

BIOLOGICAL DIVERSITY OF GROUND-DWELLING BEETLES  
(COLEOPTERA): IMPACTS OF FREQUENT CUTTING OF THE  
TREE LAYER

BIOLOGISK DIVERSITET HOS BAKKELEVENDE BILLER  
(COLEOPTERA): PÅVIRKNING AV REGELMESSIG FELLING AV  
TRESJIKTET

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## **Forord**

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## **Abstract**

Forestry is the main disturbance in forest ecosystems in Fennoscandia. Power-line corridors have some similarities with clear cuts created through modern forestry practices, but regrowth of vegetation is suppressed by regular clearing of the corridors, and the habitat is thus maintained in an early successional stage. In addition, cut trees are typically left behind after clearing of the corridors, i.e., no biomass is removed after clear cutting. Beetles (Coleoptera) are important for ecosystem services and forestry is regarded as the major threat for beetle communities. In this study, differences in ground-dwelling beetle species richness, biodiversity, community composition and composition of functional groups (predators, herbivores, detritivores and other) between two different successional stages (power-line corridors and closed canopy forests) were studied. A total of 320 pitfall traps were distributed on 160 plots at 20 sites. Half of the traps were located in early successional stages (power-line corridors) and half in late successional stages (closed canopy forests). In each plot, a number of environmental variables were also measured. We predicted that (1) species richness would be higher in early successional stages, (2) biodiversity would be higher in later successional stages, (3) species abundance distribution would be relatively similar in both habitats (4) species composition would differ between early and later successional stages, and (5) predator species would be more numerous in forest than power-line corridors. A total of 38 541 individuals and 423 species of beetles were captured. In contrast to our predictions, we found that beetle species richness did not differ between early and later successional stages, whereas beetle biodiversity was higher in early successional stages. Species abundance distribution investigated by comparing empirical cumulative distribution functions (ECDF) showed no difference between habitats. In accordance with our prediction, species composition differed significantly between early and later successional stages. However, the relative proportion of individuals and species within the main functional groups (predators, detritivores, herbivores and other) did not differ between the two habitats. In addition to successional stage, field layer and the structure of forest were additional factors that explained differences in species richness, biodiversity, species composition and functional diversity.

## Sammendrag

En av de viktigste forstyrrelsene i skogøkosystem i Fennoskandia er forårsaket av skogbruk. Kraftgater har mange likheter med hogstflater dannet av skogbruk, men gjengroing av vegetasjonen vil stadig holdes nede ved regelmessig rydding. Dette gjør at kraftgatene holdes i en tidlig suksesjonsfase. Etter rydding av kraftgatene legges trærne igjen, altså ingen biomasse blir fjernet fra kraftgatene. Biller (Coleoptera) har en viktig funksjon i økosystemene og skogbruk er en av hovedtrusselene mot billearter. I denne studien ble forskjeller i artsrikdom, biodiversitet, fordeling av artstetthet, artssammensetning og sammensetning av funksjonelle grupper (predatorer, herbivore, detrivore og andre) av biller undersøkt i to forskjellige suksesjonsfaser (kraftgater og skog). Totalt ble 320 feller fordelt på 160 plott og på 20 sites. Halvparten av fellene stod i tidlig suksesjonsfase (kraftgate) og halvparten i eldre suksesjonsfase (skog). Miljøvariabler ble registrert på hvert plot. Vi forventet at (1) artsrikdommen var høyere i tidlig suksesjonsfase, (2) biodiversiteten var høyere i eldre suksesjonsfaser, (3) fordeling av artstetthet var relativ lik mellom suksesjonsfasene, (4) artssammensetningen vil fordannes seg mellom suksesjonsfasene og (5) predatorer hadde et høyere antall arter i skogen enn i kraftgatene. Totalt ble 38 541 individ og 423 arter av biller samlet. I motsetning til våre forventninger fant vi ikke forskjell i artsrikdommen av biller i de to suksesjonsfasene, men biodiversiteten var høyere i tidlig suksesjonsfase. Sammenligning av empirisk kumulativ tetthetsfordeling viste at fordelingen av artstettheten var lik i de to suksesjonsstadiene. Som forventet var artssammensetningen påvirket av suksesjonsfasen, derimot var den relative fordelingen av individer og arter i samme funksjonelle gruppe (predatorer, detrivore, herbivore og andre) lik i begge habitat. I tillegg til suksesjonsfasen var feltvegetasjonen og skogstrukturen faktorer som forklarte forskjeller i artsrikdom, biodiversitet, artssammensetning og funksjonell diversitet.

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## 1. Introduction

Disturbances play a key role and occur in various forms in all ecosystems (White & Jentsch 2001; Turner 2010). A disturbance is an event that often changes the ecosystem, community or population structure (Pickett & White 1985). The availability of resources and substrate, as well as the physical environment, can change (Pickett & White 1985; Holt 2008).

Disturbances may change the environmental conditions and lead to changes in species composition, resulting in a heterogeneous environment. The frequency, return interval, rotation period, size and intensity of a disturbance refer to the disturbance regime (Pickett & White 1985). Succession after a disturbance is influenced by the disturbance regime, the size, shape and structure of the disturbed habitat. When disturbed patches are large, interval between disturbances is short and biotic residuals are few, succession is more variable and unpredictable (Turner et al. 1998). Disturbances can be natural or anthropogenic. In forest, natural disturbances could be caused by e.g. windthrows or insect attacks, whereas anthropogenic disturbances could be forestry and even deforestation. However, the distinction between natural and anthropogenic disturbances is not always clear. For example, forest fire can be a natural disturbance or a result from human activity (Dale et al. 1998).

Modern forestry practices have led to younger forests with shorter rotation times and new disturbance regimes (Esseen et al. 1997; Niemelä et al. 2007). With widespread use of clear cutting, forestry has replaced forest fire as the main initiator of secondary succession, and this represents the most important ecosystem change in Fennoscandian boreal forests (Esseen et al. 1997; Niemelä 1999). After fire or clear cutting, biodiversity will change throughout the succession, and all successional stages are important to maintain a high level of biodiversity at the landscape level (Heyborne et al. 2003). However, there are many differences between clear cuts and burned areas when it comes to species composition, functional capabilities and structure in forest (Franklin 1998). In addition to forestry, another anthropogenic disturbance that creates early successional stage forests, is the establishment and maintenance of power-line corridors. In 2010 approximately 40 % of Norway was covered by forest, mainly boreal (Moen et al. 1998; Statistics Norway 2011). These forested areas are intersected by a network of power-line corridors. When the power-line corridors are established, all trees are cut down. Thus power-line corridors have many similarities with clear-cuts. However, whereas clear-cuts will gradually develop into old mature forest again, regrowth of vegetation in power-line corridors will be suppressed by regular cutting, and the habitat will be maintained in an early successional stage (Smallidge et al. 1996). In addition, biomass is not removed from the

power-line corridors after clearing. Maintaining the forest in early successional stages will probably have a negative effect on specialist forest species (Niemelä et al. 1993). However, some species may benefit from the early successional stages that the power-line habitats provide. For example, Forrester et al. (2005) found that power-line corridors are a suitable habitat for the threatened Karner blue butterfly *Lycaeides melissa samuelis*, and Hollmen et al. (2008) found that power-line corridors were suitable habitats for some specialist carabid species.

Insects play an important role in ecosystem functions (Price et al. 2011). They consume living plant tissue, decompose dead organic material, are important for nutrient cycling, are a food source for other animals (Gullan et al. 2010; Price et al. 2011), and play a vital role in pollination (Didham et al. 1996). Beetles (Coleoptera) are one of the largest insect orders (Gaston 1991), and are found in almost all types of habitats except strictly marine environment (Ødegaard et al. 2010). In Norway, it is estimated that there are 3800 beetle species and approximately 95 beetle families, depending on the systematic classification used. A major part of the red listed beetles in Norway are found in forest, and forestry is regarded as the major threat (Ødegaard et al. 2010).

Many studies have addressed effects of disturbances on insects (Murdoch et al. 1972; Southwood et al. 1979) or beetle families (Niemelä et al. 1988; Niemelä 1993; Niemelä et al. 1993; Heliölä et al. 2001), and ground-dwelling beetles have been regarded as suitable bioindicators for ecosystem conditions (Bohac 1999; Rainio & Niemelä 2003; Pearce & Venier 2006). However, there have been few studies looking at the whole order of beetles and their responses to disturbances. Several studies have found that total beetle species richness increased after clear cutting (Niemelä et al. 1993; Haila et al. 1994; Spence et al. 1996). However, Paquin (2008) found carabid beetle richness to be highest in both early and late successional stages, whereas richness was lower in forests of intermediate age. Biodiversity is assumed to be higher in later successional stages, but depend most on habitat complexity (Southwood et al. 1979; Lassau et al. 2005). Niemelä et al. (1993) compared the carabid beetle assemblage in newly cut and mature forest, and found three different responses to logging. Forest generalists were not affected by logging and persisted through the succession, open habitat species increased after logging, whereas species preferring closed canopy forests decreased after logging (Niemelä et al. 1993).



In this study, we compared forest habitats maintained in early successional stages (power-line corridors) and later successional stage (closed canopy forest) with respect to ground-dwelling beetle richness, biodiversity and species composition and composition of functional groups. The overall objective was to investigate the influence on biological diversity of regular clearing of the vegetation every ten years (Skjervold 2012), without subsequent removal of biomass. Our main predictions were (1) species richness will be higher in early successional stages (Koivula et al. 2002), (2) biodiversity will be higher in later successional stages (Southwood et al. 1979), (3) species abundance distribution will be relatively similar in both habitats (Koivula et al. 2002) (4) species composition will differ between early and later successional stages (Niemelä et al. 1993) and (5) predator species will be more numerous in closed canopy forests than in power-line corridors (Barberena-Arias & Aide 2003).

## 2. Methods

### 2.1 Site selection and experimental design

The study area was located in South-Eastern Norway. In 2009, 84 sites were selected haphazardly by placing 84 crosses on a map of Statnett's power-line network in South-Eastern Norway. Out of these, 54 were randomly chosen for data collection on vegetation by drawing lots. All power-lines should be in a corridor with a minimum of 200 metres of coniferous or deciduous forest perpendicular to the edge of the power-line corridors. To determine if this criteria was fulfilled, satellite photos from "Norge i Bilder" were used. If the criteria were not fulfilled, the site was moved to the nearest suitable location. Out of these 54 sites, ten sites were chosen in 2010 and ten new sites were chosen in 2011 for data collection on beetles (Figure 1).

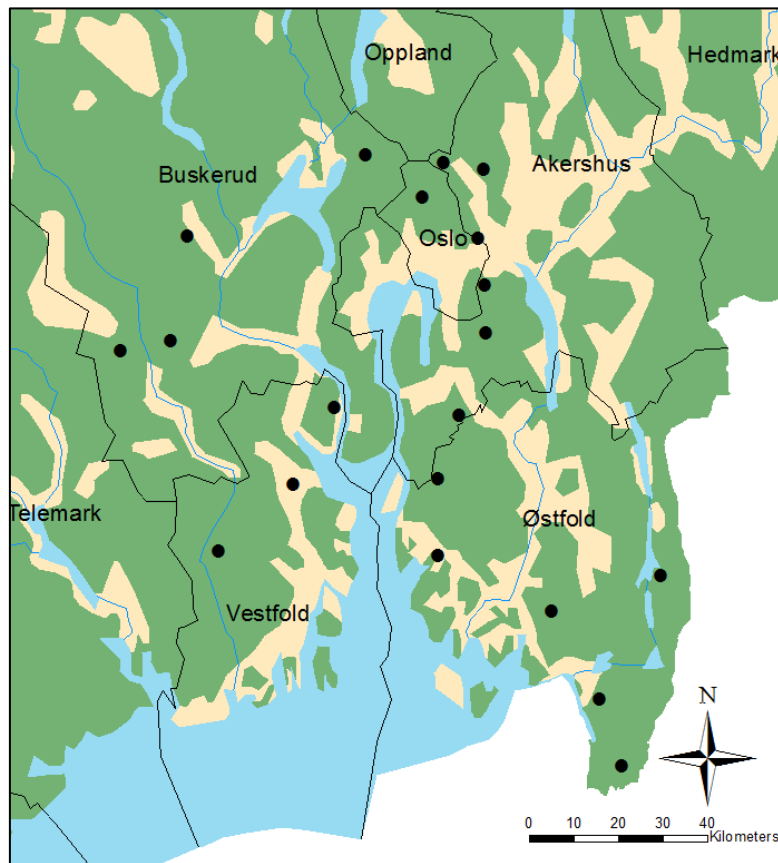


Figure 1. The geographical distribution of the 20 study sites in Eastern Norway where beetles were collected in 2010 and 2011.

Each site comprised eight rectangular plots of 4 m x 5 m. Four plots were located along the ‘centre line’ of the power-line corridor, and four plots were located along a parallel transect 100 metres into the forest from the boarder of the power-line corridor (Figure 2). Plots in the same habitat (power-line corridor or forest) were placed 50 metres apart. All plots were placed more than 50 metres from a power-line post, and in between two power-line posts. Each plot contains five sub-plots of 1 m x 1 m (Figure 2). Each plot was marked with the GPS-coordinates in the south-western corner of each sub-plot by use of a handheld GARMIN (60CSx) GPS (datum; WGS 84, UTM 32V).

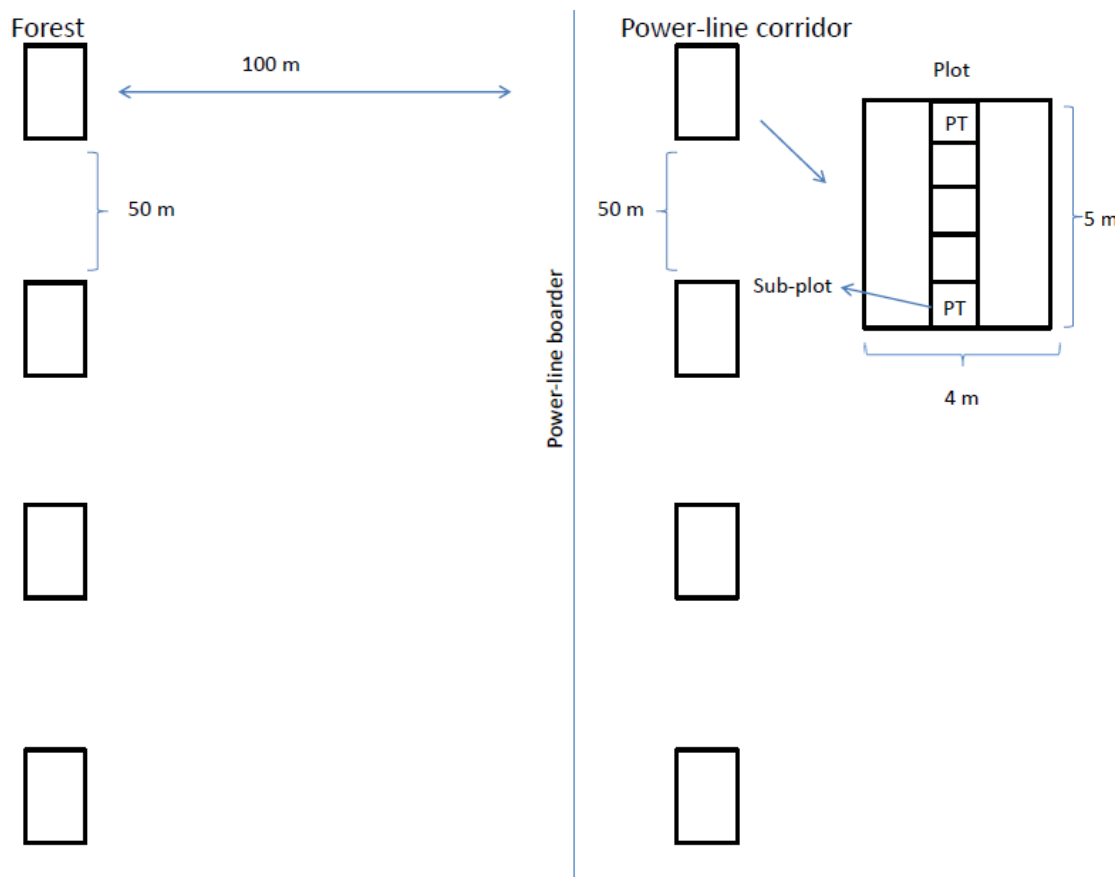


Figure 2. Schematic illustration of a study site. Each study site ( $n = 20$  sites), where one site comprised eight plots and 40 sub-plots. Pitfall traps were located in sub-plot one and five in each plot, marked with PT in the diagram. Plots in the same habitat were placed with 50 metres distance to each other. Four plots were located along the centre line of the power-line corridors and four plots were located along a parallel transect 100 metres into the closed canopy forests.

## 2.2 Data collection beetles

### 2.2.1 Field work

Pitfall traps were deployed from the start of May in 2010 and in the end of April in 2011, to September (both years). Pitfall traps (from BioQuip.com) were placed in sub-plot 1 and sub-plot 5 in each plot (Figure 2). The trap consists of two round plastic cups (height 7 cm, volume 540 ml), one removable and one stationary (Figure 3). To ensure insect preservation, the cup was filled with 1:1 mix of propylene glycol and water and a few drops of washing detergent. The traps were covered with plastic roofs to prevent rain water and small vertebrates from falling into the traps.

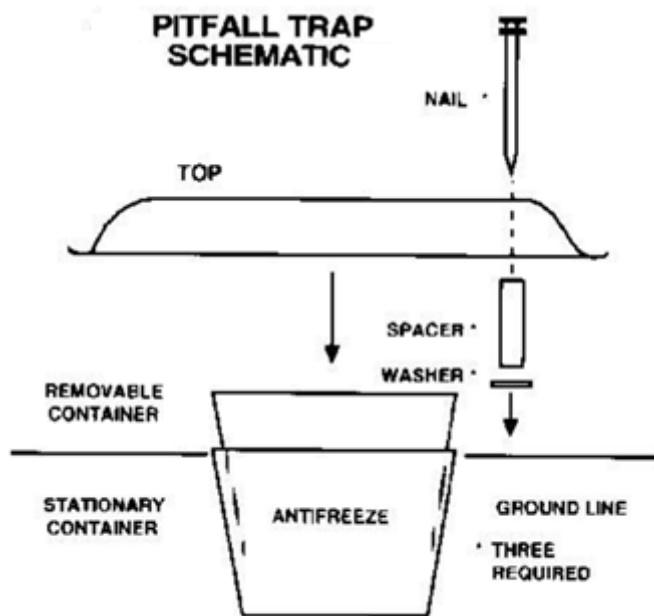


Figure 3. Schematic diagram of a pitfall trap (from BioQuip.com) .

The traps were emptied and beetles were brought back to the laboratory once every month until September 2010 and October 2011 (four data collections each year). New preservation liquid was refilled in the field at the three first collection rounds.

## **2.2.2 Laboratory material and species identification**

The beetle samples collected in the field were transported back to the laboratory. The contents of each pitfall trap was sifted through a mesh and then transferred to marked containers with 80% ethanol. If the traps contained small vertebrates or other large elements as leaves and sticks, they were removed. Thereafter, the beetle samples were sent to an beetle taxonomist (Sindre Ligaard) for species identification and categorisation. Each beetle species that occurred in the total data material was categorised according to its main ecological function as imago, and placed in one of the following functional groups according to the literature found in Appendix 1: dead wood feeders, live wood feeders, herbivores, predators, fungivores and general detritivores. Beetles were identified to species following the nomenclature of Silfverberg (2004).

## **2.3 Data collection - environmental variables**

### **2.3.1 Site level variables**

Mean annual precipitation ranged from 785 mm to 1138 mm between site locations. Mean temperature during the trapping period varied from 12.3°C to 14.7°C, whereas mean January temperature varied from -8.3°C to -3.5°C. Elevation ranged from 25 to 610 metres above sea level. Climatic data were derived from [www.eklima.no](http://www.eklima.no). We determined elevation and width of power-line corridors by digital maps and satellite photos, whereas data on number of years since establishment of the power-line corridor were provided by Statnett. Aspect of each site was measured by use of an analogue compass in the field.

### **2.3.2 Environmental variables measured at plot level in the field**

Data on vegetation were collected during 2009 and 2010. In each plot, numbers of trees of each tree species was counted. Height and diameter of crowns of the trees for all trees >1m were estimated visually. Percentage cover for herbs, shrubs, grass and trees were recorded visually within each 1 m × 1 m sub-plot (Figure 2). In addition, percentage cover of moss and lichens, rock, soil and sand were recorded within each sub-plot. A relascope was used from the middle of each plot to get the basal area of forest stand in m<sup>2</sup>/ha (Bitterlich 1984). Slope (degrees) was measured with SUUNTO clinometer for each plot where the slope was steepest. A site quality index was scored from a combination of vegetation types, latitude, dominating tree species (Norway spruce *Picea abies* or Scots pine *Pinus sylvestris*), soil depth and slope, following Nilsen & Larsson (1992).

## 2.4 Statistical analyses

Because each trap was catching beetles continuously from April/May to September/October, the material from the four collection periods was pooled for each pitfall trap. For each plot, the material from the two pitfall traps in sub-plot 1 and sub-plot 5 were pooled before further analyses of the data.

All data were analysed using SAS/STAT® 9.2 (SAS Institute, Inc., Cary, NC, USA) and R (R Development Core Team 2011).

### 2.4.1 Beetle species richness

In order to compare the difference in species richness between early successional stages (i.e. power-line corridor habitats) and later successional stages (i.e. closed canopy forest habitats), we first calculated species accumulation curves based on aggregated data from all 20 sites. However, species accumulation curves calculated for each site separately indicated substantial among-sites variation (Appendix 2). Therefore, we fitted generalised mixed models with species richness as response variable, ‘Habitat’ (power-line corridors, closed canopy forests) as fixed effect explanatory variable, and ‘Site’ as random effect. The species richness data were counts (number of species), and therefore we first fitted a model with log link function, Poisson distribution, and Gauss-Hermite Quadrature (GHQ) technique for parameter estimation (Bolker et al. 2009). However, inspection of the graphical diagnostics and the Pearson Chi-square/df value (4.47) revealed that there was substantial over-dispersion. Therefore, we adjusted the model by changing from Poisson to a negative binomial distribution, which provided a better fit to the data ( $\chi^2/df = 0.92$ ).

In addition to the fixed effect ‘Habitat’, we explored potential influence of other environmental variables measured at the site or plot level. First, we fitted a model for each environmental variable separately, and ‘Site’ as random effect. The following environmental variables measured on the site level were tested; elevation, width of power-line corridor, age of power-line corridor (number of years since establishment), aspect of corridor, difference in temperature between January and July on sites, mean temperature in plant growth season (June, July and August), and mean annual precipitation. In addition, we tested the following environmental variables measured at the sub-plot or plot level; percentage cover of shrubs, grass, dwarf shrubs, herbs, soil, stones and moss, relascope sum, number of trees, number of spruce, maximum tree height, mean tree height and mean tree crown width. Bilberry *Vaccinium myrtellis* and heather *Calluna vulgaris* were the most abundant vascular plant

species (Appendix 3.), and therefore chosen and the only individual plant species included in further analysis.

We tested the influence on species richness for each environmental variable separately, but only the environmental variables with  $p < 0.10$  were included in the more complex models. Since ‘Mean tree height’ and ‘Habitat’ was confounded, we made two separate full (most complex) models. Model 1 included ‘Habitat’, ‘Cover of herbs’ and ‘Habitat  $\times$  Cover of herbs’. Model 2 included ‘Mean tree height’, ‘Cover of herbs’ and ‘Mean tree height  $\times$  Cover of herbs’. After fitting the global models, model selection was performed by backward elimination by sequentially removing terms with the highest p-value, and always removing the interaction term before main effects. We provide Wald F tests of fixed effects as recommended by Bolker et al. (2009), and likelihood ratio (LR) tests of random effects for the model best supported by the data.

To find if it was a curvilinear relationship between mean tree height and species richness as in the study done by Paquin (2008), the formula “species richness  $\sim$  mean tree height + (mean tree height)<sup>2</sup>” was used initially, but the quadratic term was not significant.

#### **2.4.2 Beetle biodiversity**

Difference in beetle species diversity between habitats was first analysed by calculating Renyi profiles (Kindt & Coe 2005). Renyi profiles calculated for each site separately, indicated substantial among-site variation in biodiversity (Appendix 4). Therefore, we fitted generalised mixed models with biodiversity as response variable, ‘Habitat’ (power-line corridors and closed canopy forests) as fixed effect explanatory variable, and ‘Site’ as random effect. We present results of analyses with Shannon biodiversity index as response variable, but choice of the three biodiversity indices calculated in the Renyi profile, Shannon diversity index, Simpson diversity index and Berger-Parker diversity index (Kindt et al. 2006) did not qualitatively influence our results. We fitted a model with identity link function, normal distribution, and Restricted Maximum Likelihood (REML) technique for parameter estimation.

In addition to the fixed effect ‘Habitat’, we explored potential influence of other environmental variables measured at the site or plot level, following the procedure described above for analyses of beetle species richness. From environmental variables with  $p < 0.10$  (‘Cover of herbs’, ‘Number of spruce’, ‘Mean tree height’ and ‘Mean tree crown width’) new models were created. If the correlation coefficient was  $> 0.5$  between two explanatory

variables, we did not include them in the same model. This was the case for ‘Mean tree height’ and ‘Mean tree crown width’. Therefore, we constructed two alternative full models: one model with ‘Cover of herbs’, ‘Number of spruce’, ‘Mean tree height’ and all first order interactions as fixed effects, and an alternative model with ‘Cover of herbs’, ‘Number of spruce’, ‘Mean tree crown width’ and all first-order interactions as fixed effects. Model selection was done by backward elimination of non-significant terms, as described above. We provide Wald F tests of fixed effects, and likelihood ratio (LR) tests of random effects for the model best supported by the data.

### **2.4.3 Beetle species abundance distributions**

We calculated and plotted empirical cumulative distribution functions (ECDF) for each habitat, as recommended by McGill et al. (2007) and Magurran et al. (2011), to compare species abundance distributions of beetle communities between different habitats. ECDFs are mathematically stronger than rank abundance curves as they are not influenced by species richness, and thus allows for direct comparison between habitats that differ in total species richness (Magurran et al. 2011). ECDF for respectively power-line corridor habitats and closed canopy forest habitats were compared by visual inspection and Kolmogorov-Smirnov test to test if the two distributions were significantly different from each other.

### **2.4.4 Beetle species composition**

We used a Canonical Correspondence Analysis (CCA) and Monte-Carlo permutation test to determine if the variation attributed to the categorical variables ‘Site’ (20 levels = sites) and ‘Habitat’ (two levels; forest, power-line corridor) were larger than that of a random variable. In order to find significant additional variation explained by ‘Habitat’ after the variation to ‘Site’ had been explained, we performed a partial constrained ordination: First the variation to ‘Site’ was partialled out, and then the residual variation to ‘Habitat’ was found. A square root transformation was applied to the beetle species data to down-weight the influence of abundant species.

We also used a CCA and Monte-Carlo permutation test to determine the influence of the field layer variables; herbs, bilberry, heather, moss, lichens, grass and shrubs on beetle species composition. First the significance of every variable was tested separately. Variables with  $p < 0.10$  were fitted into a model by forward selection. Because of multiple testing, we applied Bonferroni corrections and Dunn-Sidak corrections, which gave approximately the same significance level (0.01429 and 0.01493, respectively).



#### **2.4.5 Functional group composition**

The data on number of individuals or species within each functional group were counts. The same type of generalised mixed model and model selection procedure as described for analyses of species richness was used (see 2.4.1). The effects of the different environmental variables, percentage cover of herb, bilberry and heather were tested. Herbs was tested because it had a significant influence on species richness and biodiversity. Heather and bilberry were tested because they were the most common species in power-line corridors and closed canopy forests, respectively. Two global models were fitted, with the fixed effects `Habitat`, `Functional group` and `Habitat × Functional group`, and respectively number of individuals and number of species as explanatory variables. These two global models were also modified by including field layer variables instead of habitat; i.e. fixed effects `Bilberry`, `Herb`, `Heather`, `Bilberry × Functional group`, `Herb × Functional group`, `Heather × Functional group` and respectively number of individuals and number of species as explanatory variables.

### 3. Results

A total of 38 541 beetle individuals belonging to 423 species and 41 families were captured. The total number of species was almost equal in power-line corridors (n = 333) and closed canopy forests (n = 317). In total the most common species were *Zyras humeralis* (n = 5828), *Geostrupes stercorosus* (n = 5277) and *Drusilla canaliculata* (n = 2404), which together comprised 35 % of the catch. In the power-line corridors the most common species were *G. stercorosus*, *Tachinus signatus* and *D. canaliculata*, which together comprised 33 % of the total catch. In the forest *Z. humeralis*, *G. stercorosus* and *D. canaliculata* comprised 45 % of the beetles (Table 1). All above mentioned species except *G. stercorosus* belong to the family Staphylinidae, which by far had the largest number of species (n = 191). A total of 106 beetle species were captured in power-line corridor sites only, and 90 species in closed canopy forest sites only. Almost 40 % of the species had only one or two captured individuals.

Predators, mainly belonging to Staphylinidae and Carabidae, were the most abundant functional group with 13 145 and 15 040 individuals in power-line corridors and closed canopy forests, respectively. Because live wood feeders (0.003 % of total number of individuals and 0.2 % total number of species, respectively), dead wood feeders (0.08 %, 4.2 %), fungivores (0.7 %, 12.9 %) and species with unknown ecological function (0.1 %, 4.9 %) made up a very small proportion of the total number of individuals and species, they were pooled together in the category “other” before further analyses of ecological functions.

Four red listed species were captured. The near threatened *Carabus arcensis* were captured in both habitats, 79 individuals in power-line corridors and 18 individuals in closed canopy forests. One individual of the near threatened *Acrotona exigua*, was captured in forest. Two vulnerable species were captured in power-line corridors, *Margarinotus purpurascens* and *Lathrobium pallidum*, with only one individual each.

Table 1. The most numerous beetle species in power-line corridors and in closed canopy forests. The count for the ten most numerous species in each habitat is in bold. The species is sorted from high to low in power-line corridors. Functional groups are represented by detritivores (DE) and predators (PR). The table is based on data from ten sites in 2010 and ten sites in 2011. The beetles were captured in the same 4 m × 5 m plot as described in Figure 2, using pitfall traps.

Species	Family	Functional group	Power-lines (No.)	Forests (No.)
<i>Geotrupes stercorosus</i>	Geotrupidae	DE	<b>2733</b>	<b>2644</b>
<i>Tachinus signatus</i>	Staphylinidae	PR	<b>1977</b>	<b>516</b>
<i>Drusilla canaliculata</i>	Staphylinidae	PR	<b>1346</b>	<b>1058</b>
<i>Liogluta micans</i>	Staphylinidae	PR	<b>824</b>	<b>620</b>
<i>Pterostichus oblongopunctatus</i>	Carabidae	PR	<b>685</b>	<b>678</b>
<i>Philonthus decorus</i>	Staphylinidae	PR	<b>652</b>	84
<i>Quedius molochinus</i>	Staphylinidae	PR	<b>574</b>	<b>323</b>
<i>Pterostichus niger</i>	Carabidae	PR	<b>570</b>	<b>512</b>
<i>Trechus secalis</i>	Carabidae	PR	<b>467</b>	271
<i>Zyras humeralis</i>	Staphylinidae	PR	<b>465</b>	<b>5363</b>
<i>Catops nigrita</i>	Leiodidae	DE	226	<b>365</b>
<i>Pterostichus melanarius</i>	Carabidae	PR	71	<b>640</b>

### 3.1 Beetle species richness

Differences in species richness between habitats increased with increasing number of sampled plots (Figure 4). The same pattern was found for family richness (Appendix 5).

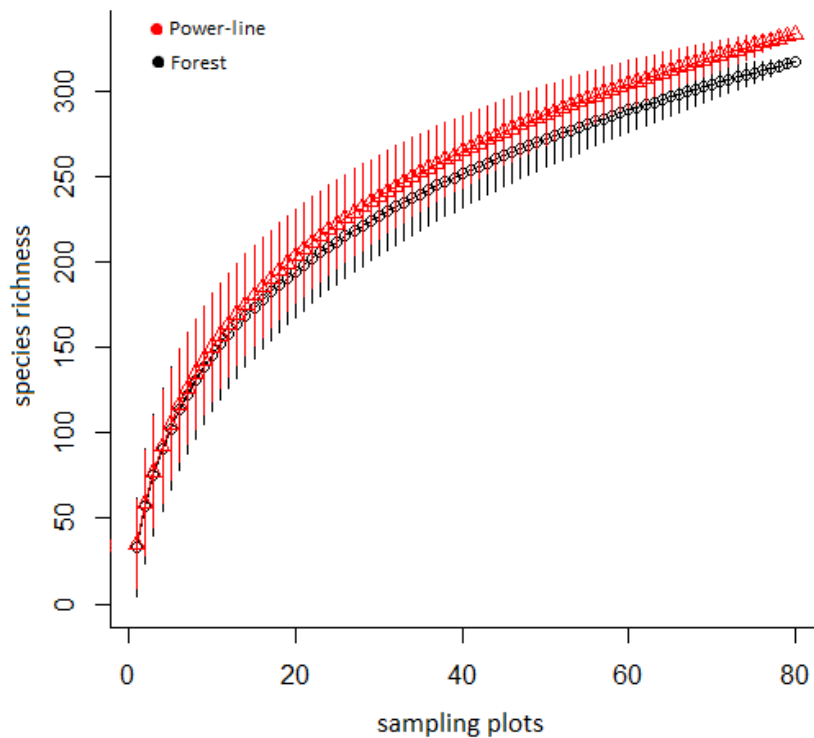


Figure 4. Species accumulation curves showing differences in beetle richness in power-line corridors and closed canopy forests. Graphs are based on aggregated data from 20 sites, with four sampling plots in power-line corridors and four sampling plots in closed canopy forests at each site. There was a significant difference in species richness between power-line corridors and closed canopy forests. Power-line corridors with low successional stage has higher richness than closed canopy forests with higher successional stage. The vertical bars indicate  $\pm 2$  standard deviations.

Estimated mean number of species per plot was 34.9 ( $\pm$  SE) in power-line corridors and 33.3 ( $\pm$  SE) in closed canopy forests. Mean species richness did not differ significantly between habitats ( $F_{1,139} = 0.5$ ,  $p = 0.48$ ). The most common vascular plant species in the field layer was bilberry and heather, but neither had a significant effect on beetle richness (heater:  $F_{1,139} = 0.67$ ,  $p = 0.41$ , bilberry:  $F_{1,136} = 2.20$ ,  $p = 0.14$ ). Per one percentage increase in cover of herbs, species richness increased with one species (Table 2). There was no significant interaction between percentage of herb cover and habitat (Table 2, Figure 5), and there was no significant effect of habitat. When tested individually, mean tree height ( $F_{1,139} = 3.3$ ,  $p = 0.07$ ) and percentage cover of herbs ( $F_{1,139} = 3.3$ ,  $p = 0.07$ ), had strongest influence on beetle species richness. When tree height increased by one metre, species richness decreased with

one individual (Table 3). There was no curve linear relationship between mean tree height and species richness ( $F_{1,138} = 1.7$ ,  $p = 0.19$ ).

Table 2. Analyses of environmental variables influencing beetle species richness. The table shows the process from full model to the most parsimonious model. Response variable was number of species captured per plot in Figure 2. Percent cover of herbs in field layer (average of sub-plots in Figure 2) and habitat (power-line corridors and closed canopy forests) was explanatory variables. Wald F tests of fixed effects and likelihood ratio tests of random effects are reported.

Explanatory variables	df	Log (likel)	$\chi^2$	<i>F</i>	<i>P</i>
<b>Model 1</b>					
Fixed effects					
Habitat	1.137			1.49	0.22
Cover of herbs	1.137			1.40	0.24
Cover of herbs × Habitat	1.137			0.73	0.4
Random effect					
Site	1	-638.7	1.91		0.08
<b>Model 2</b>					
Fixed effects					
Habitat	1.138			0.82	0.37
Cover of herbs	1.138			3.6	0.06
Random effect					
Site	1	-639.4	2.55		0.06
<b>Model 3</b>					
Fixed effects					
Cover of herbs	1.139			3.32	0.07
Random effect					
Site	1	-639.6	2.28		0.07

Generalised mixed models with log link, negative binomial distribution, and gaussian – hermite quadrature approximation parameter estimation.

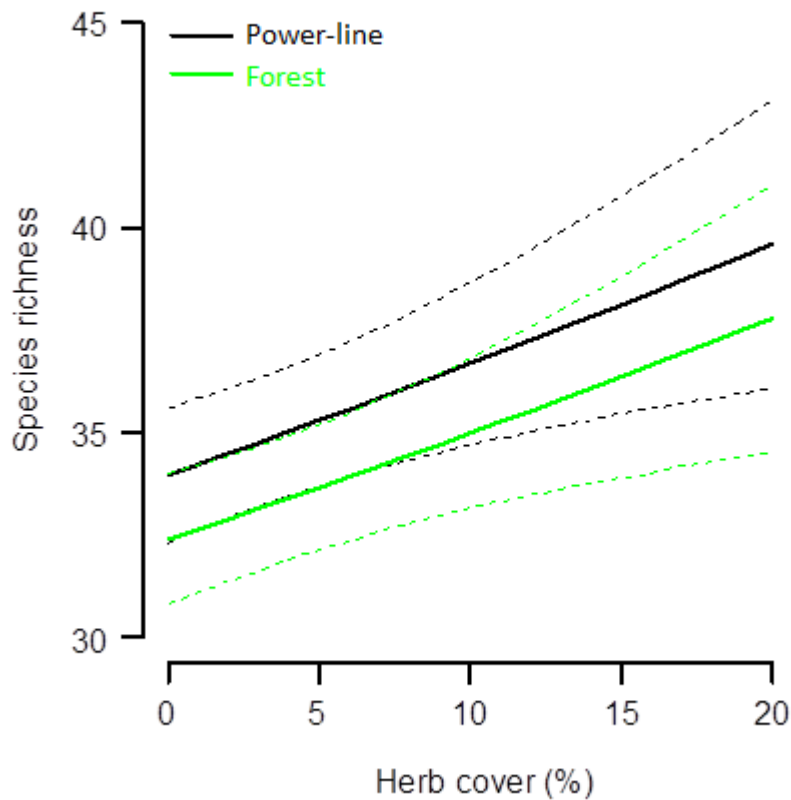


Figure 5. Relationship between beetle richness, percentages of herb cover and habitat (power-line corridors and closed canopy forests). However, species richness increased with increasing cover of herbs in both habitats. The plots give predicted values (solid lines) based on Model 2 in Table 2, and standard errors (dotted lines).

Species richness increased with percentage of herb cover at high tree height, but not at low tree height (Mean tree height  $\times$  Cover of herbs interaction:  $F_{1,137} = 4.4$ ,  $P = 0.04$ , Table 3, Figure 6).

Table 3. Analyses of environmental variables influencing beetle species richness. Response variable was number of species captured per plot. Mean tree height and cover of herbs are used as interaction. Wald F tests of fixed effects and likelihood ratio tests of random effects are reported.

Explanatory variables	df	Log (likel)	$\chi^2$	F	P
Fixed effects					
Mean tree height	1.137			7.86	0.006
Cover of herbs	1.137			0.06	0.8
Mean tree height×Cover of herbs	1.137			4.41	0.04
Random effect					
Site	1	-635.9	2.98		0.04

Generalised mixed models with log link, negative binomial distribution, and Gaussian-Hermite Quadratic approximation parameter estimation.

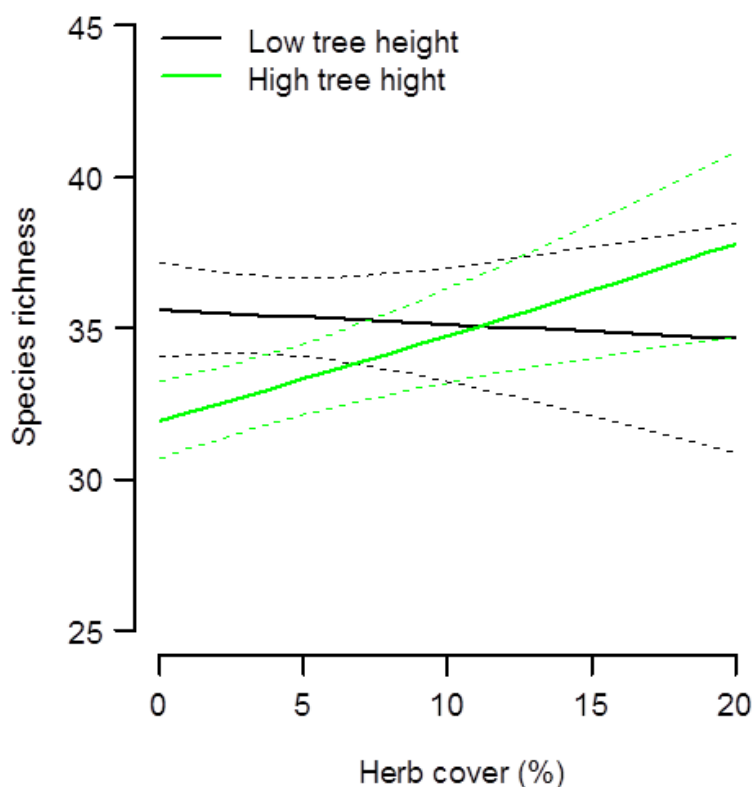


Figure 6. Relationship between percentage of herb cover, mean tree height and beetle richness. Both herb cover and tree height had a significant influence on species richness. Herb cover had a stronger influence on species richness in habitats with high trees i.e. later successional stages. The plots give predicted values (solid lines) based on the model in Table 3, and standard errors (dotted lines).

### 3.2 Beetle biodiversity

Species biodiversity was higher in power-line corridors than in the closed canopy forests ( $H\text{-alpha power-line} > H\text{-alpha forest}$  for any  $\alpha > 0$ ) (Figure 7). The less steep profile for power-line corridors indicates a slightly more even distribution of species in power-line corridors than in the closed canopy forests. A steeper curve for closed canopy forests indicates higher dominance of certain species. The species biodiversity and distribution are influenced by difference in habitats. The same pattern was found for family biodiversity (Appendix 6).

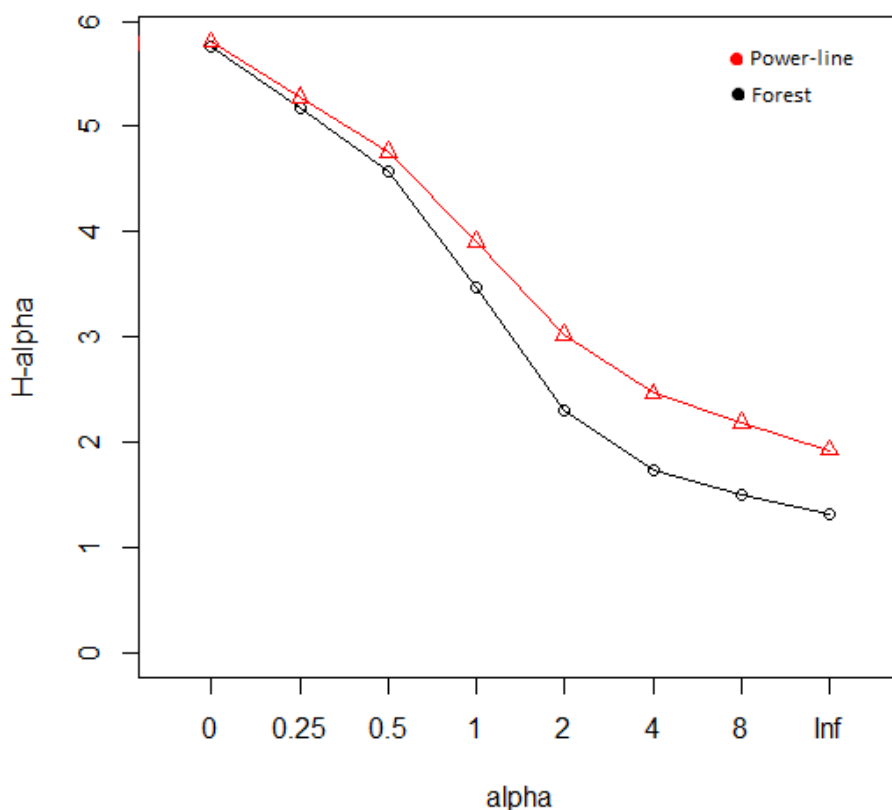


Figure 7. Renyi diversity profiles of species richness and biodiversity for beetles captured in the centre of power-line corridors and 100 m in to the closed canopy forests, perpendicular on the edge between closed canopy forests and power-line corridors. The figure is based on aggregated data from 20 sites. The beetles were captured on the same  $4\text{ m} \times 5\text{ m}$  plot as described in Figure 2. Alpha = 0 on the left side indicates species richness: profiles that start at a high level have high species richness. The antilogarithm ( $e^{H\text{-alpha}}$ ) for alpha = 0, gives species richness (power-line corridors: 333 and forests: 317). The antilogarithm ( $e^{H\text{-alpha}}$ ) for infinity gives the abundance of the most dominating species (power-line corridors:  $0.146 \approx 15\%$ , closed canopy forests:  $0.272 \approx 27\%$ ). Profiles that are higher than other profiles for all values of alpha have higher biodiversity.



We found a significant ( $F_{1,139} = 6.65$ ,  $p = 0.01$ ) difference in estimated mean biodiversity between the two habitats. Plots in power-line corridors had higher mean biodiversity (2.67) than plots in closed canopy forests (2.47) (Figure 8).

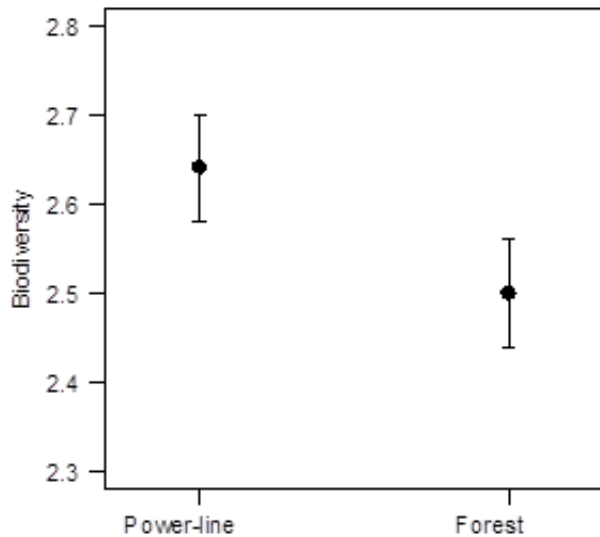


Figure 8. Estimated mean biodiversity (Shannon diversity index) and associated standard errors for power-line corridors and closed canopy forests. Power-line corridors have a significantly higher biodiversity than closed canopy forests.

Percentage of herb cover ( $F_{1,138} = 5.05$ ,  $p = 0.03$ ) and number of Norway spruce ( $F_{1,138} = 8.85$ ,  $p = 0.004$ ) had a significant influence on biodiversity (Table 4, Figure 9). One percentage increase of herbs gives an increase of 0.02 in biodiversity index (Figure 9). Norway spruce, had a negative effect on biodiversity (Figure 9). we found no significant effects of mean tree height or mean tree crown width when these variables were included in models along with herb cover and number of spruce (Table 4). We also carried out sparate tests of the two most common vascular plant species in the field layer, but non of them had a significant influence on biodiversity (bilberry:  $F_{1,139} = 1.26$ ,  $p = 0.26$ , heather:  $F_{1,139} = 1.30$ ,  $p = 0.26$ ).

Table 4. Analyses of environmental variables influencing beetle biodiversity. Response variable was Shannon biodiversity index. Mean tree height and mean tree crown width were correlated and therefore included in separate models. Models 1 and 2 have been reduced through backward elimination from initial full models including main effects and all possible interaction terms.

<b>Model 1</b>						
	Explanatory variables	df	Log (likel)	$\chi^2$	F	P
Fixed effects						
	Cover of herbs	1.137			5.37	0.02
	Number of spruce	1.137			6.18	0.01
	Mean tree crown width	1.137			3.1	0.08
Random effect						
	Site	1	-133.8	12.73		0.0002
<b>Model 2</b>						
	Explanatory variables	df	Log (likel)	$\chi^2$	F	P
Fixed effects						
	Cover of herbs	1.137			4.87	0.03
	Mean tree height	1.137			0.98	0.33
	Number of spruce	1.137			6.89	0.01
Random effect						
	Site	1	-135.8	11.77		0.0003
<b>Final model</b>						
	Explanatory variables	df	Log (likel)	$\chi^2$	F	P
Fixed effects						
	Cover of herbs	1.138			5.05	0.03
	Number of spruce	1.138			8.85	0.004
Random effect						
	Site	1	-132.9	11.76		0.0003

Generalised mixed models with identity link, noraml distribution and restricted maximum likelihood (REML) technique for parameter estimation.

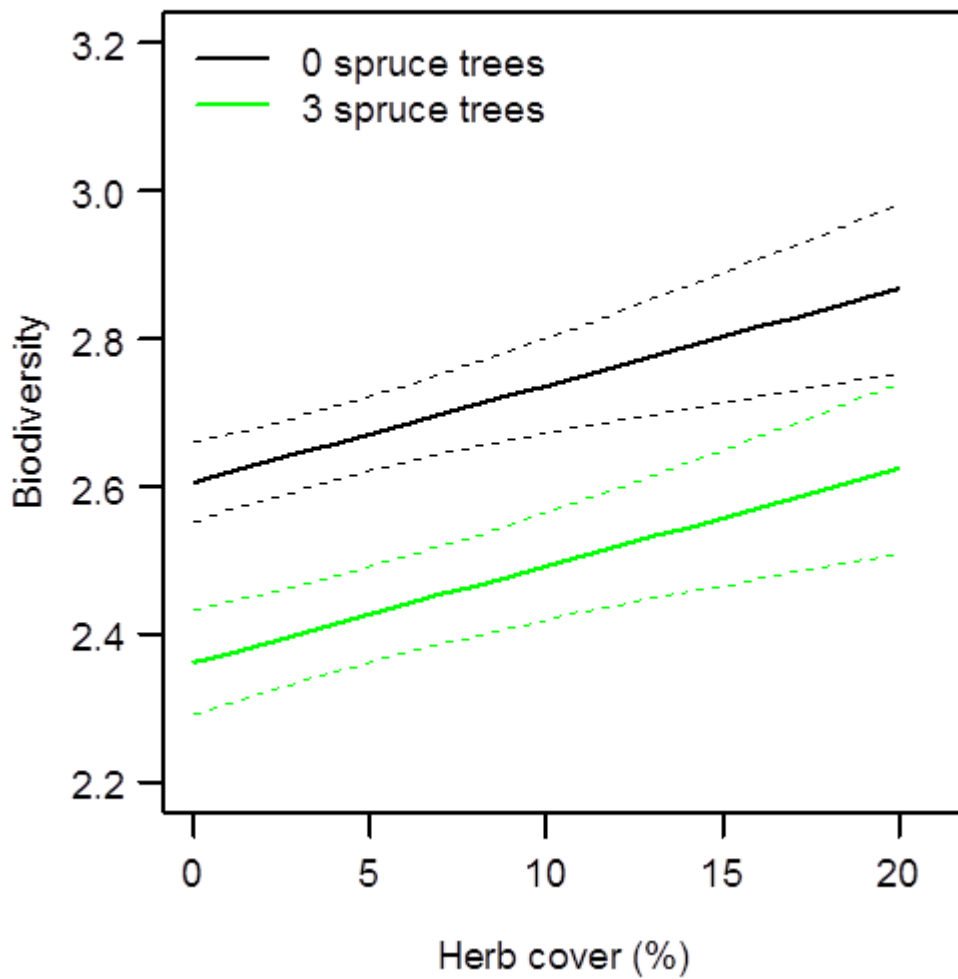


Figure 9. Relationship between percentage of herb cover, presence or absence of Norway spruce *Picea abies* and beetle biodiversity. Spruce and cover of herbs has a significant effect on biodiversity. The biodiversity is higher in habitats without trees and the amount of herb cover increases biodiversity independently of the amount of spruce trees. The graphs show predicted numbers (solid lines) based on final model in Table 4, calculated with Shannon diversity index, and standard errors (dotted lines).

### 3.3 Beetle species abundance distributions

The empirical cumulative distribution function (ECDF) of beetle species indicates that most of the species had low abundance in both habitats. Approximately 90 % of the species have abundance less than 1 % of the total number of individuals captured. The steep curve indicates high evenness in both habitats, and approximately 30 % of the species have an abundance of 0.01 %. In power-line corridors 25 % of the species have only one individual whereas in closed canopy forests 28 % of the species have one individual (Figure 10). This was confirmed by inspection of the raw data. The small difference between the curves indicates a similar species abundance distribution in both habitats, i.e. same distribution of common versus rare species, and similar evenness distributions.

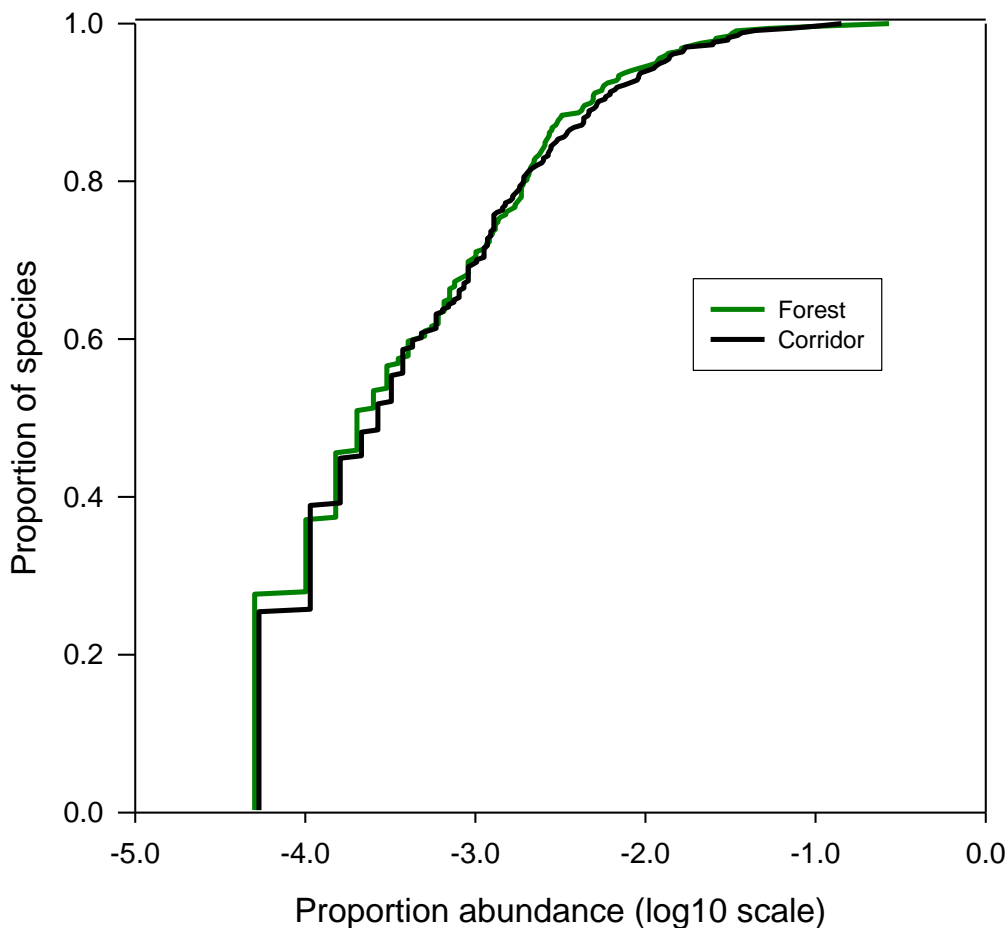


Figure 10. Empirical cumulative distribution function (ECDF) of beetle species captured using pitfall traps in power-line corridors and closed canopy forests. x-axis is log10 scale, 0 = 100%, -2 = 1%, -4 = 0.01% proportion of abundance. y-axis is abundance of species, where 1 = 100%. The steep curve indicates a high evenness in species abundance.

### 3.4 Beetle species composition

A CCA analysis showed that the site effect explained 19 % of the species composition (Monte-Carlo permutation test:  $F_{19,140} = 1.74$ ,  $p = 0.001$ , 999 permutations). A partial constrained ordination was then performed to find variation explained only by ‘Habitat’. Habitat explained 1 % of beetle composition not also explained by ‘Site’ (Monte-Carlo permutation test:  $F_{1,139} = 1.85$ ,  $p = 0.001$ , 999 permutations).

Each of the field layer variables were tested independently with site as constraining variable. Shrubs explained 0.8 % of the total variation in beetle species composition (Monte-Carlo permutation test:  $F_{1,139} = 1.53$ ,  $p = 0.001$ , 999 permutations). Moss explained 0.6 % of the total variation in beetles species composition (Monte-Carlo permutation test:  $F_{1,139} = 1.19$ ,  $p = 0.022$ , 999 permutations). The other field layer variables were not significant ( $p > 0.06$ ). We performed a forward selection procedure first including shrub, and there after moss. When shrub and moss were included together in the CCA diagram, moss was no longer significant (Monte-Carlo permutation test:  $F_{1,138} = 1.13$ ,  $p = 0.061$ , 999 permutations). The CCA diagram for effects of field layer vegetation variables also shows that shrub had most influence on species composition (Figure 11). Shrub is located slightly downwards and to the left from the origin, whereas moss is located to the right from the origin (Figure 11). This indicates that shrub and moss have different effect on beetle species composition. The species plotted close to the centre of the CCA diagram may be generalists or they may be associated with a number of habitat characteristics.

We also fitted a CCA with only species with  $\geq 100$  individuals captured (Figure 12), and this analysis also showed that shrub and moss were the most important field layer variables ( $p \leq 0.05$  when tested individually, with site as constraining variable). Most of the species with  $\geq 100$  individuals were close to the centre of the CCA diagram which may indicate they are generalists (Figure 12). Some of the speices most associated with habitats dominated by shrub were *Sciodrepoides watsoni*, *Megasternum concinnum* and *Nicrophorus vespilloides*. Some of the species most associated with moss rich habitats were *Z. humeralis*, *Carabus hortensis* and *Atheta crassicornis* (Figure 12).

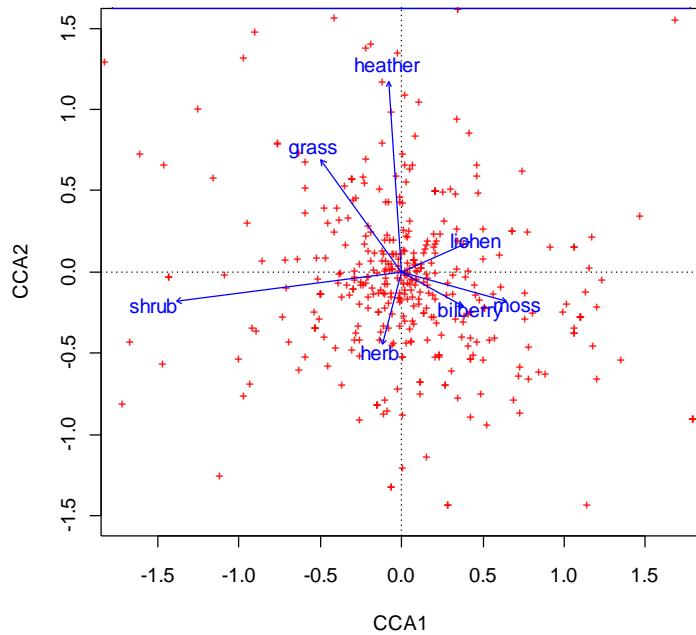


Figure 11. Canonical correspondence analysis (CCA) of the beetle species ( $n = 423$ ) composition and explanatory variables. Arrows in opposite direction indicates different species composition. The length of the arrows indicates the effect of the variable on the beetle species composition i.e variables with long arrows have stronger effect on beetle species composition than variables with short arrows. Only shrub was significant ( $p = 0.001 < \alpha = 0.015$ ), but moss was the second most important variable ( $p = 0.02$ , when constraining for effects of `shrub` and `site`). Variables are given in percentage cover of ground. Red +: beetle species.

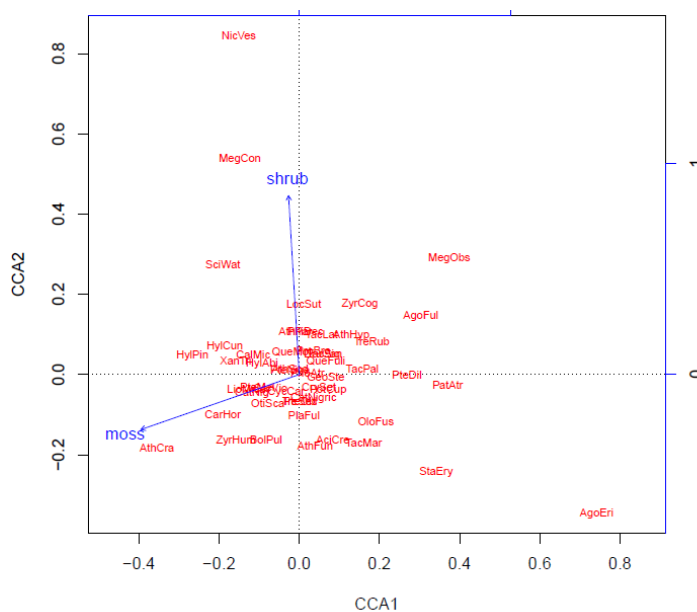


Figure 12. Canonical correspondence analysis (CCA) of the beetle species with  $\geq 100$  individuals captured, and shrub and moss as explanatory variables. Variables shrub and moss were measured as percentage cover of ground. Each beetle species are marked with 3 + 3 letter abbreviations, e.g AthCra = *Atheta crassicornis*.

### 3.5 Functional group composition

Functional group influenced the number of individuals captured, whereas habitat had no significant effect (Table 5). Number of individuals was higher for predators in forest, whereas detritivores, herbivores and other had higher number of individuals in power-line corridors (Figure 13 a). Detritivores accounted for 21 % in power-line corridors and 15 % in closed canopy forests. Herbivores accounted for 6 % in the power-line corridors and 4 % in closed canopy forests. Predators were most abundant in both habitats with 72 % and 80 % in power-line corridors and closed canopy forests, respectively. The group “other” accounted for 1 % in both habitats (Figure 13 a). However, as the habitat  $\times$  functional group interaction was non-significant, the relative difference in number of individuals within each functional group did not differ between power-line corridor habitats and closed canopy forest habitats (Table 5). Habitat had no significance on number of predator individuals ( $F_{1,139} = 0.76$ ,  $p = 0.4$ ). Percentage of bilberry cover ( $F_{1,616} = 9.16$ ,  $p = 0.003$ ) had a negative effect on the number of individuals captured ( $\beta = -0.015$ ). There was no significant interaction between functional group and cover of herb ( $F_{3,608} = 0.78$ ,  $p = 0.5$ ), bilberry ( $F_{3,605} = 0.25$ ,  $p = 0.9$ ), or heather ( $F_{3,611} = 1.15$ ,  $p = 0.3$ ).

Number of beetle species was influenced by functional groups and habitat (Table 6, Figure 13). The number of species in all functional groups was slightly higher in power-line corridors than in forest (Figure 13 b). Detritivores accounted for 13 % in power-line corridors and 12 % in closed canopy forest. Herbivores accounted for 11 % in the power-line corridors and 10 % in closed canopy forests. Predators were most abundant in both habitats with 73 % and 75 % in power-line corridors and closed canopy forests, respectively. The group “other” accounted for 4 % in power-line corridors and 3 % closed canopy forests. However, as the habitat  $\times$  functional group interaction was non-significant, the relative difference in number of species within each functional group did not differ between power-line corridor habitats and closed canopy forest habitats (Table 6). Habitat did not influence number of predator species ( $F_{1,139} = 0.01$ ,  $p = 0.9$ ). Percentage cover of herbs had a slightly positive influence ( $F_{1,615} = 6.22$ ,  $p = 0.01$ ,  $\beta = 0.010$ ) and percentage cover of bilberry had a slightly negative influence ( $F_{1,615} = 5.51$ ,  $p = 0.02$ ,  $\beta = -0.0058$ ) on number of species. There were no interactions between functional group and percentage cover of herb ( $F_{3,608} = 0.78$ ,  $p = 0.5$ ), bilberry ( $F_{3,605} = 0.25$ ,  $p = 0.9$ ), heather ( $F_{3,611} = 1.15$ ,  $p = 0.3$ ).

Table 5. Analyses of factors influencing numbers of individuals of beetles. The table shows the process from full model to most parsimonious model. Response variable was number of individuals captured per plot. The effect habitat consists of two categories; power-line corridors and closed canopy forests. The effect functional groups consists of four categories of beetles; detritivores, herbivores, predators and other.. Wald F tests of fixed effects and likelihood ratio tests of random effects are reported.

Explanatory variables	df	Log (likel)	$\chi^2$	<i>F</i>	<i>P</i>
<b>Model 1</b>					
Fixed effects					
Habitat	1.613			1.57	0.21
Functional groups	3.613			424.6	<0.0001
Habitat×Functional groups	3.613			1.60	0.19
Random effect					
Site	1	-2645.0	69.3		<0.0001
<b>Model 2</b>					
Fixed effects					
Habitat	1.616			1.27	0.26
Functional groups	3.616			422.0	<0.0001
Random effect					
Site	1	-2646.6	67.8		<0.0001
<b>Final model</b>					
Fixed effect					
Functional groups	3.617			422.3	<0.0001
Random effect					
<sup>a</sup> Site	1	-2647.4	68.0		<0.0001

<sup>a</sup>The 'Site' effect amounted to 18% of total variance in the final model. Generalized mixed models with log link function, negative binomial distribution, and Gaussian Hermite Quadrature approximation to the likelihood.



Table 6. Analyses for number of beetle species. The table shows the process from full model to most parsimonious model. Response variable was number of species captured per plot. The effect habitat consist of two categories; power-line corridors and closed canopy forests. The effect functional groups consists of four categories of beetles; detritivores, herbivores, predators and other. Wald F tests of fixed effects and likelihood ratio tests of random effects are reported.

Explanatory variables	df	Log (likel)	$\chi^2$	<i>F</i>	<i>p</i>
Fixed effects					
Habitat	1.613			5.34	0.02
Functional groups	3.613			815.9	<0.0001
Habitat×Functional groups	3.613			0.79	0.5
Random effect					
Site	1	-1538.5	20.9		<0.0001
Fixed effects					
Habitat	1.616			3.69	0.05
Functional groups	3.616			813	<0.0001
Random effect					
Site	1	-1539.9	21.3		<0.0001
Fixed effect					
Functional groups	3.617			812.2	<0.0001
Random effect					
<sup>a</sup> Site	1	-1541.2	20.3		<0.0001

<sup>a</sup>The 'Site' effect amounted to 18% to of total variance in the final model. Generalized mixed models with log link function, negative binomial distribution, and Gaussian Hermite Quadrature approximation to the likelihood

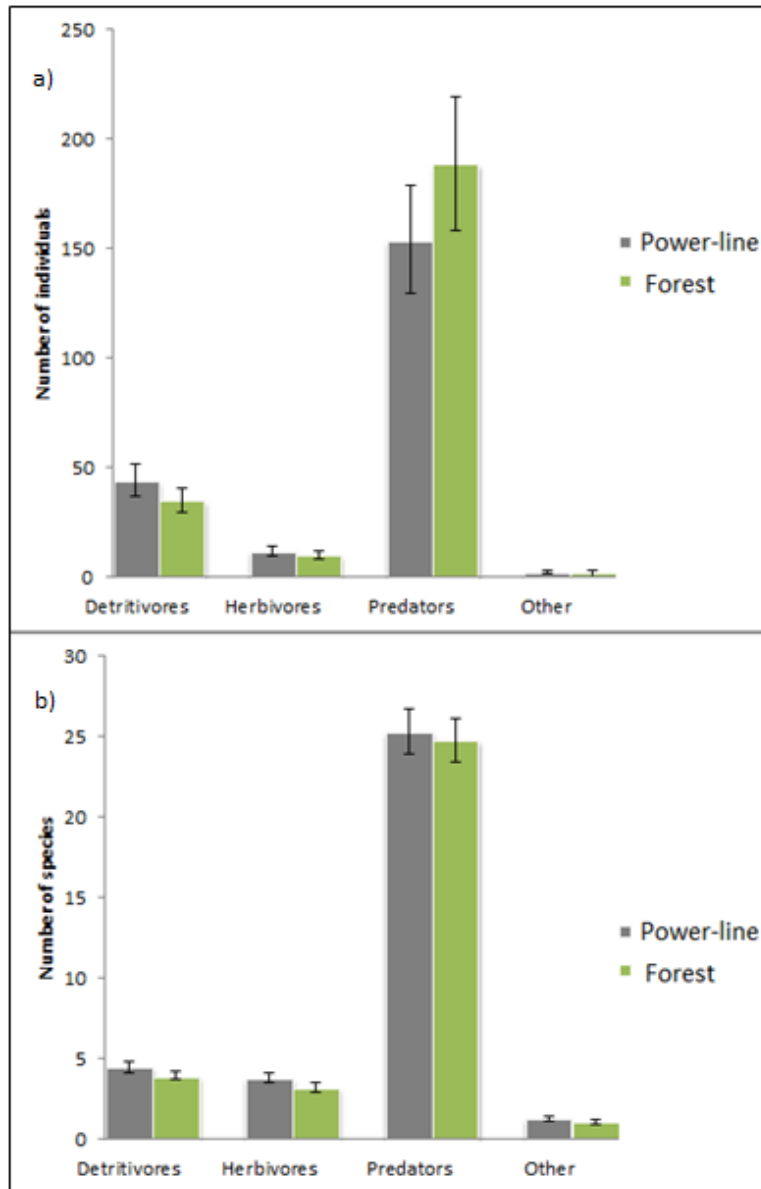


Figure 13. Number of beetle individuals (a) and species (b) in different functional groups in power-line corridors and closed canopy forests. The group other = live wood feeders, dead wood feeders, fungivores and unknown ecological functions. The figure is based on predicted values based on model in Table 5 and 6, with standard errors.

The number of species in all functional groups was higher in power-line corridors than in closed canopy forests (Figure 13 b).

## 4. Discussion

### 4.1 Beetle species richness

In this study beetle richness did not differ between early (power-line corridors) and later (closed canopy forests) successional stages. Furthermore, we found no u-shaped relationship between species richness and tree height. The result contradicts our prediction that species richness would be higher in early successional stages, as many other studies have found (Niemelä et al. 1993; Heliölä et al. 2001; Jukes et al. 2001; Koivula et al. 2002). However, Yu et al. (2007) found no differences between carabid richness in different age stands of forests, but suggested that this was due to a coarse classification of young successional stages and mature forests. After clear-cutting, forest species may survive for a few years (Koivula 2002), or colonizers from nearby mature forest can be present (Spence et al. 1996). However, it is possible that forest specialist species are on the verge of local extinction in clear cut areas (Abildsnes & Tømmerås 2000). Previous studies have suggested that richness tends to be higher in early succession because more species colonise open habitat than there are forest species disappearing (Niemelä et al. 1988; Niemelä et al. 1993; Koivula 2002). We suggest that because the power-line corridors is maintained at an early successional stage, the forest specialist species may have gone locally extinct and the beetle community may have stabilised over the years. Whereas we looked at ground-dwelling beetles in general, previous studies have focused on carabid richness. We do not think that focusing only on carabids would influence the overall result. Environmental factors such as forest types and vegetation zones is more likely to be a factor affecting the species richness. In contrast to our result, Paquin (2008) found that species richness followed a parabolic (u-shaped) pattern with highest species richness at the earliest (0-2 years) and latest (177-340 years) successional stages. However, he looked at species richness in relation to forest age, whereas we used tree height as surrogate for age. Furthermore Paquin (2008) studied successional stages after forest fires, and mean age was older in the early successional stages (power-line corridors) and younger in later successional stages (closed canopy forests) in our study, as compared with Paquin's (2008) study.

Species richness was negatively related to the height of the trees and positively related to herb cover. In successional stages with low tree height, the herb cover seemed to have less influence on species richness than in the forest with higher trees. Ings and Hartley (1999) also found that beetle richness decreased with increasing tree height. Similä et al. (2002b) and Tyler (2008) found that species richness was positively related with herb cover. When the

canopy closes, less light will reach the forest floor and the herb layer dies (Geiger 1965). This reduces habitat complexity and only a few specialist species will be able to utilise the habitat (Koivula et al. 2002). When there is a well-developed herb cover in forests, this indicates a habitat with a high nutrient status (Fremstad 1997). High trees and herb cover together make a more complex habitat, which will benefit higher trophic levels and beetle richness will increase (Abildsnes & Tømmerås 2000; Lassau et al. 2005; Janssen et al. 2009). In habitats with lower tree height, the field layer is more complex since sunlight is not a limiting factor. However, also other factors such as pH of the soil (Elek et al. 2001; Magura et al. 2003), soil organic matter (Jukes et al. 2001) or cover of leaf litter (Magura et al. 2000; Magura et al. 2003), which is not tested in this study, may be favourable for species richness in the power-line corridors.

## **4.2 Beetle biodiversity**

In contrast to our prediction, the biodiversity was higher in early (power-line corridors) than in later (closed canopy forests) successional stages. The biodiversity was negatively related to number of spruce trees and positively related to percentage of herb cover. Habitats with open canopy are found to be dominated by generalist species with low requirements to their habitat (Peltonen et al. 1997; Koivula et al. 2002). In addition, specialist species of open habitats are found in early successional stages (Heliölä et al. 2001), and this gives early successional stages high beetle biodiversity. At canopy closure (20-30 years after clear cutting), the open habitat species are replaced with specialist species which are able to live in the shaded environment (Niemelä 1993; Peltonen et al. 1997; Jukes et al. 2001). Jukes et al. (2001) found that carabid diversity was negatively related with canopy layer of spruce. Because power-line corridors represent young plant communities, there is less spruce, which may give higher beetle biodiversity. Murdoch et al. (1972) and Southwood et al. (1979) found that insect diversity increased with increasing plant diversity and more complex plant structure. At later successional stages as plant diversity fell and the structural plant diversity rised, insect diversity decreased slightly from intermediate stages (Southwood et al. 1979). However, insect biodiversity was still higher in late successional stages compared to early successional stages (Southwood et al. 1979). The forests in our study are mainly production forests, and the complexity of plant structure and biodiversity is likely low, which may give higher beetle biodiversity in the power-line corridors. The biomass left after clearing the power-line corridors, with an accumulation of dead wood and increased input of leaf litter, will also contribute to a more complex habitat beneficial for high biodiversity. Insects depending on

well developed litter mass may have high abundance here, increasing prey availability for predators. This may have cascading effects to higher trophic levels, and thus increasing biodiversity (Siemann 1998; Siemann et al. 1998; Barberena-Arias & Aide 2003).

### **4.3 Beetle species abundance distribution**

The empirical cumulative distribution function (ECDF) showed a high evenness in both early (power-line corridors) and later (closed canopy forests) successional stages, where most of the species had an abundance of less than 1 % of the total number of individuals captured. Few of the species had a high abundance. Although the evenness was approximately the same in both habitats, the dominating species were not the same (Table 1). This distribution with a few highly abundant species and many species with low abundance is common (Fisher et al. 1943; Hanski 1982; Magurran & Henderson 2003). It may reflect that the population density often is highest in the core area of a species' range, with a gradual decline towards the boundaries to other habitats (Brown 1984). Some species are always rare and their distribution on sites will vary on a much smaller scale (Brown 1984). Niemelä and Spence (1994) and Koivula et al. (2002) found a distribution with few abundant and many rare species in a carabid community. However, Niemelä (1993) found a 'gap' between the dominant and the rare carabid species in mature, thinned and newly cut forest, but not in intermediate forests (2-20 years since cutting). We did not find a 'gap' like this neither in forests nor power-line corridors.

Classification of early and late successional stages were different between the studies done by Niemelä (1993) and Koivula et al. (2002). After the definition Niemelä (1993) used in his study, the power-line corridors should be defined as intermediate forest and in that regard, the result for this habitat is consistent with Niemelä (1993). Because power-line corridors are maintained at a young successional stage, we suggest that the beetle community does not have the opportunity to develop into a specialist community. It will be an assemblage with high biodiversity of generalist and open habitat specialist beetles, and it will not house specialist species that inhabit older successional stages.

### **4.4 Beetle species composition**

Species composition was as expected different in the two habitats. Shrubs were the only variable with significant influence on species composition, although we cannot exclude the effect of mosses ( $p = 0.06$ ). In the ordination diagrams (Figure 11 and 12), the vectors for shrubs and mosses, pointed in opposite directions. Shrubs was highly associated with power-line corridors, whereas mosses was highly associated with closed canopy forests (Appendix

3). Total moss cover is reduced after cutting (Fenton et al. 2003), and a well-developed moss cover indicates later successional stages. Shrub layer, on the other hand, which is associated with early successional stages (Esseen et al. 1997), is more well-developed under power-lines (Kroodsma 1982). Niemelä and Spence (1994) and Ings and Hartley (1999) found that a large amount of variation of dominating beetle species were influenced by plant species and proportion of ground vegetation. Mosses had highest percentage cover in mature forests and carabid species preferring dense shaded environment were found here (Ings & Hartley 1999). Thus our results and previous studies suggest that moss and shrubs may be used as indicators of successional stage.

Indeed most beetle species related to moss were most abundant in forests, and most species related to shrubs were most abundant in power-line corridors. An example from the ten most common species was *Z. humeralis*, which was more abundant in forest and associated with moss (Figure 13). Early successional stages have unfavourable conditions for *Z. humeralis*, and Derunkov (2005) found that the abundance decreased remarkably from forests to open habitats. In our study *Z. humeralis* decreased with 91 % from closed canopy forests to power-lines, but was still among the top ten most abundant species in power-line corridors. Another species found in closed canopy forests in our study and which we found to be associated with moss-rich habitats was *Pterostichus melanarius* (Figure 13). Other studies have found this carabid mainly in grassland and open habitats (Luff et al. 1989; Magura 2002). Halme and Niemelä (1993) found that it was more abundant in small forest fragments than in continuous forests. However, Kålås (1985) found *P. melanarius* in forest in Norway, and it is suggested that changes microclimate can lead to colonization of the forest edge (Spence et al. 1996). However, some species closely associated with shrub habitats were actually most abundant in forests (*Megasternum concinnum*), and the opposite for species associated with moss habitats (*Bolitochara pulchra*). Although we have interpreted shrub and moss as indicators of early and later succession forests, they are not exact the same, and this may partly explain seemingly inconsistent results.

#### **4.5 Functional group composition**

The relative proportion in number of individuals and species within different functional groups did not differ between early (power-line corridors) and later (closed canopy forests) successional stages. Bilberry cover had a slightly negative effect on number of individuals. The number of species was significantly higher in power-line corridors than in closed canopy forests for all functional groups. However, the size of the difference in terms of number of

species between power-line corridors and closed canopy forests was rather small; only about one species for each functional group. The number of species within different functional groups was positively influenced by cover of herb and negatively influenced by cover of bilberry. There were no interactions between functional groups and the environmental variables, suggesting that the individual environmental variables had no effect on number of species in each functional group. Lassau et al. (2005) found the same result and suggest that the responses is more specific i.e at a finer taxonomic resolution. Woodcock and Pywell (2010) found that the total species richness for detritivore, herbivore and predatory invertebrates were negatively related to vegetation height in grasslands. Hendrix et al. (1988), Barberena-Arias and Aide (2003) and Similä et al. (2002) found that trophic composition was similar among all successional stages and forest types, suggesting that composition of functional groups recover fast after cutting. It is important to note that the functional groups include species with different specialisations (Didham et al. 1996). The most specialised species have little flexibility to cope with changes in their natural environment.

The most abundant group with regard to ecological function was predators, which is not surprising considering that Staphylinidae was the most abundant family and they are all predators. Hunter (2002) found that predators were more vulnerable to fragmentation than groups representing lower trophic levels. Barberena-Arias and Aide (2003) found that species of predators increased in number with successional stage and were more common in late successions compared with early successions, and we therefore expected a decline of predators in power-line corridors. Mean number of predators was slightly higher in forest than in power-line corridors, but the difference was not significant. The predator *Z. humeralis* accounted for 27 % of all individuals in closed canopy forests, which explains the larger number of individuals of predators in closed canopy forests. In general there were more species in the power-line corridors which may be why we found more predator species here. When looking at the composition of the different functional groups, the proportion of predators was only slightly larger in closed canopy forests (75 % of total number of species) than in power-line corridors (73 % of total number of species), but this were not significant.

We found no significant difference in the number of individuals of detritivores in the power-line corridors and the closed canopy forests. This contradict other studies that have found more detritivores in late successional stages (Didham et al. 1996; Barberena-Arias & Aide 2003). This was somewhat unexpected because litter mass increases during succession and this increases food availability for detritivores (Hector et al. 1999). Scheu et al. (2003) found

that the quality was more important than the amount of detritus. Our result may thus at least partly be due to higher quality of the detritus in power-line corridors. It may also be important that trees and shrubs, which make up a large amount of detritus, are not removed from the site after cutting. The detritivores are important in the breakdown of dead organic materials and return nutrients to the soil (Nichols et al. 2008).

The number of herbivore species was slightly higher in power-line corridors than in the closed canopy forests. According to Hunter (2002) herbivores are more tolerant to fragmentation than are species of higher trophic levels. Herbivorous species accounted for a larger part of the total catch in power-line corridors (10 % in closed canopy forests and 11% in power-line corridors). It was registered higher percentage cover of vegetation in power-line corridors (Appendix 3) which may explain this result.

#### **4.6 Sampling methodology**

Pitfall traps are mainly used to capture ground-dwelling beetles, especially carabid beetles (i.e: Niemelä et al. 1988; Heliölä et al. 2001; Koivula et al. 2002; Hollmen et al. 2008). Pitfall traps, as many other trap types, have disadvantages (Enge 2001). The result from pitfall trapping will reflect activity level and catchability of beetles, in addition to the abundance of the species (Greenslade 1964). This means that species with few numbers are not necessarily rare, but may exhibit trap avoidance behaviour, and this can influence evenness estimates (Greenslade 1964). In comparison with for example interception traps, pitfall traps capture few rare beetle species (Hyvarinen et al. 2006). However, pitfall traps captures beetles in their living habitat (Hyvarinen et al. 2006). Despite uncertainties with pitfall trapping (Fichter 1941; Woodcock 2007), this type of traps is the most reasonable for comparing different habitats with regard to abundances of ground-dwelling beetles (Fichter 1941). If the sampling sizes are large enough, the material should represent the ground-dwelling beetle community well.



## **5. Conclusion**

Frequent cutting of the tree layer in power-line corridors influenced biological diversity of ground-dwelling beetles, but the results depend on which measure of biodiversity we used. We found no significant difference in species richness between power-line corridors, (i.e., early successional forest) and closed canopy forests. In contrast, biodiversity was higher in power-line corridors. Species composition differed significantly between early and late successional stages, whereas the relative proportion of individuals and species within different functional groups (predators, herbivores, detritivores) did not. Field layer and structure of forest were additional factors that explained differences in species richness, biodiversity, species composition and functional diversity. Maintenance of power-line corridors permanently alters forest habitats and the negative impacts are likely to be strongest for forest specialist beetle species.

## 6. References

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## Appendix 1.

Beetles were categorised according to its main ecological function as imago according to the literature listed below. The categorisation was carried out by taxonomist Sidre Ligaard.

### Die Käfer Mitteleuropas

Freude, H., Harde, K.W. & Lohse, G.A. 1964-79. Die Käfer Mitteleuropas. Band 1-12. Krefeld.

Landin, B.O. 1957. Bladhorningar - Lamellicornia. Fam. Scarabaeidae. Svensk Insektfauna. Ent. Föreningen i Stockholm.

Lindroth, C.H. 1933. Olikfotade baggar. Heteromera. Svensk Insektfauna. Ent. Föreningen i Stockholm. 158 s.

Lindroth, C.H. 1942. Sandjägare och jordlöpare. Fam. Carabidae. Svensk Insektfauna. Ent. Föreningen i Stockholm.

Lindroth, C.H. (ed.) 1960. Catalogus Coleopterorum Fennoscandiae et Daniae. Ent. sällsk., Lund.

Lindroth, C.H. 1961. Sandjägare och jordlöpare. Fam. Carabidae. Svensk Insektfauna. Ent. Föreningen i Stockholm. 209 s.

Lindroth, C.H. 1967. Våra skallbaggar, del 1, 2 och 3. Bonniers, Stockholm. (Ny utgåve)

Palm, T. 1948-70. Kortvingar. Fam. Staphylinidae 1-5. Svensk Insektfauna. Ent. Föreningen i Stockholm.

### Danmarks Fauna

Bd. 76. Sandspringere og løbebiller (Hansen 1968).

Bd. 34. Vandkalve og hvirvlere (Hansen, 2. oplag 1973).

Bd. 57. Rovbiller 1 (Hansen 1951).

Bd. 58. Rovbiller 2 (Hansen 1952).

Bd. 59. Rovbiller 3 (Hansen 1954).

Bd. 77. Adselbiller, stumpbiller m.m. (Hansen, ny utgåve 1968).

Bd. 44. Blødvinger og klannere m.m. (Hansen, 2. oplag 1973).

Bd. 74. Smældere og pragtbiller (Hansen, ny utgåve 1966).

Bd. 55. Clavicornia 1 (Hansen 1950).

Bd. 56. Clavicornia 2 og Bostrychoidea (Hansen 1951).

Bd. 50. Heteromerer (Hansen, 2. oplag 1973).

Bd. 29. Torbister (Hansen 1925).  
Bd. 73. Træbukke (Hansen, ny utgave 1966).  
Bd. 31. Blad- og bønnebiller (Hansen 1927).  
Bd. 69. Snudebiller (Hansen, ny utgave 1965).  
Bd. 62. Barkbiller (Hansen 1956).

Fauna Entomologica Scandinavica.

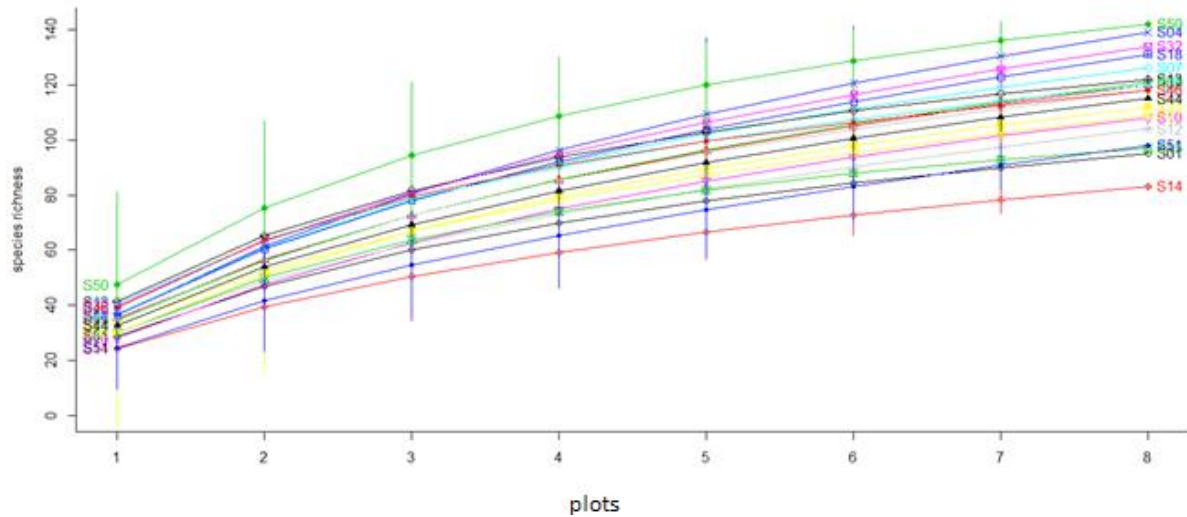
Vol. 10. The Buprestidae (Coleoptera) of Fennoscandia and Denmark (Bily 1982).  
Vol. 15. The Carabidae (Coleoptera) of Fennoscandia and Denmark (Lindroth 1985-86).  
Vol. 18. The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark (Hansen 1987).  
Vol. 20. The Aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark. I.  
Gyrinidae, Haliplidae, Hygrobiidae and Noteridae. (Holmen 1987).  
Vol. 22. Longhorn beetles (Coleoptera, Cerambycidae) of Fennoscandia and Denmark  
(Bily & Mehl 1989).

Nationalnyckeln

Skalbaggar: Långhorningar, Coleoptera: Cerambycidae

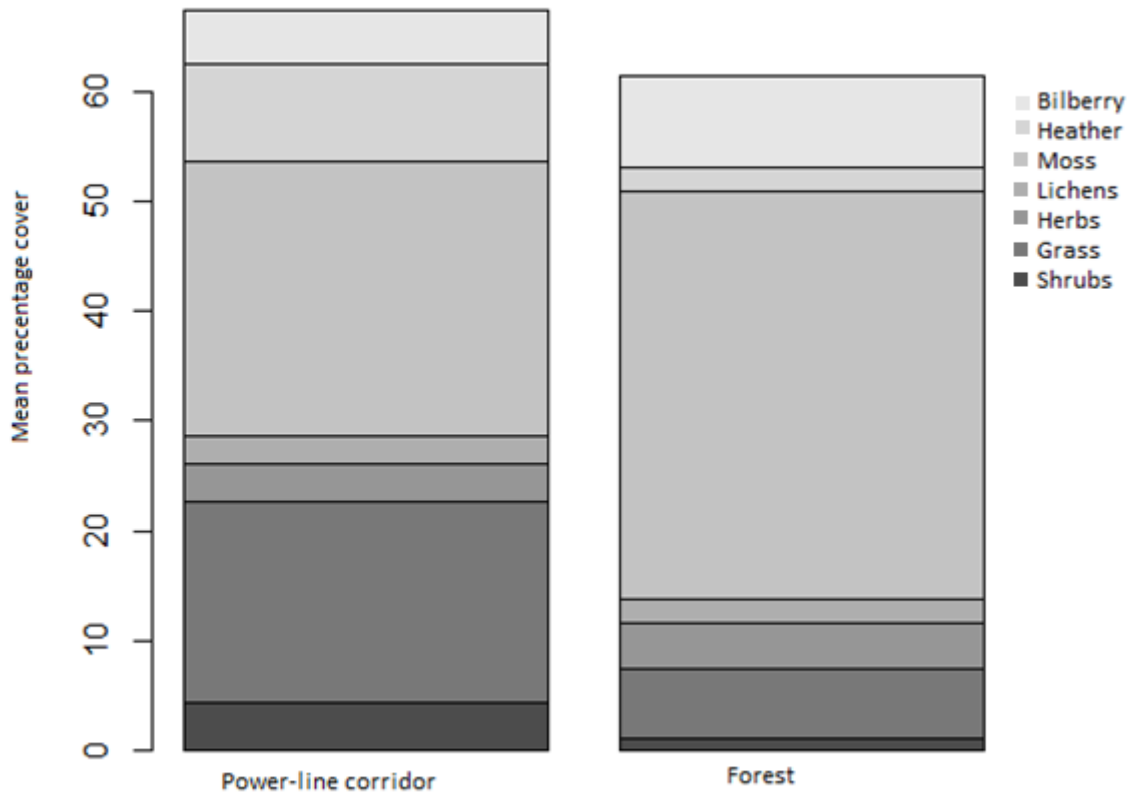
Text: Bengt Ehnström, Bild: Martin Holmer

## Appendix 2.



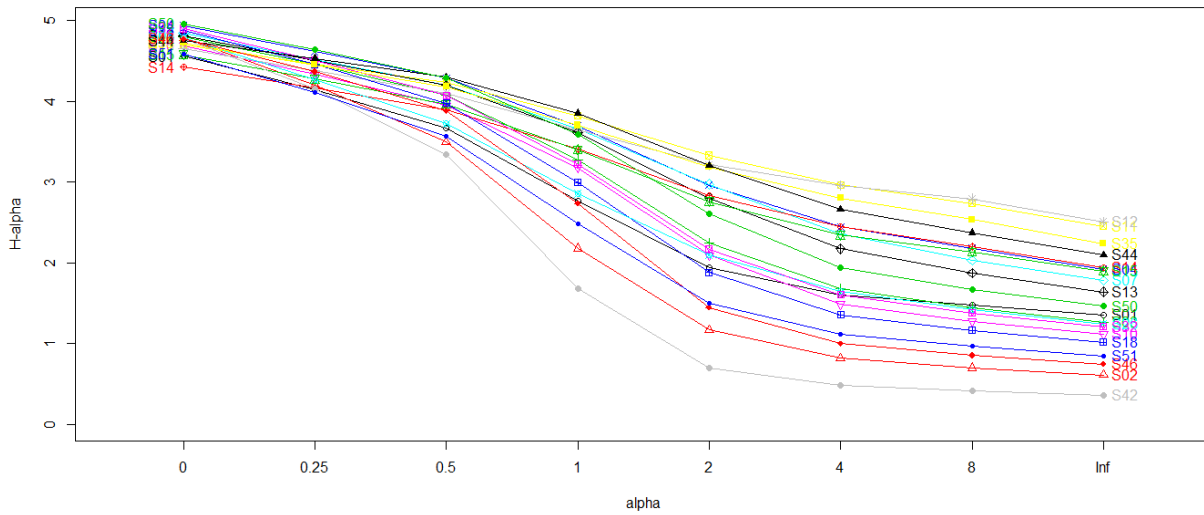
Appendix 2. Species accumulation curves for beetles, showing site differences in beetle richness in Eastern Norway. Graphs are based on aggregated data from 16 traps at each site, capturing continuously from April to September. Four sampling plots are in power-line corridors and four sampling plots are in closed canopy forests.

### Appendix 3.



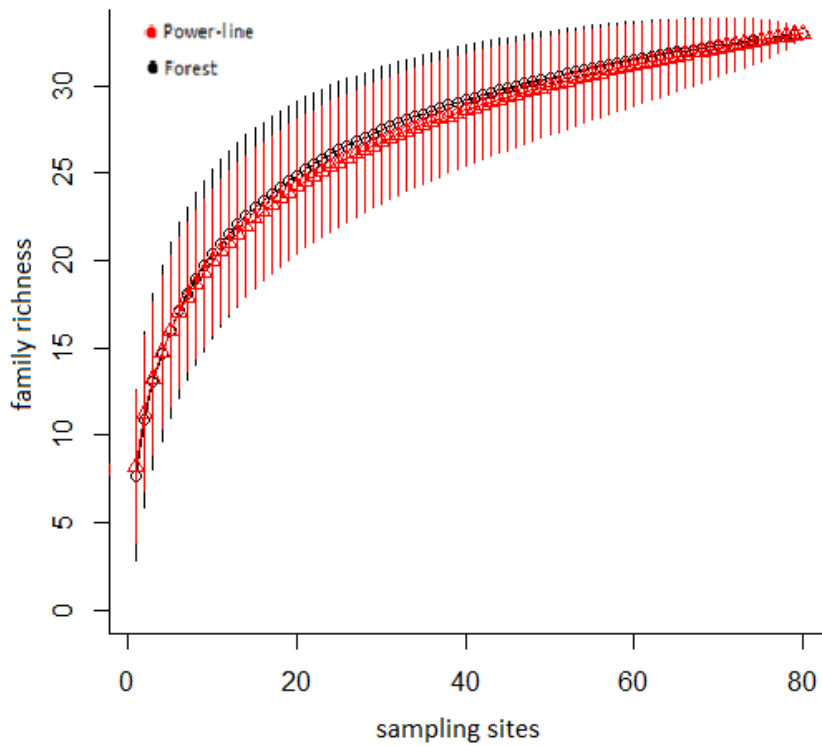
Appendix 1. Mean percentage ground cover over the most common field layer variables in power-line corridors and forests. The data are collected from 20 sites. Shrub is most common in power-line corridors and moss is most common in closed canopy forests.

## Appendix 4.



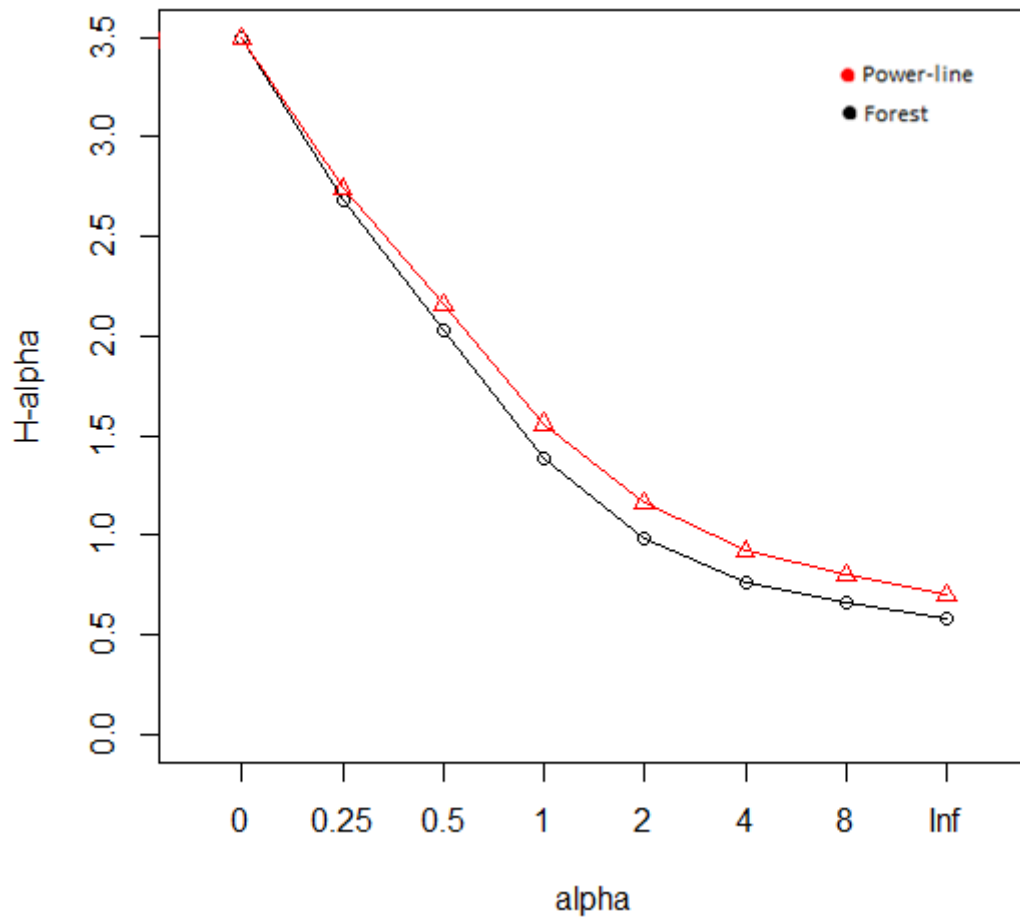
Appendix 3. Renyi profile showing differences between 20 sites for beetle species. The figure is based on aggregated data from power-line corridors and forests. Alpha = 0 on the left side indicates species richness: profiles that start at a high level have high species richness. The antilogarithm ( $e^{H-\text{alpha}}$ ) for alpha = 0, gives species richness. The antilogarithm ( $e^{H-\text{alpha}}$ ) for infinity gives the abundance of the most dominating species. Profiles that are higher than other profiles for all values of alpha have higher biodiversity.

## Appendix 5.



Appendix 4. Accumulation curves for beetle family richness in power-line corridors and closed canopy forests. Graphs are based on aggregated data from 20 sites, with four sampling plots in power-line corridors and four sampling plots in closed canopy forests at each site. There is no significant difference in family richness between power-line corridors and forests. The vertical bars indicate  $\pm 2$  standard deviations.

## Appendix 6.



Appendix 5. Renyi diversity profiles for family richness and biodiversity for beetles captured in the centre of power-line corridors and 100 m in to the forests, perpendicular on the edge between closed canopy forests and power-line corridors. The figure is based on aggregated data from 20 sites. The beetles were captured on the same 4 m × 5 m plot as described in Figure 2. Alpha = 0 on the left side indicates species richness: profiles that start at a high level have high species richness. The antilogarithm ( $e^{H-\text{alpha}}$ ) for alpha = 0, gives species richness. The antilogarithm ( $e^{H-\text{alpha}}$ ) for infinity gives the abundance of the most dominating species. Profiles that are higher than other profiles for all values of alpha have higher biodiversity.