqrs	Df	R2	F	P
	Bray-Curtis	Forest treatment	1.0708	2	0.06	1.59	0.047
		Residual	17.2245	51	0.94		
		Total	18.2954	53	1		
	Jaccard	Forest treatment	0.7078	2	0.04	1.07	0.352
		Residual	16.8125	51	0.96		
		Total	17.5203	53	1		
Spiders	**Bray-Curtis**	Forest treatment	1.5333	2	0.11	2.99	0.001
		Residual	12.5756	49	0.89		
		Total	14.1089	51	1		
	Jaccard	Forest treatment	1.1663	2	0.08	2.00	0.001
		Residual	14.2603	49	0.92		
		Total	15.4266	51	1		

Table 2: Results of the BETADISPER model showing comparable distances to the group centroids

Carabids	**Bray-Curtis**	**Average distance to median**		
		Clearcut	Retention	Setaside
		0.5541	0.5647	0.5348
	Jaccard	0.5567	0.5725	0.5034
Spiders	**Bray-Curtis**	**Average distance to median**		
		Clearcut	Retention	Setaside
		0.4392	0.4855	0.5115
	Jaccard	0.4791	0.5329	0.5410

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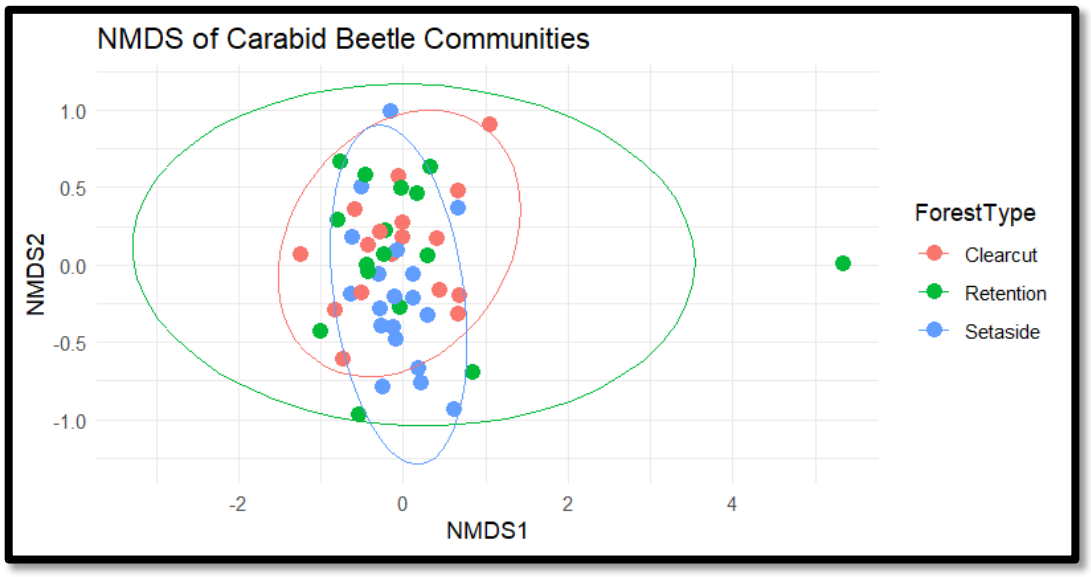

Figure 4: Carabid NMDS based on Bray-Curtis's distance matrix. The small shift of treatments along NMDS1 represents the small but significant shift detected by PERMANOVA ($R^2 \approx 0.06$, $P = 0.046$). The three ellipses overlapping shows that there is no difference in within-group spread (ANOVA P=0.8).

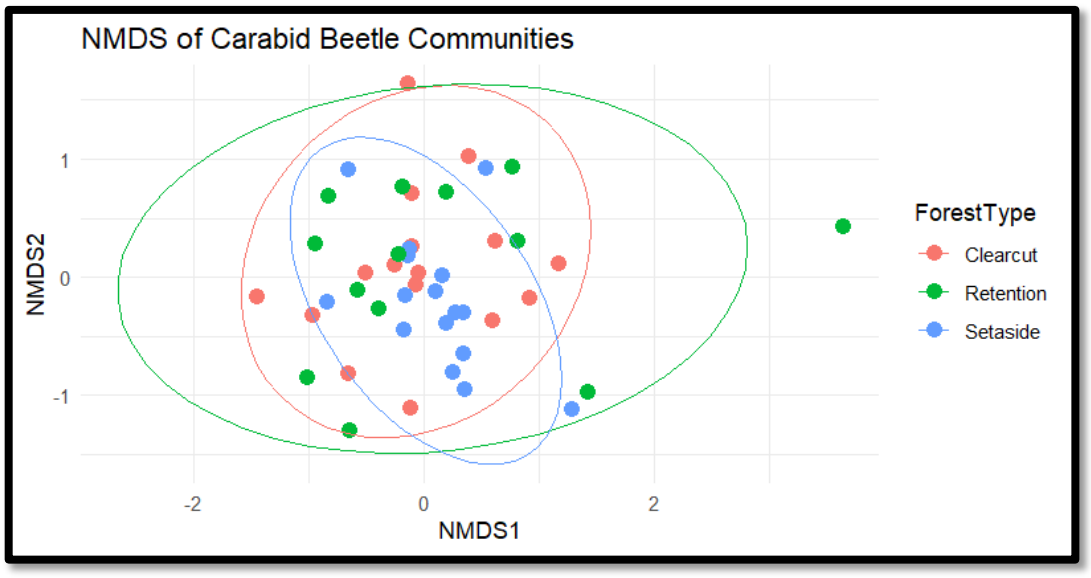

Figure 5: Carabid NMDS based on Jaccard distance matrix. Here the treatments are clustered together with no directional separation of centroids, consistent with the non-significant PERMANOVA ($R^2 \approx 0.04$, $P = 0.345$) and homogenous dispersion (ANOVA P=0.30).

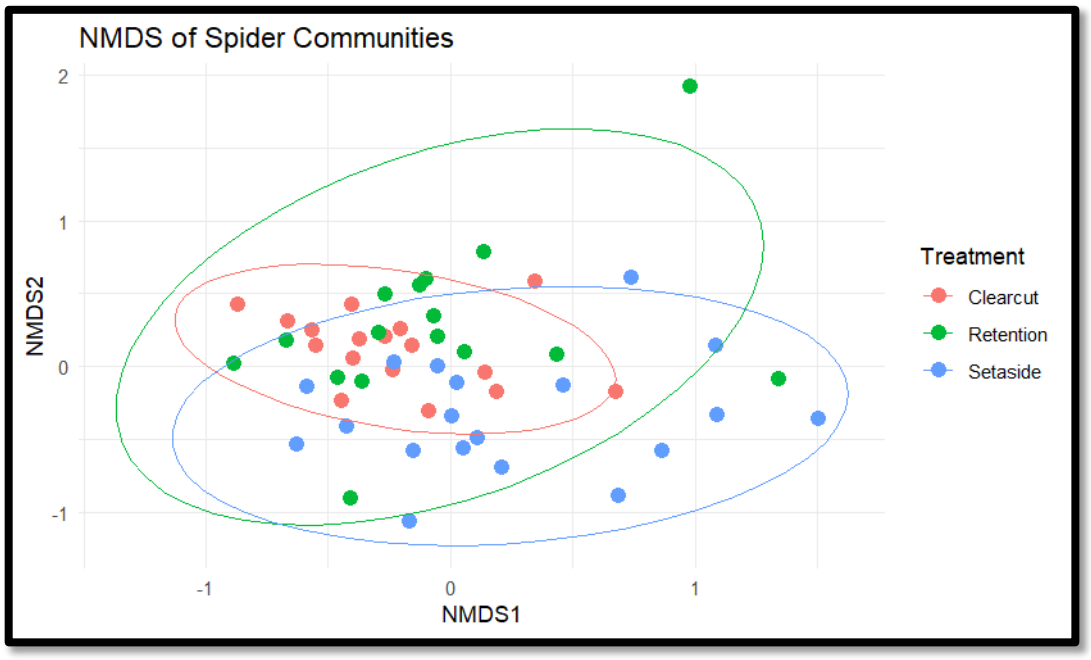

Figure 6: Spider NMDS based on Bray-Curtis distance matrix. The separation of clouds along the ordination reflects the strong PERMANOVA effect ($R^2 \approx 0.11$, $P = 0.001$) and equally uniform dispersion (ANOVA P=0.16).

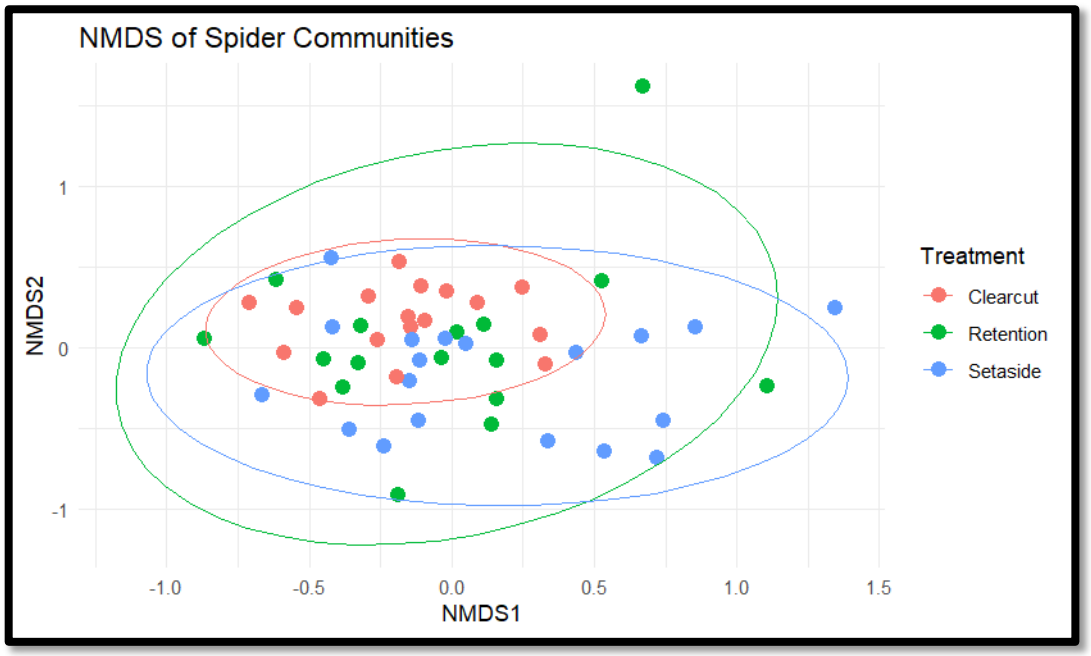

Figure 7: Spider NMDS based on Jaccard distance matrix. Set aside points spread more widely reflecting the significantly higher dispersion in incidence data (ANOVA P=0.041). The significant Jaccard PERMANOVA ($R^2 \approx 0.076$, $P = 0.001$) is reflected by the clear non-overlap of centroids.

Discussion

This study investigated how clear-cutting, retention patches and set asides differ in regards to carabid beetle and spider communities in Swedish boreal forests 30 years post-implementation. The findings revealed taxon-specific responses to forest management treatments across multiple aspects of diversity, providing insights into the ecological implications of different forestry strategies.

Alpha Diversity: Contrasting Patterns in Abundance

Our results showed that species richness and evenness remained unaffected by forest treatment in both spiders and carabids. Only abundance showed significant differences for both studied taxa. Interestingly, the results showed opposite trends between those studied groups. Carabids showed highest numbers in set asides followed by retention patches and clear-cuts. On the other hand, spider abundances were highest in clear-cuts, followed by retention patches and lowest in set asides.

One explanation of the carabid abundance distribution is the broad categorisation of beetles into open-habitat species, forest generalists and mature forest specialists (Belluz et al., 2022) and the drastic change in canopy cover 20 to 30 years post-implementation as described in Niemelä et al. (2007). After this period, canopy closure drives out open-habitat species and usually species that are dependent on mature forest stands with stable microhabitats and complex litter structures replace them. However, as previously mentioned, clear-cutting is a high disturbance practice which alters habitat structure by removing most of the forest components and scarring the soil. Not only does this alter microclimate resulting in higher temperatures and lower humidity but also leads to habitat fragmentation (e.g. break in deadwood and continuous litter) and ultimately affects prey communities. The clear-cuts and retention patches may therefore lack sufficient structural complexity, microclimatic stability, or prey availability required by forest adapted species even after three decades (Kotze & O'Hara, 2003).

In the case of spiders, previous studies have reported that particularly wolf spiders (*Lycosidae*), are well adapted to colonise and maintain viable populations in highly disturbed environments and that this effect is not limited to recent disturbances alone (Larrivée et al., 2005, Paradis & Work, 2011, Pearce et al., 2004 in Bouchard & Hébert, 2021). Their ability to quickly colonize new habitats is a result of their wandering behaviour coupled with their visual and active hunting strategy as well as the use of

“ballooning”, a technique in which webs act as balloons allowing areal dispersion through wind movements (McIver et al., 1992). The two most abundant species in this study were *Paradosa lugubris* and *Trochosa terricola* which both belong to the previously mentioned family (Appendix 1). This being said, the higher abundance in clear-cuts does not necessarily indicate a richer or functionally stable community but rather a numerical dominance existing because of a few generalist species. This might indicate that clear-cutting acts as an ecological filter, favouring disturbance adapted species over forest specialists.

Mitigating Effects of Retention Patches

Given the slightly higher abundances of carabid beetles in retention patches, we can conclude that the latter practice only partially mitigates the loss of individuals caused by clear-cutting. This does not hold true for the spiders where total abundances showed slight reductions in retention patches compared to the clear-cuts. One theory that can explain both outcomes is that the retention patches acted as “archipelagos” with higher structural complexity that facilitated the recolonisation of clear-cuts for spiders (Hamřík et al., 2024) but also acted as “life boats” for carabid beetles which helped preserving part of the original community structure (Fedrowitz et al., 2014; Skłodowski, 2021). This being said, species richness and evenness remained unaffected, which may point to an early successional or simplified structure even decades after disturbance and this suggests that retention patches do not restore community composition to pre-disturbance conditions.

It is important to consider here that the effectiveness of retention patches is highly debated (Fedrowitz et al., 2014; Gustafsson et al., 2010; Skłodowski, 2021) and depends on many factors such as forest age, forest cover type (i.e. deciduous or coniferous), the proportion of retained trees (%), the size of retention and the choice of spatial arrangement of trees (i.e. aggregated islands or dispersed, single trees (Hamřík et al., 2024; Roberge et al., 2015; Sultaire et al., 2021), information that has not been considered in this study.

Beta-Diversity and Community Composition

The exploration of negative treatment effects on community composition (i.e. beta-diversity) has yielded complex and taxon-specific results.

Carabid composition showed significant differences in abundance structure but not in species composition. This implies that the same species persisted across treatments. This resilience in presence/absence is supported by long-term carabid research in boreal forests. Belluz et al. (2022) and Niemelä et al. (2007) reported that carabids are able to recolonize clear-cut

and retention stands relatively quickly due to their mobility and generalist traits but that species typically found in closed-canopy forests often remain rare and underrepresented for several decades. This is also reflected in this study where clear-cuts and retention patches are still missing the abundance structure of set asides, though the species pool itself seems intact. This also suggests dominance of generalists in the regional species pool, masking losses of rarer specialists. Moreover, the size and distribution of retention patches is important. Sultaire et al. (2021) found that small patches may act as ecological traps or “micro-edge” environments that mimic open areas, rather than true refuges. Thus, the lack of significant Jaccard-based differences may reflect the persistence of highly mobile or generalist species, not necessarily the full recovery of the community structure.

For spiders, both Bray-Curtis and Jaccard-based PERMANOVA tests revealed statistically significant effects of treatment, implying that forest management influences both abundance structure and species identity. NMDS ordinations further confirm this separation among treatments, indicating long-term divergence in spider assemblages even 30 years post-disturbance. These shifts likely reflect replacement of forest specialists by generalists or open-habitat species, particularly members of *Lycosidae* and *Linyphiidae* which dominate clear-cut and retention plots. These results are reflected in Larrivée et al. (2005) who reported that spider assemblages in clear-cuts were significantly different from those of un-treated stands, even years after logging, due to changes in microclimatic conditions and loss of vertical structures. Furthermore, Elek et al. (2018) demonstrated that spiders showed greater sensitivity than carabids to clear-cutting and retention practices, particularly in terms of species turn-over. The findings of this study support this given the increased dissimilarity between clear-cuts and set asides under the Jaccard index and confirm that even 30 years post treatment, legacy effects persist.

The difference in multivariate dispersion between set asides and clear-cuts may suggest that spider communities in disturbed areas are not only different on average but also more heterogenous, potentially due to patchy recolonization, edge effects or unstable environmental conditions (Paradis & Work, 2011; Pearce et al., 2004).

Study Limitations and implementations for future studies

The limitation of this study lies in the first place in the use of only one variable, this being forest treatment. This oversimplifies the ecological reality as multiple interacting factors are responsible for shaping community

composition. Some of the important factors include canopy cover and vertical complexity which affect temperature, humidity and light input (Tews et al., 2004), deadwood abundance and quality (Roberge et al., 2015) and landscape context and connectivity which influences recolonization rates and population viability (Hamřík et al., 2024).

Another important consideration regards the lack of information of development since implementation. Even though we consider the different treatments to be undisturbed for the last 30 years, it goes without saying that environmental impacts alter development of the stands. The lack of historical and timely legacies denies the inference of successional trajectories or temporal stability of the carabid and spider communities. To fully understand recovery trajectories and thus the effect of treatments, longer ecological monitoring is needed.

Finally, there is a need for increased effort to reach full sample coverage in some plots. The current heterogeneity in sample completeness introduces potential bias in richness estimates and reduces power to detect real treatment effects. Although rarefaction improves comparability, future studies should ensure higher and more uniform trapping effort per plot, particularly in clear-cuts.

Conclusion and management implications

Three decades after the implementation of the forestry practices, clear-cuts still favour disturbance-tolerant species while retention patches only partially reestablish carabid abundances but do not restore community structure to set aside conditions for either taxon. To promote both beetle and spider diversity, future forestry management and the continued study of their practices need to continue taking into account retention effects by increasing retention size and structural complexity and promoting connectivity. Long-term monitoring of canopy cover, deadwood resources and in general landscape context is essential to refine retention designs and ensure true recovery of assemblages over time.

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Popular Science Summary

The management of our forests is often a means to an end. We want to extract trees for different purposes but after that, we don't really think about what it does to the residents of our forests.

This research looks at the differences in spider and beetle diversity and community structure after three decades in three different forest management practices. These include old undisturbed forests (i.e. set asides), clear-cuts where all natural elements have been cut down and retention patches which retain a certain amount of trees.

We found that beetles are most abundant in the undisturbed areas whereas spiders, especially wolf spiders, are most abundant in clear-cuts. However, the number of different species (species richness) and how evenly they were distributed (evenness) didn't change much across forest types. It is interesting to see that, while beetle communities remained relatively stable regardless of forest type, spider communities changed noticeably, showing that some species benefit from disturbance, while others disappear.

Retention patches showed some benefits but didn't fully recreate the biodiversity seen in untouched forests. These findings suggest that while retention forestry helps, it's not a substitute for protecting natural habitats when it comes to conserving biodiversity, even decades after logging.

Appendix 1: Species and species abundance list

Table 3: Carabid species abundances for each of the forest treatments and total abundances.

Species	Clearcut	Retention	Setaside	Total
Carabus violaceus	29	31	54	114
Pterostichus oblongopunctatus	14	12	88	114
Agonum fuliginosum	15	10	56	81
Calathus micropterus	26	16	31	73
Carabus hortensis	6	9	29	44
Cychrus caraboides	3	15	16	34
Carabus coriaceus	4	0	26	30
Pterostichus niger	5	8	0	13
Carabus glabratus	2	0	8	10
Carabus nemoralis	0	0	6	6
Amara aenea	2	1	0	3
Loricera pilicornis	0	2	1	3
Notiophilus reitteri	0	1	2	3
Pterostichus nigrita	0	0	3	3
Pterostichus strenuus	3	0	0	3
Notiophilus germinyi	1	1	0	2
Notiophilus palustris	1	1	0	2
Patrobus assimilis	0	2	0	2
Pterostichus melanarius	0	2	0	2
Amara brunnea	1	0	0	1
Harpalus laevipes	1	0	0	1
Nothiophilus aestuans	0	1	0	1

Table 4: Spider species abundances for each of the forest treatments and total abundances.

Family	Species	Retention	Setaside	Clearcut	Total
Lycosidae	*Pardosa lugubris*	301	42	181	524
Lycosidae	*Trochosa terricola*	93	88	170	351
Linyphiidae	*Tapinocyba pallens*	86	91	130	307
Linyphiidae	*Pocadicnemis pumila*	34	20	93	147
Linyphiidae	*Walckenaeria dysderoides*	38	35	51	124
Liocranidae	*Agroeca brunnea*	22	69	22	113
Miturgidae	*Zora spinimana*	46	23	19	88
Linyphiidae	*Centromerus arcanus*	23	36	23	82
Lycosidae	*Alopecosa taeniata*	33	9	39	81

Lycosidae	*Alopecosa aculeata*	20	6	54	80
Linyphiidae	*Walckenaeria cucullata*	21	19	38	78
Tetragnathidae	*Pachygnatha listeri*	7	33	30	70
Linyphiidae	*Minyriolus pusillus*	13	25	27	65
Linyphiidae	*Agyneta cauta/olivacea*	18	4	38	60
Theridiidae	*Euryopis flavomaculata*	28	12	18	58
Miturgidae	*Zora nemoralis*	19	9	21	49
Gnaphosidae	*Haplodrassus soerenseni*	28	5	9	42
Lycosidae	*Piratula uliginosa*	3	11	24	38
Lycosidae	*Pardosa sphagnicola*	10	12	15	37
Linyphiidae	*Diplocentria bidentata*	10	16	10	36
Lycosidae	*Pardosa riparia*	18	0	17	35
Cybaeidae	*Cryphoeca silvicola*	11	21	1	33
Linyphiidae	*Tenuiphantes alacris*	8	8	17	33
Linyphiidae	*Walckenaeria mitrata*	4	4	19	27
Thomisidae	*Xysticus audax*	8	9	10	27
Thomisidae	*Ozyptila trux*	10	11	5	26
Gnaphosidae	*Micaria aenea*	3	2	19	24
Linyphiidae	*Dicymbium tibiale*	3	8	13	24
Linyphiidae	*Abacoproeces saltuum*	12	6	5	23
Lycosidae	*Alopecosa pinetorum*	3	19	1	23
Gnaphosidae	*Haplodrassus signifer*	6	4	12	22
Gnaphosidae	*Zelotes clivicola*	3	5	12	20
Linyphiidae	*Microneta viaria*	8	3	8	19
Linyphiidae	*Macrargus rufus*	5	9	4	18
Linyphiidae	*Semljicola faustus*	3	15	0	18
Linyphiidae	*Walckenaeria antica/alticeps*	5	0	12	17
Lycosidae	*Alopecosa pulverulenta*	12	1	4	17
Linyphiidae	*Agyneta conigera*	7	9	0	16
Amaurobiidae	*Amaurobius fenestralis*	9	6	0	15

Gnaphosidae	*Gnaphosa bicolor*	3	0	12	15
Linyphiidae	*Bathyphantes parvulus*	6	1	8	15
Linyphiidae	*Oryphantes angulatus*	1	5	6	12
Salticidae	*Evarcha falcata*	1	8	3	12
Linyphiidae	*Agyneta ramosa*	1	10	0	11
Segestriidae	*Segestria senoculata*	4	3	4	11
Theridiidae	*Robertus scoticus*	2	8	0	10
Thomisidae	*Xysticus luctuosus*	1	3	6	10
Thomisidae	*Xysticus obscurus*	2	4	4	10
Linyphiidae	*Diplocentria rectangulata*	0	5	4	9
Linyphiidae	*Walckenaeria cuspidata*	3	3	3	9
Linyphiidae	*Cnephalocotes obscurus*	1	1	6	8
Linyphiidae	*Oreonetides vaginatus*	1	6	1	8
Hahniidae	*Hahnia ononidum*	2	2	2	6
Linyphiidae	*Asthenargus paganus*	1	4	1	6
Phrurolithidae	*Phrurolithus festivus*	0	0	6	6
Linyphiidae	*Ceratinella brevis*	0	2	3	5
Linyphiidae	*Hilaira herniosa*	0	5	0	5
Linyphiidae	*Tenuiphantes tenebricola*	1	4	0	5
Linyphiidae	*Walckenaeria karpinskii/clavicornis*	1	4	0	5
Liocranidae	*Apostenus fuscus*	0	4	1	5
Gnaphosidae	*Drassodes cupreus*	3	0	1	4
Gnaphosidae	*Drassodes pubescens*	1	0	3	4
Linyphiidae	*Agyneta suecica*	2	0	2	4
Linyphiidae	*Diplocephalus picinus*	3	1	0	4
Linyphiidae	*Gonatium rubellum*	2	2	0	4
Linyphiidae	*Hilaira pervicax*	3	1	0	4
Linyphiidae	*Tenuiphantes cristatus*	0	2	2	4
Linyphiidae	*Zornella cultrigera*	1	3	0	4
Lycosidae	*Piratula hygrophila*	1	3	0	4
Theridiidae	*Robertus lividus*	3	0	1	4

Clubionidae	*Clubiona comta*	2	1	0	3
Clubionidae	*Clubiona subsultans*	1	1	1	3
Gnaphosidae	*Gnaphosa leporina*	0	0	3	3
Gnaphosidae	*Gnaphosa muscorum*	0	2	1	3
Linyphiidae	*Diplocephalus latifrons*	1	1	1	3
Linyphiidae	*Maro minutus*	3	0	0	3
Linyphiidae	*Micrargus apertus*	1	0	2	3
Linyphiidae	*Oedothorax gibbosus*	0	0	3	3
Linyphiidae	*Palliduphantes antroniensis*	2	1	0	3
Linyphiidae	*Pelecopsis mengei*	3	0	0	3
Linyphiidae	*Porrhomma pallidum*	1	1	1	3
Linyphiidae	*Walckenaeria atrotibialis*	1	0	2	3
Lycosidae	*Trochosa spinipalpis*	1	2	0	3
Pisauridae	*Pisaura mirabilis*	0	0	3	3
Clubionidae	*Clubiona kulczynskii*	0	0	2	2
Gnaphosidae	*Zelotes subterraneus*	1	0	1	2
Linyphiidae	*Agyneta subtilis*	0	2	0	2
Linyphiidae	*Centromerus brevipalpus*	1	1	0	2
Linyphiidae	*Ceratinella brevipes*	1	0	1	2
Linyphiidae	*Gonatium rubens*	1	0	1	2
Linyphiidae	*Stemonyphantes lineatus*	0	0	2	2
Linyphiidae	*Walckenaeria nudipalpis*	1	1	0	2
Linyphiidae	*Walckenaeria unicornis*	0	0	2	2
Lycosidae	*Acantholycosa lignaria*	0	0	2	2
Mimetidae	*Ero furcata*	0	1	1	2
Salticidae	*Neon reticulatus*	1	1	0	2
Araneidae	*Cercidia prominens*	1	0	0	1
Gnaphosidae	*Drassyllus pusillus*	0	0	1	1
Gnaphosidae	*Gnaphosa montana*	0	0	1	1
Gnaphosidae	*Micaria pulicaria*	0	1	0	1

Gnaphosidae	*Zelotes latreillei*	1	0	0	1
Linyphiidae	*Agyneta affinis*	1	0	0	1
Linyphiidae	*Bathyphantes gracilis*	0	1	0	1
Linyphiidae	*Bathyphantes nigrinus*	0	1	0	1
Linyphiidae	*Centromerus sylvaticus*	0	0	1	1
Linyphiidae	*Evansia merens*	1	0	0	1
Linyphiidae	*Hilaira nubigena*	0	1	0	1
Linyphiidae	*Lophomma punctatum*	0	1	0	1
Linyphiidae	*Maso sundevalli*	0	1	0	1
Linyphiidae	*Micrargus herbigradus*	1	0	0	1
Linyphiidae	*Neriene clathrata*	0	0	1	1
Linyphiidae	*Nusoncus nasutus*	1	0	0	1
Linyphiidae	*Obscuriphantes obscurus*	0	1	0	1
Linyphiidae	*Palliduphantes pallidus*	1	0	0	1
Linyphiidae	*Pelecopsis elongata*	1	0	0	1
Linyphiidae	*Pelecopsis parallela*	1	0	0	1
Linyphiidae	*Peponocranium ludicrum*	0	0	1	1
Linyphiidae	*Walckenaeria obtusa*	0	1	0	1
Liocranidae	*Agroeca proxima*	1	0	0	1
Lycosidae	*Pardosa pullata*	0	1	0	1
Lycosidae	*Xerolycosa nemoralis*	0	0	1	1
Salticidae	*Euophrys frontalis*	0	0	1	1
Tetragnathidae	*Metellina merianae*	1	0	0	1
Theridiidae	*Crustulina guttata*	1	0	0	1
Theridiidae	*Pholcomma gibbum*	0	1	0	1
Theridiidae	*Phycosoma inornatum*	0	0	1	1
Theridiidae	*Robertus lyrifer*	0	1	0	1
Thomisidae	*Ozyptila atomaria*	0	0	1	1

Appendix 2: TukeyHSD tables

Table 5: Pairwise comparisons between the forest treatments using the "emmeans" package to test which forest types differ significantly in terms of abundance, species richness and evenness.

Tukey Comparison				
Abundance				
Comparison	Estimate	SE	Z.Ratio	P.Value
Setaside-Clearcut	10.35	3.02	3.423	0.0018
Setaside-Retention	9.00	3.18	2.829	0.0129
Clearcut-Retention	-1.35	1.82	-0.740	0.7397
Species Richness				
Comparison	Estimate	SE	Z.Ratio	P.Value
Setaside-Clearcut	0.450	0.555	0.811	0.6959
Setaside-Retention	0.613	0.577	1-061	0.5381
Clearcut-Retention	0.163	0.557	0.292	0.9542
Evenness				
Comparison	Estimate	SE	T.Ratio	P.Value
Setaside-Clearcut	-0.03	0.0850	-0.386	0.9213
Setaside-Retention	-0.08	0.0904	-0.934	0.6225
Clearcut-Retention	-0.05	0.0929	-0.556	0.8442

Table 6: Tukey multiple comparison of means compares each pair of treatments to see which differ in dispersion. It displays the mean difference in mean distances to centroid, lower and upper confidence intervals and p-values which reflect statistical significance.

Tukey multiple comparison of means				
Carabids-Bray-Curtis				
Comparison	Mean difference	Lower CI	Upper CI	Adjusted p
Retention-Clearcut	0,0106	-0,1005	0,1218	0,9711
Setaside-Clearcut	-0,0193	-0,1256	0,0870	0,8998
Setaside-Retention	-0,0299	-0,1410	0,0812	0,7935
Carabids-Jaccard				
Comparison	Mean difference	Lower CI	Upper CI	Adjusted p

Retention-Clearcut	0,0158	-0,0970	0,1285	0,9393
Setaside-Clearcut	-0,0534	-0,1612	0,0544	0,4614
Setaside-Retention	-0,0691	-0,1819	0,0436	0,3087

Spider-Bray-Curtis

Comparison	Mean difference	Lower CI	Upper CI	Adjusted p
Retention-Clearcut	0,0463	-0,0483	0,1410	0,4686
Setaside-Clearcut	0,0723	-0,0184	0,1630	0,1421
Setaside-Retention	0,0260	-0,0662	0,1181	0,7759

Spider-Jaccard

Comparison	Mean difference	Lower CI	Upper CI	Adjusted p
Retention-Clearcut	0,0538	-0,0100	0,1176	0,1141
Setaside-Clearcut	0,0619	0,0007	0,1230	**0,0467**
Setaside-Retention	0,0081	-0,0540	0,0703	0,9466

Appendix 3: Coverage-based rarefaction table

Table 7: Coverage-based rarefaction using the DataInfobet3D function of the iNEXT.beta3D package. This function is used to evaluate the completeness and comparability of species sampling across different forest treatments. It helps determine how thoroughly each plot's species diversity was captured and whether increased sampling would yield more species. n determines the sample size, or the number of individuals sampled in a given plot (i.e. assemblage), S.obs is the number of observed species in the sample, SC(n) reflects the sample coverage estimate at the observed sample size with values close to 1 signifying almost complete sampling, SC(2n) shows the projected coverage if the sampling effort were doubled (i.e. assessment of how much more would be gained by further effort) and f1-5 reflects the number of species found in 1, 2, 3, 4 and 5 individuals, respectively. These are frequency counts of rare species and are used in estimating undetected species. Bold numbers show low coverage and highlighted numbers in red show assemblages where doubling the coverage still doesn't result in more representative sampling.

Carabids

Dataset	Assemblage	n	S.obs	SC(n)	SC(2n)	f1	f2	f3	f4	f5
Clearcut	H5O	14	3	1,000	1,000	1	0	0	1	0
Clearcut	H7O	14	5	0,867	0,953	2	1	0	1	0
Clearcut	HJ1O	2	2	0,667	0,963	2	0	0	0	0
Clearcut	HL10O	1	1	1,000	1,000	1	0	0	0	0
Clearcut	HL13O	5	4	**0,486**	0,762	3	1	0	0	0
Clearcut	HL1O	6	4	0,583	0,860	3	0	1	0	0
Clearcut	HL21O	9	6	**0,477**	0,697	5	0	0	1	0
Clearcut	HL81O	13	4	0,934	0,991	1	1	1	0	0
Clearcut	HL8O	1	1	1,000	1,000	1	0	0	0	0
Clearcut	T12O	5	4	**0,486**	0,762	3	1	0	0	0
Clearcut	T18O	9	3	1,000	1,000	1	0	0	2	0
Clearcut	T23O	4	2	1,000	1,000	1	0	1	0	0
Clearcut	T24O	6	3	0,881	0,984	1	1	1	0	0
Clearcut	T25O	3	3	**0,333**	0,802	3	0	0	0	0
Clearcut	T26O	1	1	1,000	1,000	1	0	0	0	0
Clearcut	T30O	3	3	**0,333**	0,802	3	0	0	0	0

Clearcut	T30R	15	6	0,813	0,934	3	0	2	0	0
Clearcut	T32O	1	1	1,000	1,000	1	0	0	0	0
Clearcut	T40O	10	4	0,836	0,978	2	0	1	0	1
Clearcut	T41O	1	1	1,000	1,000	1	0	0	0	0
Clearcut	Pooled assemblage	123	15	0,976	0,997	3	3	1	2	1
Clearcut	Joint assemblage	123	61	0,684	0,756	39	5	7	5	1
Retention	H5R	9	3	1,000	1,000	0	2	0	0	1
Retention	H7R	14	5	0,867	0,953	2	1	1	0	0
Retention	HJ1R	8	4	0,920	0,998	1	2	1	0	0
Retention	HL10R	1	1	1,000	1,000	1	0	0	0	0
Retention	HL13R	7	5	0,649	0,914	3	2	0	0	0
Retention	HL1R	9	3	1,000	1,000	1	0	1	0	1
Retention	HL21R	9	4	0,822	0,976	2	0	1	1	0
Retention	HL81R	13	2	1,000	1,000	0	0	0	0	0
Retention	HL8R	6	2	1,000	1,000	1	0	0	0	1
Retention	T12R	3	2	0,833	0,979	1	1	0	0	0
Retention	T15R	1	1	1,000	1,000	1	0	0	0	0
Retention	T18R	17	4	1,000	1,000	0	1	0	2	0
Retention	T23R	7	4	0,755	0,917	2	1	1	0	0
Retention	T24R	8	3	1,000	1,000	1	0	1	1	0
Retention	T25R	6	3	1,000	1,000	0	3	0	0	0
Retention	T26R	7	1	1,000	1,000	0	0	0	0	0
Retention	T32R	1	1	1,000	1,000	1	0	0	0	0
Retention	T41R	3	2	0,833	0,979	1	1	0	0	0
Retention	Pooled assemblage	129	16	0,954	0,983	6	3	0	0	0
Retention	Joint assemblage	129	50	0,862	0,971	18	14	6	4	3

Setaside	N18C	10	3	1,000	1,000	1	0	1	0	0
Setaside	N19C	16	3	1,000	1,000	1	0	1	0	0
Setaside	N20C	30	6	1,000	1,000	0	2	2	0	0
Setaside	N25C	27	6	1,000	1,000	0	1	4	0	0
Setaside	N28C	13	5	0,781	0,892	3	1	0	0	0
Setaside	N2C	15	4	1,000	1,000	0	2	1	0	0
Setaside	N36C	22	4	1,000	1,000	1	0	0	2	0
Setaside	NR2C	21	2	1,000	1,000	0	0	0	1	0
Setaside	NR4C	19	3	1,000	1,000	1	0	0	1	0
Setaside	T12C	6	3	0,881	0,984	1	1	1	0	0
Setaside	T15C	4	3	0,625	0,881	2	1	0	0	0
Setaside	T16C	5	4	**0,486**	0,762	3	1	0	0	0
Setaside	T18C	4	1	1,000	1,000	0	0	0	1	0
Setaside	T23C	12	3	1,000	1,000	1	0	0	0	1
Setaside	T25C	15	1	1,000	1,000	0	0	0	0	0
Setaside	T26C	1	1	1,000	1,000	1	0	0	0	0
Setaside	T30C	42	8	0,954	0,983	2	1	1	0	2
Setaside	T40C	12	4	0,929	0,991	1	1	1	0	0
Setaside	T41C	46	2	1,000	1,000	0	0	0	0	0
Setaside	Pooled assemblage	320	12	0,997	1,000	1	1	1	0	0
Setaside	Joint assemblage	320	66	0,944	0,984	18	11	12	5	3

Spiders

Dataset	Assemblage	n	S.obs	SC(n)	SC(2n)	f1	f2	f3	f4	f5
Clearcut	H5O	127	32	0,883	0,954	15	7	2	1	1
Clearcut	H7O	57	21	0,828	0,949	10	6	2	0	2
Clearcut	HJ1O	29	11	0,832	0,926	5	2	1	1	1

Clearcut	HL10O	45	17	0,802	0,874	9	2	0	1	3
Clearcut	HL13O	99	23	0,930	0,978	7	4	5	2	2
Clearcut	HL1O	39	16	0,827	0,959	7	5	0	3	0
Clearcut	HL21O	114	24	0,913	0,952	10	3	2	1	1
Clearcut	HL8O	83	19	0,917	0,980	7	5	1	1	0
Clearcut	T12O	100	26	0,891	0,964	11	6	2	2	1
Clearcut	T15O	55	16	0,875	0,961	7	4	2	0	0
Clearcut	T18O	38	11	0,844	0,889	6	1	0	2	1
Clearcut	T23O	108	20	0,926	0,955	8	2	2	4	0
Clearcut	T24O	70	21	0,829	0,878	12	2	2	1	0
Clearcut	T25O	62	12	0,904	0,931	6	1	0	1	0
Clearcut	T26O	70	21	0,844	0,910	11	3	4	0	0
Clearcut	T30R	92	28	0,882	0,961	11	6	3	1	1
Clearcut	T32O	100	25	0,871	0,941	13	5	1	1	0
Clearcut	Pooled assemblage	1288	83	0,981	0,991	24	9	7	5	2
Clearcut	Joint assemblage	1288	343	0,880	0,947	155	64	29	22	13
Retention	H5R	21	12	0,732	0,931	6	4	1	1	0
Retention	HJ1R	36	17	0,725	0,818	10	2	2	2	0
Retention	HL13R	73	18	0,891	0,934	8	2	3	1	2
Retention	HL1R	58	24	0,795	0,896	12	4	4	2	1
Retention	HL21R	155	31	0,891	0,932	17	4	1	1	0
Retention	HL81R	2	2	0,667	0,963	2	0	0	0	0
Retention	HL8R	90	22	0,879	0,930	11	3	1	2	0
Retention	T15R	78	24	0,834	0,878	13	2	3	2	2
Retention	T18R	19	14	0,374	0,475	12	1	0	0	1
Retention	T23R	56	15	0,895	0,962	6	3	1	1	1

Retention	T24R	52	11	0,925	0,973	4	2	1	1	0
Retention	T25R	100	23	0,901	0,964	10	5	3	0	1
Retention	T26R	59	19	0,867	0,951	8	4	2	1	1
Retention	T32R	111	26	0,874	0,906	14	2	2	0	1
Retention	T41O	95	19	0,916	0,961	8	3	2	1	1
Retention	T41R	70	17	0,888	0,968	8	5	0	1	2
Retention	Pooled assemblage	1075	92	0,967	0,977	36	7	14	2	2
Retention	Joint assemblage	1075	294	0,861	0,925	149	46	26	16	13
Setaside	N18C	27	14	0,669	0,737	9	1	2	1	0
Setaside	N19C	40	23	0,553	0,644	18	2	1	1	0
Setaside	N20C	32	9	0,814	0,868	6	1	0	0	0
Setaside	N25C	52	19	0,848	0,929	8	3	4	1	0
Setaside	N28C	9	7	0,495	0,786	5	2	0	0	0
Setaside	N2C	24	12	0,853	0,992	4	6	0	2	0
Setaside	N36C	42	17	0,788	0,865	9	2	2	2	1
Setaside	NR2C	49	21	0,778	0,872	11	3	3	1	1
Setaside	NR4C	21	13	0,581	0,736	9	2	0	2	0
Setaside	T12C	61	25	0,806	0,916	12	5	2	2	0
Setaside	T15C	51	18	0,867	0,968	7	5	3	0	1
Setaside	T16C	32	19	0,565	0,624	14	1	3	0	0
Setaside	T18C	81	22	0,853	0,911	12	3	2	2	0
Setaside	T23C	28	12	0,717	0,781	8	1	1	1	0
Setaside	T25C	52	13	0,905	0,936	5	1	2	1	2
Setaside	T26C	80	19	0,914	0,973	7	4	2	0	2
Setaside	T32C	62	20	0,856	0,908	9	2	3	1	1
Setaside	T40C	23	13	0,613	0,702	9	0	2	2	0

Setaside	T41C	59	19	0,849	0,904	9	2	3	2	0
Setaside	Pooled assemblage	825	85	0,970	0,984	25	8	6	8	5
Setaside	Joint assemblage	825	315	0,793	0,879	171	46	35	21	8

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