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*Chapter 2*

## COMMUNITY ASSEMBLY OF SAPROXYLIC BEETLES IN OLD-GROWTH FOREST AND RECENTLY BURNT FOREST

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### ABSTRACT

Community assembly is the trajectory exhibited over time regarding species composition and community structure as species colonize an empty patch. Chase (2007) distinguish two basic types of assembly where a niche-assembled community is constrained by species interactions and competitive hierarchies whereas a dispersal-assembled community is unaffected by competition. The first wood-living (saproxylic) beetles to colonize a dead tree are sub-cortical, cambial-living species with a larval development-time of one year or less. Important community assembly events could therefore take place the first summer after tree death.

Community assembly was studied during the eight weeks immediately after tree death. By exposing 0.5 m long stem sections (bolts) of Norway spruce, *Picea abies*, to colonization for increasingly longer times (0.5, 1, 2, 4, and 8 weeks) a temporal sequence was created. A total of 140 bolts at four forest sites in central Sweden were studied with six to eight replicates per site. Two of the sites were old-growth forest and the other two were forest sites subjected to burning right before the experiment started. I used community ecology measures to describe assembly patterns and emphasize findings that would have gone unnoticed in an analysis confined to the 8-week final state.

In total 8802 beetles of 56 species were reared from the bolts. Two fire-dependent species were found in burnt forest, this is noteworthy since unburnt bolts were used in both forest types. The total number of emerged beetles per bolt was similar in the two forest types in early assembly but later this density was higher in the old-growth forest. During assembly the community-level carrying capacity was reached in old-growth forest but not in burnt forest. During assembly, community evenness and taxonomic richness

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was higher in the burnt forest than in old-growth forest but at eight weeks these community measures had converged. The two forest types became more dissimilar regarding species composition as the community assembly progressed. Old-growth forest also had a lower bolt-to-bolt variation in species composition than burnt forest. Cambivores was the functional group that made up the largest proportion of individuals in both forest types but the proportion was highest in old-growth forest. The proportion fungivores was highest in burnt forest. The proportion predators peaked early in both forest types and then decreased during assembly. In old-growth forest, 74 % of the bolts were numerically dominated by the cambivorous scolytine *Dryocoetes autographus*. In burnt forest only 33 % of the bolts were dominated by that species. Furthermore, burnt forest also had fungivores as bolt dominants, for example the fire-favoured corticarid *Corticara rubripes*, whereas old-growth forest bolts were always dominated by cambivores.

In conclusion, the beetle assemblages in the two forest types followed different assembly trajectories. The beetle assemblage in burnt forest conforms to a dispersal-assembled community whereas that in old-growth forest conforms to a niche-assembled community (*sensu* Chase 2007). The biology of fire-adapted beetles is discussed in light of these findings.

## INTRODUCTION

Community assembly (Diamond 1975) is the process deciding species inclusion/exclusion as well as determining the relative species abundance in a local community (Weiher and Keddy 1999). Community assembly implies change over time and can be viewed as the trajectory, regarding species composition and community structure, a community exhibits over time (Drake et al. 1999). Studying the final state of communities is important but by ignoring community assembly, the final states might seem idiosyncratic, especially if the species acting during assembly, such as a key-stone predator (Warren et al. 2003), is no longer present in the final state (Drake 1991). Community patterns can either be created by environmental differences between patches or by biotic interactions within patches. In this respect community assembly can be viewed as sequential species filtering (Weiher and Keddy 1999) where abiotic filtering removes species for which the patch does not fulfil environmental niche criteria and biotic filtering, i.e. community ecology interactions such as resource competition and predation, exclude further species.

Saproxyllic beetles depend on dead wood and are an important group in the heterotrophic succession in coarse woody debris (CWD) (Stokland et al. 2012). After tree-death, insects colonize the thin, nutrient-rich sub-cortical layer (phloem, cambium, and outer sapwood) (Dajoz 2000). Beetle larvae are the main primary consumers (cambivores) (Esseen et al. 1992) with scolytines and cerambycids being two important groups. The sub-cortical layer is consumed in less than two years and is the most ephemeral resource in dead trees. Most cambial-living saproxyllic beetles have a larval development-time of one year or less (Ehnström and Axelsson 2002), so the time for community assembly is short and significant assembly events could be expected to be separated by weeks only.

Forest fire is the major large-scale disturbance in natural boreal forest (Zackrisson 1977, Niklasson and Granström 2000). The newly burnt forest is rich in sun-exposed coarse woody debris (CWD) for many years (Boulanger and Sirois 2007, Stokland et al. 2012). The forest then develop through a young-forest stage with very little CWD (Stokland et al. 2012). Later,

when the forest becomes an old-growth stand, more CWD is again produced during small-scale tree-mortality events (self-thinning, drought, wind throw, or fungus infestations) (Siitonen 2001). For saproxylic insects, a natural boreal landscape is therefore a forest-patch mosaic where most available dead wood is found in patches of old-growth forest and burnt forest. Therefore, community assembly in saproxylic beetles is probably a result of interactions developed in these two forest stages.

If community structure and composition can be recorded non-invasively then community assembly can be studied directly. For example Jenkins and Buikema (1998) did this when they used biweekly plankton sampling to study community assembly in ponds. Saproxylic insects, however, complete their larval development hidden within the dead wood and inspecting the community by bark removal would destroy the process under study. In this experiment, I therefore exposed stem sections, bolts (0.5 m long), of Norway spruce *Picea abies* to natural colonization for increasingly longer times (0.5 to 8 weeks). Beetles reared from the bolts offered community assembly “snapshots”, providing quantitative community data along the assembly trajectory. This methodology has been used to study insects in dung and carrion (Koskela and Hanski 1977, Kuusela and Hanski 1982).

Chase (2007) distinguish two community types based on the species-interaction intensity. (1) A *niche-assembled community* is constrained by species interactions in the patch. Competitive hierarchies and species traits determine community assembly. An increased species-composition similarity during assembly is predicted. (2) In a *dispersal-assembled community*, colonization and extinction are unaffected by species competitive traits (as in the neutral theory of Hubbell 2001). These communities have a high patch-to-patch variation in species composition. I predicted that burnt forest would have a dispersal-assembled community whereas old-growth forest would have a niche-assembled community. The reasoning behind this was: (1) that the intensity of density-dependent effects (such as larval resource competition) is predicted to be lower in burnt forest than in old-growth forest (Esseen et al. 1992, Wikars 1992); and (2) that burnt forest attracts colonizers on a landscape scale (Boulanger et al. 2010) which could lead to a wider taxonomic range of colonizing species. I used increasingly fine-scaled community-measures, such as evenness, importance of nutritional functional groups and species composition in an attempt to describe important community-level patterns during community assembly. I emphasize patterns that would not have been found in an analysis of first-year final states only.

## METHODS

### Study Sites

The study was performed in central Sweden, an area dominated by managed, boreal forest. The dominating tree species in the area are Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. Some deciduous species, mainly birch *Betula* spp., aspen *Populus tremula*, and alder *Alnus* spp., also occur but in low densities. The managed forest has a very low level of dead wood, only 2-6 m<sup>3</sup> ha<sup>-1</sup> (Fridman and Walheim 2000). The experiment was performed in two pairs of burnt and old-growth forest sites (inter-pair distance 135 km). The burnt sites were surrounded by managed forest and in both pairs, the only available old-

growth site within a 60 km radius of the burnt site were used. The first burnt site, Eggåsen (B1) (61°05' N, 16°00' E), was burnt for conservation purposes on June 11 1997. Before the fire, the site was mature, managed forest that was thinned the winter before burning, leaving 25 mature Scots pine, trees per hectare. Approximately 20 % of the stand was left untouched before the fire and the study area was established in this part (see Wikars and Schimmel 2001, for details of Eggåsen). The old-growth site, Rödmyrberget (OG1) (61°04' N, 16°03' E), was situated 3 km from Eggåsen.

This was a set-aside, excluded from forest management due to high conservation values. Rödmyrberget had a mixed tree-species composition and an uneven tree-age structure (see Wikars 2002, for details of Rödmyrberget). The second burnt site, Galhån (B2) (62°00' N, 14°38' E), was burnt by a wildfire that started June 3 1997 and continued until June 11. Galhån was managed forest, with a stand age of approximately 60 years (the rotation period is 90 years). The corresponding old-growth site, Ryggen (OG2) (62°12' N, 14°20' E), was situated 15 km from the burnt site. Just like Rödmyrberget this was a set-aside with a mixed tree-species composition and an uneven tree-age structure.

## Field Experiment

The experiment had a two-way factorial design with forest type and exposure time as factors. The experiment ran in the field from June 12 to August 7 and started one day after the fire at the burnt sites and one day later still at the old-growth sites. The experimental units were 140 bolts (0.5 m long, diameter 15-25 cm) from eight Norway spruce trees taken at site B1. This is a common host tree in both forest types. From each tree, 20 bolts were taken and divided so that each individual tree was represented as a 5-bolt group at each site. The bolts in each such group were randomly subjected to one of five exposure treatments: 0.5, 1, 2, 4, or 8 weeks. Each tree was therefore a blocking variable.

The bolt bark area was calculated after measuring the circumference and length of each bolt. The bark area was a measure of the amount of substrate available to saproxylic insects and it was used as a covariate in all analyses where that was possible. The bark area was  $0.324 \pm 0.058 \text{ m}^2$  (mean  $\pm$  SD), but there was no treatment differences (ANOVA; B1/OG1:  $F_{9,70} = 0.70$ ,  $P = 0.70$ ; B2/OG2:  $F_{9,50} = 0.59$ ,  $P = 0.80$ ).

The bolt-groups were placed within a 250 x 250 m study area at the centre of each site with a minimum distance between groups of 10 m. Distance between bolts within group was 0.5 m. When the experiment started, all bolts were exposed to colonization. Terminating the exposure was done by enclosing the bolt in a cloth mesh cage (mesh size 1 mm). The number of exposure replicates was eight in B1/OG1 and six in B2/OG2. Please note that neither the bolts in the old-growth forest nor the bolts in the burnt forest were scorched by fire.

The 8-week bolts were the first-year final stage. This is not the end of the heterotrophic succession but it is the end of most of the season for the focal species that year (Vanderwel et al. 2006). If a longer exposure time than eight weeks had been used then the species with the shortest larval development time would have left the bolts before the experiment ended (e.g. *Pityogenes chalcographus*).

In natural logs, the colonization would undoubtedly commence anew the following year (Boulanger and Sirois 2007) but my study focused on the first-year community assembly.

The bolts were hanged in individual emergence traps at each original bolt-exposure site on August 8-10. Traps were emptied four times: (1) November 1997; (2) July 1998; (3) October 1998; and (4) October/November 1999. Regrettably, at emptying number four, most traps at study site B1 had been destroyed. Therefore, the analyses were made on beetles from emptying 1-3 in B1/OG1 and from emptying 1-4 in B2/OG2.

## Species Ecology

The species reared with this method belong to successional stage one in the 4-stage successional sequence in Norway spruce (Esseen et al. 1992). All beetles except 423 *Dryocoetes spp.* were determined to species (these individuals belonged to either *Dryocoetes autographus* or *Dryocoetes hectographus*). Species were assigned to one of four functional groups based on the literature (Martikainen et al. 1999, Dajoz 2000, Ehnström and Axelsson 2002, Lieutier et al. 2004, Johansson et al. 2007, Hjältén et al. 2010): (1) *cambivores* feed directly on inner bark or outer sapwood; (2) *fungivores* feed on subcortical mycelium; (3) *predators* feed on other arthropods; and (4) *facultative predators* are predators but also feed as fungivores or as detritivores (feeding on the remains of other saproxylics). Out of all 56 species, 51 could be assigned (99.8 % of all individuals).

Species were classified as fire-dependent or fire-favoured based on the most recent classification of Swedish insects in relation to fire (Wikars 2006). Fire-favoured species are regularly abundant in burnt forest but also occur in other habitats whereas fire-dependent species are confined to burnt forest.

## Community Variables and Analysis

A range of community variables were calculated. The *total abundance* ( $N_{\text{tot}}$ ) and the *number of species* of all beetles emerging from each bolt were calculated. *Evenness*, in each bolt was measured with the index  $E_{\text{var}}$  (Smith and Wilson 1996). *Taxonomic diversity* was measured with average taxonomic distinctness ( $AvTD$ ) (Warwick and Clarke 1995). This index measures the average path length, along a taxonomic tree, between species in the sample.  $AvTD$  was calculated using software PRIMER (version 6.1.10, PRIMER-E, Plymouth).

I used the taxonomic information in Lundberg and Gustafsson (1995). Both  $AvTD$  and  $E_{\text{var}}$  are relatively unaffected by total species number and abundance (Magurran 2004) which is advantageous since species number and abundance was positively correlated with exposure time. I tested the effect on the *relative abundance of each functional group* for the four functional groups. For example, for cambivores this was the effect on  $N_{\text{cambivores}}/N_{\text{tot}}$ . As exposure times increase so does total abundance in the bolts and the relative abundance control for this in order to get an unbiased measure of the importance of the different functional groups.

All tests on those community variables were performed using procedure GLIMMIX in SAS version 9.3. (SAS institute, Cary, NC). They were analysed with two-way factorial ANCOVAs with the treatment factors *forest type* and *exposure time*. The *bark area* for each bolt was used as a covariate. The variables *substrate tree* (the eight Norway spruce trees) and

*study site pair* (B1/OG1 and B2/OG2 respectively) were used as random variables (blocking variables).

Further tests of simple effects (slices) were done as described in Littell et al. (2006). For  $N_{\text{tot}}$  a Poisson error distribution (suitable for counts) and log link was used. A quasi-likelihood model was used to compensate for overdispersion (Quinn and Keough 2002). Another preplanned test, a contrast between the 4- and 8-week exposures to detect a “levelling-off” in beetle density, was also done for this measure. The two indices,  $AvTD$  and  $E_{\text{var}}$ , were arcsine square root transformed, with additional multiplication by  $2/\pi$  to rescale values to the original scale as described by McCune and Grace (2002). The functional groups were tested using the events/trials syntax in procedure GLIMMIX (Littell et al. 2006). For example, when testing the effect on cambivores, an event was  $N_{\text{cambivores}}$  and a trial was  $N_{\text{tot}}$ . For tests on the two functional groups fungivores and facultative predators, there was too few observation in the 0.5-week exposure for the model to converge. Therefore a model without the 0.5-week exposure was fitted instead.

More detailed measures took species identity into account. Bolt-dominants, the most abundant species, in each bolt were visualized using a mosaic plot. The most detailed community measure, species composition, uses species identity and abundance of all species in a bolt. I tested the difference in species composition between forest types in the 8-week bolts with an analysis of similarity (ANOSIM) (Clarke and Warwick 2001) using Bray-Curtis similarity and 4<sup>th</sup> root transformed abundances (to dampen the influence of the most abundant species) in software PRIMER.

The test statistic,  $R$ , ranges from 0 to 1 and is a measure of difference in species composition. Further testing was done using similarity percentage analysis (SIMPER) (Clarke and Warwick 2001) to decompose the forest-type difference into the percentage contribution of each species to that dissimilarity. Species with a high SIMPER value for a particular habitat are said to characterize that habitat (Clarke and Gorley 2006). I also used within-treatment Bray-Curtis similarity to test for differences in bolt-to-bolt similarity along the assembly trajectory. This was modelled with a two-way ANOVA with study site pair as random factor.

To visualize the assembly trajectory, regarding species composition, I performed a non-metric multidimensional scaling (NMDS) ordination of  $R$ -values from an ANOSIM testing for differences between all treatments. This analysis involved four steps (all in software PRIMER): (1) ANOSIM testing for differences between treatments; (2) a similarity-matrix was constructed using these  $R$ -values; (3) this matrix was used in an NMDS ordination with Euclidian distances between treatments now showing  $R$ -values; (4) the matrix was also used in a group-average linking (UPGMA) cluster analysis; (5) circles indicating  $R$ -distances, obtained from the clustering, were added to the NMDS ordination to increase interpretability.

I used as many bolts as was meaningful in each analysis. This meant using all 140 bolts when testing  $N_{\text{tot}}$  and number of species. In the more derived measures fewer bolts could be used. For example, calculating  $E_{\text{var}}$  is not meaningful with too few individuals in a bolt. In the analyses of species composition I restricted the analysis to bolts with  $> 6$  individuals reared. This criterion was met for 88 bolts, 46 in old-growth forest and 42 in burnt forest (for the exposure times 0.5-8 weeks the sample sizes in burnt forest were 5, 8, 6, 10, 13 and in the old-growth forest 4, 7, 8, 13, and 14).

## Environmental Variables and Analysis

I kept bolt-group sun-exposure similar in the two forest types by setting out bolts in sun-exposed sites at the old-growth sites. I took a canopy-cover picture at each bolt-group and calculated sun-exposure as the proportion sky in the pictures using software ImageJ (version 1.38). Trees and CWD were inventoried in November 1997, the same year as the experiment. Diameter at breast height and species was recorded for all trees and CWD (with a diameter > 10 cm) within five circular plots (10 m radius) placed in a pre-determined grid at each forest site. CWD was classified into two classes: (1) fresh CWD (0-2 years old), and (2) old CWD (> 2 years old). I summed the basal area of each class for each of the five circular plots (as m<sup>2</sup> ha<sup>-1</sup>). I tested for forest-type differences in with one-way ANOVAs for each factor and study-site pair.

## RESULTS

More individuals were reared from the old-growth forest, 6787 individuals, than from the burnt forest, 2015 individuals. Among the 56 species reared, the dominating groups were Scolytinae (81 % of all individuals), other Curculionidae (7 %), Cerambycidae (6 %), and Staphylinidae (3 %) (Appendix 1). Two fire-dependent species, *Henoticus serratus* and *Cryptophagus corticinus* were reared in burnt forest. Nine fire-favoured species were found, five of those only in burnt forest (Appendix 1).

Burnt forest and old-growth forest showed forest-type specific community assembly regarding all nine univariate community measures (Figure 1) since there were significant (or in the case of evenness borderline significant,  $P = 0.052$ ) exposure x forest type interactions for all measures (Table 1). The total abundance of beetles reared per bolt increased during assembly in both forest types (Table 1, Figure 1). Between the 2-week and 8-week exposures the abundance rose and reached a plateau in old-growth forest (difference between 4- and 8-week exposure,  $t_{2,121} = 1.00$ ,  $P = 0.32$ ) but not in burnt forest ( $t_{2,121} = -2.99$ ,  $P = 0.0034$ ). The number of species increased 2.6 times (from 1.6 to 4.2 species) during assembly in burnt forest and 5.2 times in old-growth forest (from 1.4 to 7.3 species) (Table 1, Figure 1). The taxonomic diversity was significantly higher in burnt forest than in old-growth forest in the 0.5-week exposure and marginally so in the 2-week exposure (Table 1, Figure 1). During assembly there was then a forest type convergence in taxonomic diversity. Evenness remained the same in burnt forest during assembly whereas it decreased during assembly in old-growth forest. Evenness was therefore significantly higher in burnt forest in the 4-week exposure but in the 8-week exposure there was forest-type convergence (Table 1, Figure 1). Within exposure treatment, the old-growth bolts were more similar regarding species composition than the burnt forest bolts since the Bray-Curtis similarity was higher in old-growth bolts in the 0.5-, 4-, and 8-week exposures (Table 1, Figure 1).

The forest-type differences in the relative abundance of each functional group were larger during assembly than in the first-year final states where there was a tendency towards forest-type convergence (Table 1, Figure 1). Cambivores and fungivores differed most between the forest types during assembly (Table 1, Figure 1). Cambivores made up the largest proportion in all treatments but the proportion was significantly lower in burnt forest than in old-growth

forest during assembly. The proportion fungivores was significantly higher in burnt forest than in old-growth forest during assembly. The proportion predators peaked early during assembly and made up 5-20 % of total abundance in the 1- and 2-week exposures (Table 1, Figure 1). After that, the proportion decreased to 1-2 %. The peak came earlier on old-growth forest (1-week bolts) than in burnt forest (2-week bolts). The proportion facultative predators made up the smallest proportion overall (Table 1, Figure 1). Forest-type differences were not significant for this functional group, except for 8-week bolts, but the overall pattern was very similar to that of the predators.

The assemblages followed forest-type specific assembly trajectories regarding species composition (Figure 2). The forest types became more and more dissimilar as the community assembly progressed (Figure 2). There was a pronounced difference in species composition in the final state (8-week bolts, burnt forest versus old-growth forest: ANOSIM,  $R = 0.42$ ,  $P = 0.001$ ) and nine species contributed  $> 4$  % each to this difference according to the SIMPER analysis. Old-growth forest was characterized by four cambivores *Dryocoetes autographus* (17.0 % contribution to the dissimilarity according to the SIMPER), *Tetropium castaneum* (9.8 %), *Hylastes cunicularius* (7.5 %), and *Dryocoetes hectographus* (5.2 %); one fire-favoured predator *Phloeonomus sjoebergi* (6.7 %); and one facultative predator *Rhizophagus ferrugineus* (5.2 %). Burnt forest was characterized by two cambivores *Pissodes gyllenhalii* (10.4 %) and *Pityogenes chalcographus* (7.1 %); and one fire-favoured fungivore, *Atomaria pulchra* (4.2 %). Of the 20 most abundant species, two were only reared from burnt forest, the fire-favoured fungivores *A. pulchra* and *Corticaria rubripes*, whereas four species were only reared from old-growth forest, *Dendroctonus micans*, *D. hectographus*, *Rhizophagus dispar*, and *Leptusa pulchella*, (Appendix 1). A total of 25 species were only reared from exposure times shorter than eight weeks (Appendix 1).

In old-growth forest only cambivores were bolt dominants (the most abundant species in a bolt) and *D. autographus* dominated 74 % of the bolts (Figure 3). There was a wider selection of bolt-dominant species in burnt forest where *D. autographus* dominated only 33 % of the bolts. In burnt forest another cambivore, *P. gyllenhalii*, dominated 31 % of the bolts and two fire-favoured fungivores, *A. pulchra* and *C. rubra*, and a fire-favoured predator, *P. sjoebergi*, dominated a total of six bolts (Figure 3).

Sun exposure at the bolt-groups was similar in the two forest types (% sky in the canopy-cover pictures) (B1/OG1:  $F_{1,14} = 1.40$ ,  $P = 0.26$ ; B2/OG2:  $F_{1,10} = 0.36$ ,  $P = 0.56$ ) (Table 2). In OG1 there was a larger living-tree basal area than in B1 ( $F_{1,8} = 9.18$ ,  $P = 0.016$ ) but there was no difference in B2/OG2 ( $F_{1,8} = 1.46$ ,  $P = 0.26$ ) (Table 2). The amount of old CWD was similar in the two forest types (B1/OG1:  $F_{1,8} = 0.03$ ,  $P = 0.86$ ; B2/OG2:  $F_{1,8} = 0.05$ ,  $P = 0.83$ ) (Table 2). The amount of fresh CWD was probably severely underestimated in the burnt sites and is not presented. There was more living Norway spruce in the old-growth sites than in the burnt sites (Table 2).

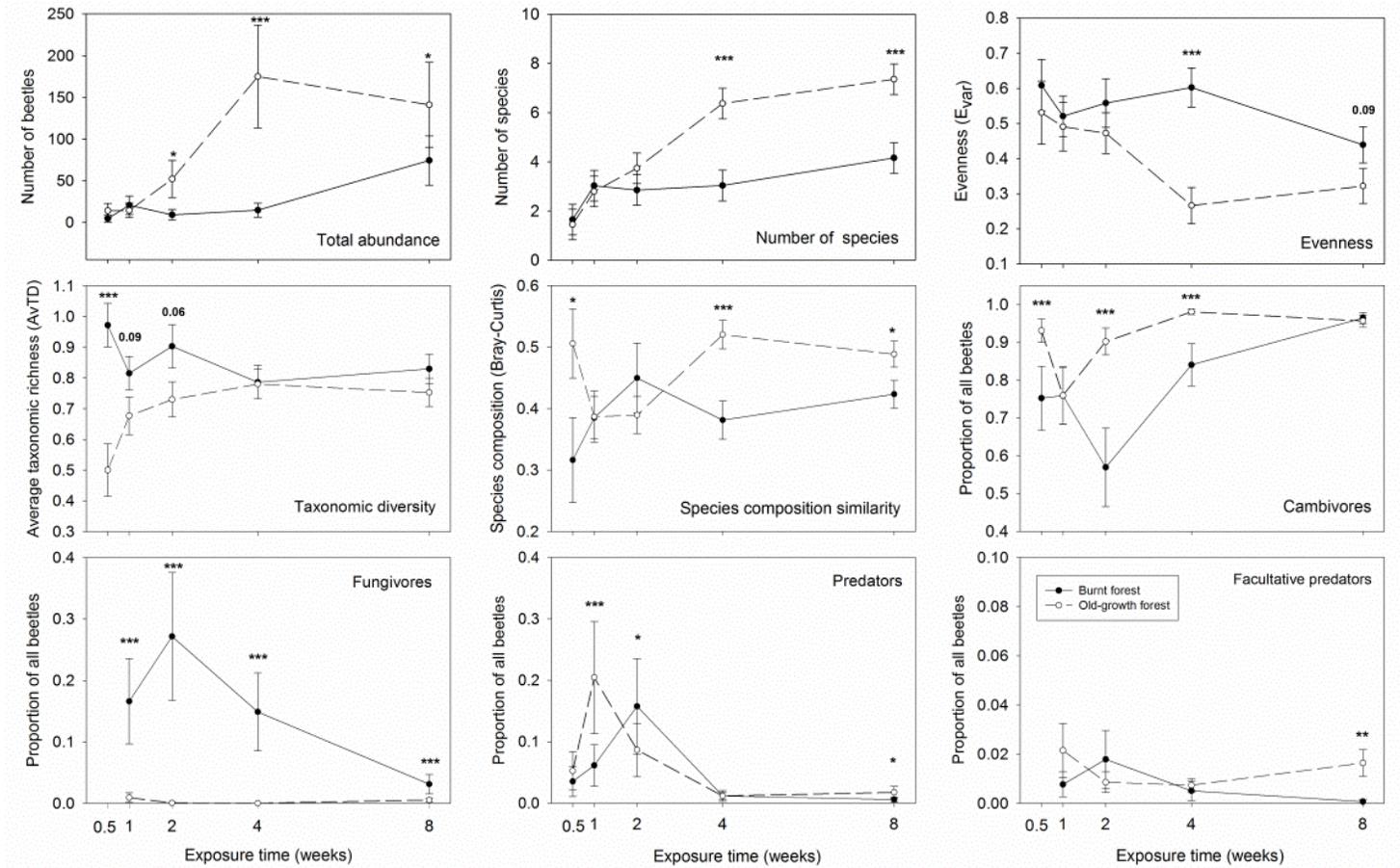


Figure 1. Community structure changes during community assembly. Means and SE from the ANCOVA/ANOVAs. Note different scale on Y-axes for the functional groups. Asterisks denote significant forest-type differences in that exposure treatment (simple effects from the ANCOVAs): \*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ . Differences with a significance level between 0.05 and 0.09 indicated by actual  $P$ -value.

**Table 1. Results from ANCOVA and ANOVA analyses testing the effects of forest type and exposure time on nine community measures of the beetle assemblage reared from 140 Norway spruce *Picea abies* bolts at four sites in central Sweden. The actual number of bolts used in each test differ (see text for details). Statistically significant differences ( $P < 0.05$ ) are shown in bold**

Source of variation	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
	<i>Total beetle abundance</i>			<i>Number of species</i>			<i>Evenness (<math>E_{var}</math>)</i>		
Forest type	1,121	14.23	<.001	1,121	18.65	<.001	1,76	11.10	<b>0.001</b>
Exposure	4,121	13.58	<.001	4,121	20.32	<.001	4,76	3.14	<b>0.02</b>
Forest type x Exposure	4,121	3.87	<b>0.005</b>	4,121	5.90	<.001	4,76	2.47	0.05
Bark area	1,121	9.22	<b>0.003</b>	1,121	0.60	0.44	1,76	1.06	0.31
Simple effect: burnt forest	4,121	6.26	<.001	4,121	3.00	<b>0.02</b>	4,76	1.68	0.16
Simple effect: old-growth forest	4,121	12.76	<.001	4,121	23.03	<.001	4,76	3.86	<b>0.007</b>
Simple effect: exposure 0.5 weeks	1,121	1.29	0.26	1,121	0.07	0.79	1,76	0.48	0.49
Simple effect: exposure 1 week	1,121	0.31	0.58	1,121	0.10	0.75	1,76	0.12	0.73
Simple effect: exposure 2 weeks	1,121	6.43	<b>0.01</b>	1,121	1.50	0.22	1,76	0.98	0.33
Simple effect: exposure 4 weeks	1,121	23.81	<.001	1,121	21.25	<.001	1,76	22.06	<.001
Simple effect: exposure 8 weeks	1,121	4.96	<b>0.03</b>	1,121	19.36	<.001	1,76	3.03	0.09
	<i>Taxonomic diversity (AvTD)</i>			<i>Species composition similarity (Bray-Curtis)</i>			<i>Proportion cambivores</i>		
Forest type	1,74	20.18	<.001	1,191	6.43	<b>0.01</b>	1,106	76.15	<.001
Exposure	4,74	0.52	0.72	4,191	1.54	0.19	4,106	58.72	<.001
Forest type x Exposure	4,74	3.34	<b>0.01</b>	4,191	2.68	<b>0.03</b>	4,106	25.34	<.001
Bark area	1,74	0.25	0.62	n.t.	n.t.	n.t.	1,106	13.45	<.001
Simple effect: burnt forest	4,74	1.37	0.25	4,191	0.96	0.43	4,106	31.38	<.001
Simple effect: old-growth forest	4,74	2.30	0.07	4,191	4.24	<b>0.003</b>	4,106	50.17	<.001
Simple effect: exposure 0.5 weeks	1,74	18.08	<.001	1,191	4.49	<b>0.04</b>	1,106	14.50	<.001
Simple effect: exposure 1 week	1,74	2.86	0.09	1,191	0.00	0.97	1,106	0.00	0.99
Simple effect: exposure 2 weeks	1,74	3.67	0.06	1,191	0.88	0.35	1,106	66.94	<.001
Simple effect: exposure 4 weeks	1,74	0.01	0.93	1,191	12.98	<.001	1,106	104.47	<.001

Source of variation	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
	<i>Taxonomic diversity (AvTD)</i>			<i>Species composition similarity (Bray-Curtis)</i>			<i>Proportion cambivores</i>		
Simple effect: exposure 8 weeks	1,74	1.34	0.25	1,191	4.46	<b>0.04</b>	1,106	0.71	0.40
	<i>Proportion fungivores</i>			<i>Proportion predators</i>			<i>Proportion facultative predators</i>		
Forest type	1,85	110.39	<b>&lt;.001</b>	1,106	4.22	<b>0.04</b>	1,85	5.53	<b>0.02</b>
Exposure	3,85	4.12	<b>0.009</b>	4,106	33.46	<b>&lt;.001</b>	3,85	2.16	0.10
Forest type x Exposure	3,85	11.73	<b>&lt;.001</b>	4,106	6.46	<b>&lt;.001</b>	3,85	3.54	<b>0.02</b>
Bark area	1,85	24.80	<b>&lt;.001</b>	1,106	0.11	0.74	1,85	0.48	0.49
Simple effect: burnt forest	3,85	17.27	<b>&lt;.001</b>	4,106	13.61	<b>&lt;.001</b>	3,85	2.72	<b>0.049</b>
Simple effect: old-growth forest	3,85	5.14	<b>0.003</b>	4,106	52.11	<b>&lt;.001</b>	3,85	3.84	<b>0.01</b>
Simple effect: exposure 0.5 weeks	n.t.	n.t.	n.t.	1,106	0.50	0.48	n.t.	n.t.	n.t.
Simple effect: exposure 1 week	1,85	16.52	<b>&lt;.001</b>	1,106	18.69	<b>&lt;.001</b>	1,85	2.09	0.15
Simple effect: exposure 2 weeks	1,85	36.17	<b>&lt;.001</b>	1,106	5.07	<b>0.03</b>	1,85	1.12	0.29
Simple effect: exposure 4 weeks	1,85	45.42	<b>&lt;.001</b>	1,106	0.00	0.97	1,85	0.25	0.62
Simple effect: exposure 8 weeks	1,85	22.77	<b>&lt;.001</b>	1,106	5.17	<b>0.02</b>	1,85	9.81	<b>0.002</b>

Notes: n.t. means that that effect is not tested for that particular community measure.

**Table 2. Environmental variables at two burnt forest sites (B) and two old-growth forest (OG) sites in central Sweden. Sun exposure is a measure of percent sky ( $\pm$  SE) from photos taken at each of the bolt groups. Basal area, in  $\text{m}^2$  / ha, of trees and CWD are means  $\pm$  SE for five circular plots per study site (10 m radius). Tree species composition (percent basal area) are based on all five plots pooled within study site. Species are: Scots pine (*Pinus sylvestris*) / Norway spruce (*Picea abies.*) / deciduous species (mainly *Betula spp.*)**

Variable	B1	OG1	B2	OG2
Area (ha)	30	25	15	25
Sun exposure	54 $\pm$ 4.6	48 $\pm$ 1.9	62 $\pm$ 2.4	65 $\pm$ 5.1
Basal area				
living trees	13.3 $\pm$ 3.6	29.9 $\pm$ 4.1	25.0 $\pm$ 3.4	18.5 $\pm$ 4.2
old CWD	2.6 $\pm$ 1.2	2.3 $\pm$ 1.5	4.3 $\pm$ 2.1	4.9 $\pm$ 1.4
Tree species composition				
living trees	92 / 3 / 5	42 / 44 / 14	100 / 0 / 0	67 / 27 / 6
old CWD	74 / 0 / 9	57 / 18 / 0	100 / 0 / 0	45 / 19 / 14

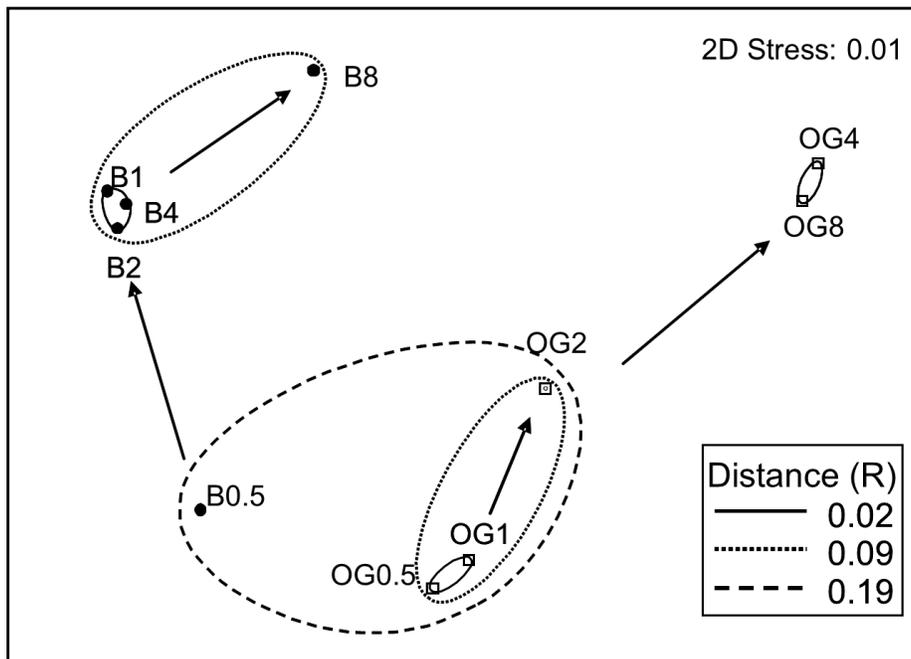


Figure 2. Beetle community assembly in species-composition space. Non-metric multi-dimensional scaling (NMDS) ordination of R-values from an analysis of similarity (ANOSIM) of all treatments (using Bray-Curtis similarity and 4<sup>th</sup> root transformed abundances). Arrows indicate assembly trajectory along the exposure-time sequence. Euclidian distances represent ANOSIM R-values (ranging from 0 to 1), a measure of how different treatments are from each other in species composition. Circles with R-value distances (from a cluster analysis on the same data) added to increase interpretability. B: burnt-forest bolts; OG: old-growth-forest bolts. Exposure time in weeks: 0.5, 1, 2, 4, 8.

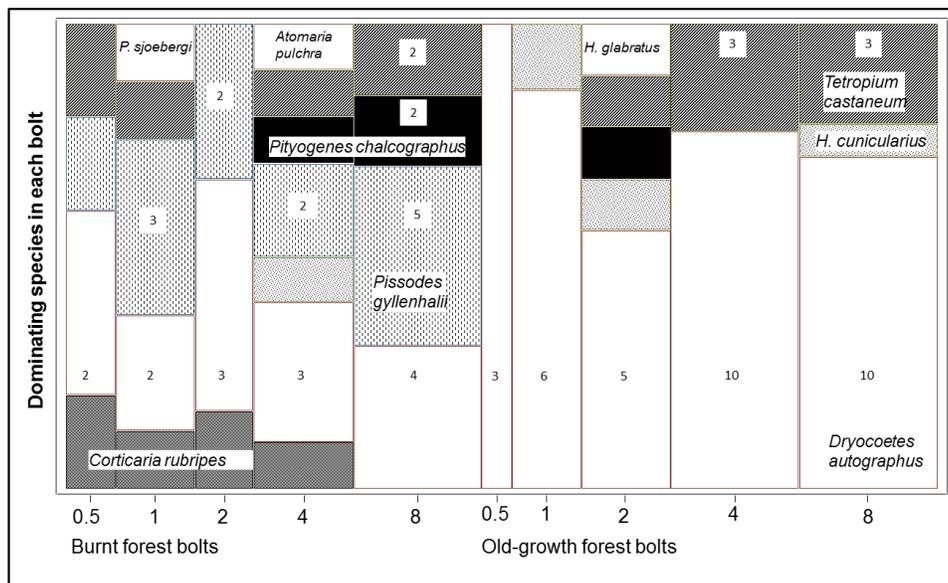


Figure 3. Bolt-dominants in each bolt. Mosaic plot showing proportion of bolts in each treatment that were dominated by a particular species. *Phloeonomus sjoebergi*, *Atomaria pulchra*, and *Hylastes glabratus* dominated one bolt each; all other bolts indicated in white are *Dryocoetes autographus*. Number of bolts indicated (no indication = 1 bolt). Exposure time in weeks: 0.5, 1, 2, 4, 8.

## DISCUSSION

### Two Types of Community Assembly

Based on the two community types distinguished by Chase (2007), the community in burnt forest conformed to a dispersal-assembled community whereas that in old-growth forest conformed to a niche-assembled community. This is supported by five results.

Firstly, total abundance, the number of beetles emerging per bolt, reached the community-level carrying capacity (the increase levelled off) already after four weeks of exposure in the old-growth sites but not in the burnt sites. Resource competition is important in saproxylic beetles (Anderbrant et al. 1985, Rankin and Borden 1991, Schlyter and Anderbrant 1993, Schroeder and Weslien 1994, Weslien 1994, Denno et al. 1995, Victorsson 2012) and it is likely that larval resource competition created the levelling off in the number of emerging beetles in the old-growth bolts for two reasons: (1) Analogous results in the scolytines *Tomicus piniperda* (Sauvard 1989) and *Ips typographus* (Anderbrant et al. 1985), where the density also levelled off when the number of colonists increased, are interpreted as an effect of larval resource competition that offsets the increase in number of colonists (Dajoz 2000); (2) Competition is expected to be most intense within guilds (Pianka 1980) and in the old-growth 4- and 8-week bolts, where 95 % of all beetles were cambivores, intraguild resource competition among those cambivores probably created the levelling off in the number of emerging beetles. Density-dependent predation would be an alternative explanation but in both forest types predators were important only in the 1- and 2-week bolts

whereas in the 4- and 8-week bolts, the predators could not follow the rapid increase in cambivore abundance and those treatments contained only 1-2 % predators.

Secondly, in the burnt forest, species similarity was low in replicate bolts during assembly which is consistent with a dispersal-assembled community where a high patch-to-patch variation in species composition is predicted. In the old-growth forest, on the other hand, species-composition varied less between replicate bolts as is predicted for niche-assembled communities.

Thirdly, the greater selection of bolt-dominating species in burnt forest shows that those assemblages had a less absolute competitive hierarchy, which is predicted for a dispersal-assembled community. The fact that most old-growth forest bolts were dominated by *D. autographus* indicates that the competitive hierarchy was quite strict in that forest type, an observation consistent with a niche-assembled community.

Fourthly, in 4- and 8-week bolts there were twice as many species per bolt in old-growth forest as in burnt forest. This indicates that the available niche space was more filled up in old-growth forest than in burnt forest. Furthermore, the higher taxonomic diversity in burnt forest early during assembly also indicates a dispersal-assembled community, where colonists come from a wider taxonomic range in burnt forest than in old-growth forest.

Fifthly, the higher evenness in burnt forest during assembly indicates an open community with colonization less constrained by species competitive traits since higher evenness means that species get a more equal share of resources. Buddle et al. (2000) also found increased evenness in burnt forest when studying spiders and conclude that this is an effect of lower levels of competition when spiders colonize a competition-relaxed habitat.

Two explanations for the forest-type specific community assembly could be important. Firstly, a wider selection of colonist species in burnt forest could explain the higher bolt-to-bolt variation in that forest type. Insects can colonize CWD from either within the stand, internal colonization, or from the surrounding forest, external colonization. In burnt forest, beetles present in bark-covered CWD (the source of potential colonists) would suffer high mortality during the fire since these trees often are destroyed by the fire (pers. obs. at site B1). Species residing deep inside old dead wood suffer less mortality whereas subcortical species are negatively affected by the fire (Ulyshen et al. 2010). Furthermore, Boulanger et al. (2010) show that the amount of internal CWD in burnt forest is unimportant as a colonist source. Insects are instead attracted to burnt forest from long distances by smoke or infrared radiation (Evans 1962, 1971, Schmitz et al. 1997, Schutz et al. 1999). For example the fire-dependent beetles in the genus *Melanophila* can detect fires at a distance of 130 km (Schmitz and Bousack 2012). The burnt sites therefore receive beetles from many CWD patches in the surrounding landscape. These patches differ in quality and this gives a wide selection of colonizing species which in turn could increase the variation in species composition and bolt dominants. In old-growth forest, internal colonists make up a larger proportion of all colonists since in that forest type the CWD still harbour subcortical colonists. This means that old-growth forest colonists are drawn from a narrower range of within-stand CWD types. The selection of colonizing species in this forest type should therefore be limited compared to that in burnt forest, as seen in the lower taxonomic richness in old-growth forest during assembly. The difference in tree-species composition between the two forest types, with more Norway spruce (the bolt species) in the old-growth sites than in the burnt-forest sites, is therefore not crucial for the results. Regardless of tree-species composition, the colonization mode for burnt forest is still external. (2) A high amount of CWD in the burnt sites could explain why

the community-level carrying capacity was not reached in burnt forest. The colonizers arriving at the burnt sites would be spread out over the CWD created by the fire and the densities in individual CWD units would be low. The amount of fresh CWD is generally very high in newly burnt forest (Uotila et al. 2001, Stokland et al. 2012). The amount of CWD was most likely severely underestimated in the burnt sites in my study. A possible reason for this is that the CWD-inventory was done the same year as the fires. At this stage, it is difficult to estimate whether an injured tree will die or survive. Many of the trees classified as living at the time of inventory were probably sufficiently damaged by the fire (primarily by leaf-needle mortality) to be suitable as substrate for the focal species. Furthermore, Wikars and Schimmel (2001), who also did an experiment at Eggåsen, estimate that 50 % of the trees in that site were killed by fire. Also the high abundance of *Pissodes gyllenhalii* in burnt forest in the present study is important in this context as it is normally a rare and local species but can reach high abundance when there is locally a large amount of CWD (e.g. after stormfellings: Ehnström and Axelsson 2002). In my study it characterized burnt forest and was also bolt dominant in 31 % of the bolts in that forest type. *Pissodes gyllenhalii* could therefore indicate that the CWD amount was high in the burnt forest sites. However, further studies are clearly needed to establish whether the amount of CWD is the mechanism behind the forest-type specific community assembly.

### **Cambivore Specialization**

The forest-type convergence in the proportion of cambivores and the forest-type difference in the species identity of those cambivores showed that the cambivore role offers opportunity for forest-type specialization. Patch quality, such as tree species, decay stage, and sun-exposure all affect saproxylic beetles (e.g. Vanderwel et al. 2006, Hjältén et al. 2007). Therefore, I used standardized bolts with standardized sun-exposure at the bolt group. However, the burnt sites were a more structurally open forest-habitat at the stand level, mainly because shrubs and small trees were consumed by the fire. The charred ground in the burnt forest could also increase heat retention. All this could increase temperatures on a forest-stand level in the burnt forest, a difference in microclimate that could be a basis for abiotic filtering. A pattern consistent with abiotic filtering was obvious for four cambivorous species. Old-growth forest had a higher abundance of *Dryocoetes autographus*, *Dryocoetes hectographus* and *Tetropium castaneum*, three species more common in closed forest than in sun-exposed forest (Ehnström and Axelsson 2002), whereas burnt forest had a higher abundance of *Pityogenes chalcographus*, a common species also in clear-cuts, a very open habitat (Ehnström and Axelsson 2002). *Pissodes gyllenhalii* also preferred burnt forest and the most important factor for this species could be the CWD amount as previously explained. Furthermore, as could be expected the fire-favoured cambivorous cerambycid *Rhagium inquisitor* was more abundant in burnt forest.

### **Erased Importance of Functional Groups**

Fungivores, predators and facultative predators were all more important early during assembly than in the first-year final states. Their importance had become “erased” (as

discussed in Drake 1991) and would not have been detected in a study of first-year final states only. This clearly points to the importance of community assembly studies in order to understand natural communities. In the present study fungivores made up 15-27 % of the individuals during the 1- to 4-week exposures in burnt forest whereas in old-growth forest they made up less than 1 %. Furthermore, the two fire-favoured fungivores, *Atomaria pulchra* and *Corticaria rubripes*, were even bolt dominants in burnt forest. This indicates that burnt forest is even more important for fungivores than previous studies on first-year final states indicate (Wikars 2002). Fungivorous beetles is a group that suffer from habitat fragmentation in managed forest (Komonen et al. 2000, Victorsson and Jonsell 2013) and prescribed burning of forest might be especially important for this group.

The pattern for the predators was driven by the staphylinids *Phloeonomus sjoeborgi* and *Phloeonomus planus* since they were the most abundant predators. The prey choice for these species is scolytine eggs and larvae (Palm 1951, Nuorteva 1956). Likewise *Thanasimus formicarius* is a predator known to feed on scolytines (Kenis et al. 2004). The predator proportion was initially high in both forest types but later decreased as the number of scolytines increased. Such a pattern has been described by Aukema and Raffa (2004) as a predator-diluting effect contingent on scolytine biology. They conclude that the predators are unable to track the rapid, pheromone-mediated, increase of the scolytines. The pattern for the predators in the present study could have the same explanation. The pattern for the facultative predators was a scaled-down copy of the predator pattern. Among these species, the three *Rhizophagus* species as well as the *Epurea* species are associated with scolytines (Kenis et al. 2004) as predators and detritivores of dead scolytines and exuviae. It is noteworthy that the predator *P. sjoeborgi* preferred old-growth forest (129 individuals) over burnt forest (37) even though it is fire-favoured (Wikars 2006). Predators must of course follow their prey and the much higher abundance of scolytines in old-growth forest compared to burnt forest could explain this result.

## Fire-Dependent Species

The result that the community-level carrying capacity was not reached in burnt forest suggests that burnt forest can be a competition-reduced habitat for saproxylic beetles, as has previously been proposed (Esseen et al. 1992, Wikars 1992). Obviously, given an exposure time long enough, the community-level carrying capacity would be reached also in the burnt sites. However, the longest exposure time in the present study included most of the remaining season for the focal species (Vanderwel et al. 2006). In natural CWD, colonization would restart the following year (Boulanger and Sirois 2007) and the community-level carrying capacity might be reached also in burnt forest. However, even if larval resource competition becomes important in burnt forest over the years following the fire, my results suggest that it is unimportant during the fire-year.

Some beetle species are adapted to the burnt-forest habitat and depend on burnt forest for their reproduction. Such pyrophilous (fire loving) species are threatened by the lack of burnt forest in areas dominated by forestry (Wikars 1992, Esseen et al. 1997, Wikars 2002). Fire-adaptation in beetles can include long-range dispersal capacity, the ability to develop in sun-exposed CWD, specialized senses for fire-detection, a propensity to mate near still glowing fire, and possibly coloration (Evans 1964, Schmitz et al. 1997, Schutz et al. 1999, Allison et

al. 2004, Evans 2010, Schmitz and Bousack 2012). I found two fire-dependent and nine fire-favoured species in burnt forest (*sensu* Wikars 2006). Such species generally prefer scorched CWD (Wikars 2002, Johansson et al. 2007) but the results presented here, where I used unscorched bolts, show that also factors other than scorching are important. The results in this chapter indicate that the dispersal-assembled community in burnt forest could be important. Pyrophilous species could invade these competition-reduced habitats and gain priority over more competitive, later-arriving species. In a niche-assembled community in old-growth forest such species might not be able to establish due to poor competitive abilities. Priority effects are important in saproxylic beetles (Weslien et al. 2011, Victorsson 2012) and arrival order could be crucial for pyrophilous species.

## CONCLUSION

Community assembly differed in many respects between burnt and old-growth forest. The saproxylic beetle assemblage in old-growth forest conformed to a niche-assembled community (*sensu* Chase 2007) since the community-level carrying capacity was reached during assembly and most bolts were dominated by the same species, the cambivorous scolytine *D. autographus*. In contrast, the beetle assemblage in burnt forest conformed to a dispersal-assembled community (*sensu* Chase 2007) since the community-level carrying capacity was not reached and the bolts were dominated by a variety of species. Furthermore, there was a wider bolt-to bolt variation in species composition and a higher evenness in burnt forest. Additionally, the burnt forest bolts harboured only half the number of species per bolt as the old-growth bolts which could indicate that the available niche space was not filled up in burnt forest.

These results indicate that pyrophilous species could be adapted not only to the burnt wood *per se* but also to the dispersal-assembled community type developing in burnt forest. To conserve pyrophilous species it seems imperative that prescribed burning creates competition-reduced habitats where pyrophilous species can develop. In this respect, the practice of burning clear-cuts as a conservation measure seems less than perfect. If a large amount of CWD is created on the clear-cut, a prescribed burning might have some value but the importance of burning intact forest cannot be overemphasized.

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## APPENDIX 1.

Abundance of all saproxylic beetles reared from 140 Norway spruce *Picea abies* bolts at two old-growth and two burnt forest sites in central Sweden. The bolts were exposed for colonization for 0.5, 1, 2, 4, or 8 weeks. The species biology, functional group and relation to fire, were taken from the literature (see text for details). Red list categories are from the Swedish national red list (threat category and publication year in parenthesis after the species name).

Family	Species	Biology	Burnt forest					Old-growth forest					Total
			0.5 w	1 w	2 w	4 w	8 w	0.5 w	1 w	2 w	4 w	8 w	
Ptiliidae	<i>Pteryx suturalis</i>	f					1					1	2
Staphylinidae	<i>Acrulia inflata</i>	f										3	3
	<i>Hapalarea linearis</i>	p										2	2
	<i>Phloeonomus planus</i>	p	2	2	1	1	1	6	21	12	11	10	67
	<i>Phloeonomus lapponicus</i>	p, FF		1	1	1						5	8
	<i>Phloeonomus sjoeborgi</i>	p, FF	3	12	16	2	4	4	8	45	38	34	166
	<i>Coryphium angusticolle</i>									1			1
	<i>Dadobia immersa</i>	f					2						2
	<i>Dinaraea aequata</i>						2						2
	<i>Dinaraea linearis</i>										1		1
	<i>Leptusa pulchella</i>	f								1	1	7	9
	<i>Placusa tachyporoides</i>	p		1									1
	<i>Placusa incompleta</i>	p							5				5
	<i>Placusa suecica</i>	p		1	2				5	2	1		11
	<i>Placusa atrata</i>	p, FF		1						1			2
Cantharidae	<i>Malthodes brevicollis</i>	p						1					1
Anobiidae	<i>Ptinus villiger</i>		1										1
	<i>Ptinus subpilosus</i>	f							1			2	3

Family	Species	Biology	Burnt forest					Old-growth forest					Total
			0.5 w	1 w	2 w	4 w	8 w	0.5 w	1 w	2 w	4 w	8 w	
Cleridae	<i>Thanasimus formicarius</i>	p								5	1	1	7
Nitidulidae	<i>Epuraea angustula</i>	fac			1	1			1			2	5
	<i>Epuraea boreella</i>	fac		1		1		3	3	5	7	11	31
	<i>Epuraea pygmaea</i>	fac									1	1	2
	<i>Epuraea rufomarginata</i>	fac		1									1
	<i>Glischrochilus quadripunctatus</i>	fac,FF		1									1
Monotomidae	<i>Rhizophagus ferrugineus</i>	fac					1				12	26	39
	<i>Rhizophagus dispar</i>	fac							2	2	1	4	9
	<i>Rhizophagus parvulus</i>	fac			1						1		2
Silvanidae	<i>Silvanus bidentatus</i> (NT 2005)	fac, FF			1								1
Cryptophagidae	<i>Henoticus serratus</i>	FD			1								1
	<i>Cryptophagus corticinus</i>	f, FD	1										1
	<i>Atomaria morio</i>	f							1				1
	<i>Atomaria fuscipes</i>	f					1						1
	<i>Atomaria elongatula</i>	f			1	1							2
	<i>Atomaria pulchra</i>	f, FF	3	10	12	15	11						51
Latridiidae	<i>Corticaria rubripes</i>	f, FF	13	23	11	18	3						68
	<i>Corticaria ferruginea</i>	f, FF	1	5			1						7
Salpingidae	<i>Salpingus ruficollis</i>	p							1				1
Cerambycidae	<i>Tetropium castaneum</i>	c	11	33		15	13			41	197	208	518
	<i>Tetropium fuscum</i>	c									1		1
	<i>Rhagium inquisitor</i>	c, FF		4	5	7	2		1			1	20
	<i>Pogonocherus fasciculatus</i>	c									2		2
Curculionidae	<i>Hylobius piceus</i>	c										1	1
	<i>Pissodes glyllenhalii</i>	c	10	128	29	67	210		13	45	29	51	582

(Continued)

Family	Species	Biology	Burnt forest					Old-growth forest					Total
			0.5 w	1 w	2 w	4 w	8 w	0.5 w	1 w	2 w	4 w	8 w	
Scolytinae	<i>Hylurgops glabratus</i>	c							1	16	25		42
	<i>Hylurgops palliatus</i>	c						1	1				2
	<i>Hylastes brunneus</i>	c		1			1				2		4
	<i>Hylastes cunicularius</i>	c	1	3	1	7	19	1	7	25	77	74	215
	<i>Xylechinus pilosus</i>	c								1			1
	<i>Tomicus piniperda</i>	c		1									1
	<i>Dendroctonus micans</i>	c									28		28
	<i>Pityogenes chalcographus</i>	c		2		16	702			67			787
	<i>Pityogenes bidentatus</i>	c					2						2
	<i>Dryocoetes autographus</i>	c	39	119	77	111	163	205	149	478	2148	1652	5141
	<i>Dryocoetes hectographus</i>	c							22		256	234	512
	<i>Dryocoetes</i> spp.	c	1	4	1	2	10	9	13	28	146	209	423
	<i>Crypturgus pusillus</i>	c								1			1
	<i>Trypodendron lineatum</i>	f										1	1
	<b>Total</b>		86	354	161	265	1149	230	255	776	2986	2540	8802

Abbreviations: w, weeks of exposure; NT, near threatened; c, cambivorous; f, fungivorous; p, predator; fac, facultative predator (also feeds as a detritivore or fungivore).FD, fire-dependent; FF, fire-favoured.

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**REFERENCES**

- Allison, J. D., Borden, J. H. & Seybold, S. J. (2004). A review of the chemical ecology of the Cerambycidae (Coleoptera). *Chemoecology*, *14*, 123-150.
- Anderbrant, O., Schlyter, F. & Birgersson, G. (1985). Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. *Oikos*, *45*, 89-98.
- Aukema, B. H. & Raffa, K. F. (2004). Does aggregation benefit bark beetles by diluting predation? Links between a group-colonisation strategy and the absence of emergent multiple predator effects. *Ecological Entomology*, *29*, 129-138.
- Boulanger, Y. & Sirois, L. (2007). Postfire succession of saproxylic arthropods, with emphasis on coleoptera, in the north boreal forest of Quebec. *Environmental Entomology*, *36*, 128-141.
- Boulanger, Y., Sirois, L. & Hébert, C. (2010). Distribution of saproxylic beetles in a recently burnt landscape of the northern boreal forest of Québec. *Forest Ecology and Management*, *260*, 1114-1123.
- Buddle, C. M., Spence, J. R. & Langor, D. W. (2000). Succession of boreal forest spider assemblages following wildfire and harvesting. *Ecography*, *23*, 424-436.
- Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 17430-17434.
- Clarke, K. R. & Gorley, R. N. (2006). PRIMER v6: user manual/tutorial. PRIMER-E Ltd., Plymouth.
- Clarke, K. R. & Warwick, R. M. (2001). Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E Ltd., Plymouth.
- Dajoz, R. (2000). Insects and forests: the role and diversity of insects in the forest environment. Intercept, Paris.
- Denno, R. F., McClure, M. S. & Ott, J. R. (1995). Interspecific interactions in phytophagous insects - competition reexamined and resurrected. *Annual Review of Entomology*, *40*, 297-331.
- Diamond, J. M. (1975). Assembly of species communities. Pages 342-444 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Drake, J. A. (1991). Community assembly mechanics and the structure of an experimental species ensemble. *American Naturalist*, *137*, 1-26.
- Drake, J. A., Zimmerman, C. R., Purucker, T. & Rojo, C. (1999). On the nature of the assembly trajectory. Pages 233-250 in E. Weiher and P. Keddy, editors. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge.
- Ehnström, B. & Axelsson, R. (2002). Insektsnag i bark och ved. ArtDatabanken, SLU, Uppsala.
- Esseen, P. A., Ehnström, B., Ericson, L. & Sjöberg, K. (1992). Boreal forests-the focal habitats of Fennoscandia. Pages 252-325 in L. Hansson, editor. Ecological principles of nature conservation. Elsevier Applied Science, Amsterdam.
- Esseen, P. A., Ehnström, B., Ericson, L. & Sjöberg, K. (1997). Boreal forests. *Ecological Bulletins*, *46*, 16-47.

- Evans, W. G. (1962). Notes on the biology and dispersal of *Melanophila*. *The Pan-Pacific Entomologist*, 38, 59-63.
- Evans, W. G. (1964). Infra-red receptors in *Melanophila acuminata* DeGeer. *Nature*, 202, 211.
- Evans, W. G. (1971). The attraction of insects to forest fires. Pages 115-127 in Tall Timbers conference on ecological animal control by habitat management, proceedings, Tall Timbers Research Station, Tallahassee, Florida.
- Evans, W. G. (2010). Reproductive Role of Infrared Radiation Sensors of *Melanophila acuminata* (Coleoptera: Buprestidae) at Forest Fires. *Annals of the Entomological Society of America*, 103, 823-826.
- Fridman, J. & Walheim, M. (2000). Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management*, 131, 23-36.
- Hjältén, J., Johansson, T., Alinvi, O., Danell, K., Ball, J. P., Pettersson, R., Gibb, H. & Hilszczanski, J. (2007). The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. *Basic and Applied Ecology*, 8, 364-376.
- Hjältén, J., Stenbacka, F. & Andersson, J. (2010). Saproxylic beetle assemblages on low stumps, high stumps and logs: Implications for environmental effects of stump harvesting. *Forest Ecology and Management*, 260, 1149-1155.
- Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Jenkins, D. G. & Buikema, A. L. (1998). Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecological Monographs*, 68, 421-443.
- Johansson, T., Hjältén, J., Gibb, H., Hilszczanski, J., Stenlid, J., Ball, J. P., Alinvi, O. & Danell, K. (2007). Variable response of different functional groups of saproxylic beetles to substrate manipulation and forest management: implications for conservation strategies. *Forest Ecology and Management*, 242, 496-510.
- Kenis, M., Wermelinger, B. & Grégoire, J. C. (2004). Research on parasitoids and predators of scolytidae, a review. Pages 237-290 in F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire, and H. F. Evans, editors. *Bark and wood boring insects in living trees in Europe, a synthesis*. Springer, Dordrecht.
- Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. (2000). Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos*, 90, 119-126.
- Koskela, H. & Hanski, I. (1977). Structure and succession in a beetle community inhabiting cow dung. *Annales Zoologici Fennici*, 14, 204-223.
- Kuusela, S. & Hanski, I. (1982). The structure of carrion fly communities - the size and the type of carrion. *Holarctic Ecology*, 5, 337-348.
- Lieutier, F., Day, K. R., Battisti, A., Grégoire, J. C. & Evans, H. F. editors. (2004). *Bark and wood boring insects in living trees in Europe, a synthesis*. Springer, Dordrecht.
- Littell, R., Milliken, G., Stroup, W., Wolfinger, R. & Schabenberger, O. (2006). *SAS for Mixed Models*. 2 edition. SAS Press, Cary.
- Lundberg, S. & Gustafsson, B. (1995). *Catalogus Coleopterorum Sueciae*. Naturhistoriska riksmuseet & Entomologiska föreningen Stockholm, Stockholm.
- Magurran, A. E. (2004). *Measuring biological diversity*. Blackwell Publishing, London.

- Martikainen, P., Siitonen, J., Kaila, L., Punttila, P. & Rauh, J. (1999). Bark beetles (Coleoptera, Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. *Forest Ecology and Management*, 116, 233-245.
- McCune, B. & Grace, J. B. (2002). Analysis of ecological communities. MJM Software Design, Gleneden Beach, Oregon.
- Niklasson, M. & Granström, A. (2000). Numbers and sizes of fires: Long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology*, 81, 1484-1499.
- Nuorteva, M. (1956). Über den Fichtenstamm-Bastkäfer, *Hylurgops palliatus* Gyll., und seine Insektenfeinde. *Acta Entomologica Fennica*, 13, 1-116.
- Palm, T. (1951). Die Holz- und Rinden-Käfer der nordschwedischen Laubbäume. Esselte, Stockholm.
- Pianka, E. R. (1980). Guild structure in desert lizards. *Oikos*, 35, 194-201.
- Quinn, G. P. & Keough, M. J. (2002). Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.
- Rankin, L. J. & Borden, J. H. (1991). Competitive interactions between the Mountain pine-beetle and the Pine engraver in Lodgepole pine. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 21, 1029-1036.
- Sauvard, D. (1989). Multiplication capacities of *Tomicus piniperda* L. (Col, Scolytidae).1. Effects of attack density. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie*, 108, 164-181.
- Schlyter, F. & Anderbrant, O. (1993). Competition and niche separation between two bark beetles - existence and mechanisms. *Oikos*, 68, 437-447.
- Schmitz, H., Bleckmann, H. & Murtz, M. (1997). Infrared detection in a beetle. *Nature*, 386, 773-774.
- Schmitz, H. & Bousack, H. (2012). Modelling a historic oil-tank fire allows an estimation of the sensitivity of the infrared receptors in pyrophilous *Melanophila* beetles. *Plos One* 7.
- Schroeder, L. M. & Weslien, J. (1994). Interactions between the phloem-feeding species *Tomicus piniperda* (Col, Scolytidae) and *Acanthocinus aedilis* (Col, Cerambycidae), and the predator *Thanasimus formicarius* (Col, Cleridae) with special reference to brood production. *Entomophaga* 39, 149-157.
- Schutz, S., Weissbecker, B., Hummel, H. E., Apel, K. H., Schmitz, H. & Bleckmann, H. (1999). Insect antenna as a smoke detector. *Nature*, 398, 298-299.
- Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 49, 11-42.
- Smith, B. & Wilson, J. B. (1996). A consumer's guide to evenness indices. *Oikos*, 76, 70-82.
- Stokland, J. N., Siitonen, J. & Jonsson, B. G. (2012). Biodiversity in dead wood. Cambridge University Press, Cambridge.
- Ulyshen, M. D., Horn, S., Barnes, B. & Gandhi, K. J. K. (2010). Impacts of prescribed fire on saproxylic beetles in loblolly pine logs. *Insect Conservation and Diversity*, 3, 247-251.
- Uotila, A., Maltamo, M., Uuttera, J. & Isomäki, A. (2001). Stand structure in semi-natural and managed forests in eastern Finland and Russian Karelia. *Ecological Bulletins*, 49, 149-158.
- Vanderwel, M. C., Malcolm, J. R., Smith, S. A. & Islam, N. (2006). Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. *Forest Ecology and Management*, 225, 190-199.

- Warren, P. H., Law, R. & Weatherby, A. J. (2003). Mapping the assembly of protist communities in microcosms. *Ecology*, *84*, 1001-1011.
- Warwick, R. M. & Clarke, K. R. (1995). New "biodiversity" measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology-Progress Series*, *129*, 301-305.
- Weiher, E. & Keddy, P. editors. (1999). Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Cambridge, UK.
- Weslien, J. (1994). Interactions within and between species at different densities of the bark beetle *Ips typographus* and its predator *Thanasimus formicarius*. *Entomologia Experimentalis et Applicata*, *71*, 133-143.
- Weslien, J., Djupström, L. B., Schroeder, M. & Widenfalk, O. (2011). Long-term priority effects among insects and fungi colonizing decaying wood. *Journal of Animal Ecology*, *80*, 1155-1162. .
- Victorsson, J. (2012). Semi-field experiments investigating facilitation: arrival order decides the interrelationship between two saproxylic beetle species. *Ecological Entomology*, *37*, 395-401.
- Victorsson, J. & Jonsell, M. (2013). Effects of stump extraction on saproxylic beetle diversity in Swedish clear-cuts. *Insect Conservation and Diversity*, *6*, 483-493.
- Wikars, L. O. (1992). Skogsbränder och insekter. *Entomologisk Tidskrift*, *113*, 1-11.
- Wikars, L. O. (2002). Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. *Journal of Insect Conservation*, *6*, 1-12.
- Wikars, L. O. (2006). Åtgärdsprogram för bevarande av brandinsekter i boreal skog.
- Wikars, L. O. & Schimmel, J. (2001). Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. *Forest Ecology and Management*, *141*, 189-200.
- Zackrisson, O. (1977). Influence of forest fires on the North Swedish boreal forest. *Oikos*, *29*, 22-32.