UNIVERSITY OF TROMSØ UiT

FACULTY OF BIOSCINCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

Master thesis in
Ecology

Do saproxylic beetles respond numerically to rapid changes in dead wood availability following moth outbreaks?

Sabrina Schultze

May, 2012
Tromsø

BIO-3910 Master`s thesis in Biology

Master thesis in
Ecology

Do saproxylic beetles respond numerically to

rapid changes in dead wood availability

following moth outbreaks?

BIO-3910

Sabrina Schultze

May 2012

University of Tromsø

Faculty of Biosciences Fisheries and Economics
Department of Arctic and Marine Biology

Table of contents

Abstract

Outbreaks of defoliating insects periodically cause mass mortality of trees, thereby generating pulses of dead wood resources for saproxylic (i.e. dead-wood dependent) organisms. This study investigated the responses of saproxylic beetles to a dead wood resource pulse caused by recent (2001-2009) outbreaks of geometrid moths in the subarctic mountain birch forest of the Varanger region in northern Norway. A large scale (20 km) transect design, implementing window (flight interception) traps and replicated in two areas, was used to compare beetle community structure between outbreak (dead wood) and non-outbreak (live wood) locations. The overall abundance and species richness of saproxylic beetles did not differ consistently between live- and dead wood sections of the transects. However, the two most common early successional saproxylic species, *Hylecoetus dermestoides* and *Rabocerus foveolatus*, were significantly more abundant in the dead wood sections of both transects, while no such responses were found in later successional saproxylic species. With respect to trophic groups, mycetophagous beetles were significantly more abundant in dead wood, but this response was entirely driven by *H. dermestoides.* Moreover, carnivorous beetles strongly dominated the beetle community along the entire transects, regardless of wood vitality. The lack of an overall response from saproxylic beetles to dead-wood-availability, combined with the raised abundance of a few early successional species, suggests that four to eight years after the moth outbreaks saproxylic beetle succession in the Varanger region is still in an initial phase.

Introduction

Outbreaks of defoliating insects constitute a major natural disturbance for many forest ecosystems, periodically causing mass mortality of trees over vast areas (Kamata 2002, Jepsen *et al.* 2008, Kurz *et al.* 2008). The causes for mass insect outbreaks (Myers 1998, Liebhold *et al.* 2000, Jepsen *et al.* 2009a), as well as their direct impacts on nutrient availability and the potential for regeneration of plants (Lovett and Ruesink 1995, Lovett *et al.* 2002, Yang 2004) have been extensively studied. Meanwhile, little attention has been paid to the fact that outbreaks create a resource pulse [i.e. an occasional event of ephemeral resource superabundance" (Yang 2004)] for decomposing (saproxylic) organisms, in the form of huge amounts of dead wood material made available in a very short time. As a result, the ecological consequences of the outbreak-induced resource superabundance for saproxylic organisms are still mostly unknown. It is the saproxylic

community, however, which sets the basis for the successful regeneration of the forest following insect outbreaks by remineralization of lignified plant tissues indigestible to most organisms, and by gradually releasing nutrients into the forest floor over a long period of time (Maser and Trappe 1984, Siitonen 2001). More studies on how saproxylic organisms respond to outbreak-induced resource pulses are, therefore, necessary.

Saproxylic species are per definition "dependent, during some part of their life cycle, upon dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics" (Speight 1989), although species that are strongly associated with, but not strictly dependent on, dead wood are also commonly referred to as saproxylic (Dahlberg and Stokland 2004, Menke 2006). This diverse saproxylic community includes several different insect orders as well as other invertebrates, fungi, plants, vertebrates and microorganisms, but is still overall very poorly understood. (Maser and Trappe 1984, Menke 2006). Saproxylic beetles (Coleoptera) have a key role in decomposition processes, since pioneer beetle species are known to initiate the colonization of dead wood material (Hammond *et al.* 2001). The galleries bored into the wood by early successional beetle species effectively connect the outside world with the inside of the tree and thus facilitate the arrival of fungi, microorganisms and further insects. Those new arrivals again lay the foundation for the colonization by organisms of later successional stages through successional facilitation and exclusion processes within the rapidly diversifying habitat of the dead tree trunk (Maser and Trappe 1984, Weslien *et al.* 2011). The very early colonizing beetles are often dependent on rapidly perishing resources such as the nutrient-rich phloem layer of the inner bark and the cambium of host trees (Maser and Trappe 1984, Wermelinger *et al.* 2002). They are characterized by short development times and can thus be expected to respond rapidly and with high population growth rates to newly available resources, if a source population is in residence within reach (Wermelinger *et al.* 2002). Intermediate to late successional species are increasingly dependent on the established fungal community, which to a large degree is introduced by the pioneer colonizers (Ulyshen and Hanula 2010). Secondary colonizers are also expected to show a clear numerical response to a dead wood pulse, but with a certain time lag and less pronounced than the primary colonizers, since they are often characterized by longer larval development times (Wermelinger *et al.* 2002). During all successional stages, a changing host of specialist and generalist predatory beetles are present within or in the direct vicinity of the trunk

(Maser and Trappe 1984). Information on predatory beetle succession, is, however, scarce. While several studies exist about saproxylic organisms, especially beetles, for often managed temperate (Köhler 1995, Menke 2006) to middle boreal forests in Europe (Väisänen *et al.* 1993, Martikainen *et al.* 1999, Sverdrup-Thygeson and Ims 2002), information is still lacking for most northern sub-arctic European ecosystems (but see Siitonen (1994) for northern Finland). Additional studies of saproxylic communities in northern regions would, therefore, be particularly valuable.

The Fennoscandian mountain birch (*Betula pubescens* ssp. *czerepanovii* Orlova) forest is subject to cyclic outbreaks by the two geometrid (Lepidoptera: Geometridae) moth species autumnal moth (*Epirrita autumnata* Bkh.) and winter moth (*Operophtera brumata* L.) at approximately decadal intervals (Tenow 1972, Bylund 1999). The two moth species can cause severe defoliation of birch trees and also secondary in the understory vegetation. Two prolonged, successive outbreaks of first the autumnal moth (2001-2004) and then the winter moth (2005-2009) recently caused extensive mortality of birch forest in the Varanger region in Finnmark county in northern Norway. In the most heavily affected areas, several hundreds of square kilometres of birch forest died. These severe outbreaks led to an unusually strong dead wood resource pulse, which both spans large areas and is easy to pinpoint in time. Moreover, the particular spread of the two moth outbreaks, from north towards south-east, led to a mosaic of areas with different outbreak histories with regard to forest damage and time since outbreak (Klemola *et al.* 2008, Jepsen *et al.* 2009a, Jepsen *et al.* 2009b) (fig. 2b). While numerical responses to unexpected changes in a system are typically difficult and time consuming to investigate, needing pre- as well as extensive post-disturbance data, the spatiotemporal patterning of the moth outbreaks favours analyses of numerical population changes within a much smaller timescale. In particular, areas with different outbreak histories can be compared with the background of the respective non-outbreak areas, as an alternative to following the succession of only one place over a long period of time.

The primary focus of this study is thus to use a spatial comparative approach to investigate whether, and to what degree, the beetle community in the Varanger region has responded numerically to the recent dead wood resource pulse. Within the beetle community, an emphasis will be put on the most commonly occurring species and

functional groups, with a focus on (known) saproxylic species as these could be expected to respond most clearly.

Material and Methods

Study Area

Fieldwork was conducted in June to August 2011 in the Varanger region (approx. 70° north) in the county of Finnmark, northern Norway (fig. 1). The forest in this region is very strongly dominated by mountain birch, although aspen (*Populus spp.*) and coniferous trees also occur patchily and in very low numbers (fig. 2a). The climate in the study area is characterized by low precipitation [approx. 400-500 mm per year (Moen *et al.* 1999)] and cold winters, with average January temperature of – 11.8°C at the weather station north west of the Varanger area (weather station Rustefjelbma) and -12.2°C at a nearby eastern station (weather station Kirkenes lufthavn) [monthly normal temp 1961-1990 by Norwegian Meterological institute (http://eklima.met.no)]. Summer temperatures are comparatively high for northern Norway, with an average July temperature of 12.3°C at Rustefjelbma and 12.1°C at Kirkenes lufthavn.
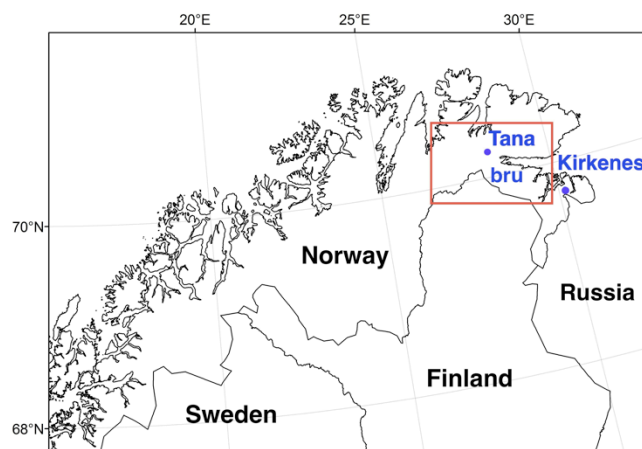
Fig. 1: **Overview map** of northern Norway, with locations of the towns
Tana bru and Kirkenes (blue dots) and the study area (red rectangle).

Study design and sampling

Two transects (Kirkenes and Tana) were established in areas with different defoliation backgrounds: The Tana area was defoliated primarily in 2006-2007 and the Kirkenes area in 2007-2009 (fig. 2b). The two transects spanned localities of both dead and live forest and consisted of 10 stations each, which were selected at an interval of approx. 2 km from

one another. The Kirkenes transect is characterised by a more variable terrain with regard to elevation, mean slope and VRM (Vector ruggedness measure, see explanation in appendix 4) than the Tana transect (appendix 4). In the Tana transect, most stations located on slopes were facing southeast-wards, while in southern and nothwestern slope directions were most common in Kirkenes (appendix 4).

In addition to the transect stations, two reference areas were established; a dead wood reference (Varangerbotn) and a live wood reference (Tana). Both references were selected within large homogenous areas of the respective wood vitality type to gain representative examples for each wood vitality category (fig. 2b). They were made up of one station respectively. The area of the dead wood reference was defoliated during two outbreak waves between 2003 and 2006 and almost all of the birch forest in this area has died. In contrast, the area of the live wood reference was not defoliated in the past outbreaks and is situated at least 20km from the nearest outbreak zone (fig. 2b). Almost all of the trees killed by the moth outbreaks remained standing at all locations at the time of the study, with the bark firmly attached. The trunks generally showed high resistance to knife testing, suggesting that wood decay or rot had not progressed far in the birch trunks (S. Schultze, personal observation).
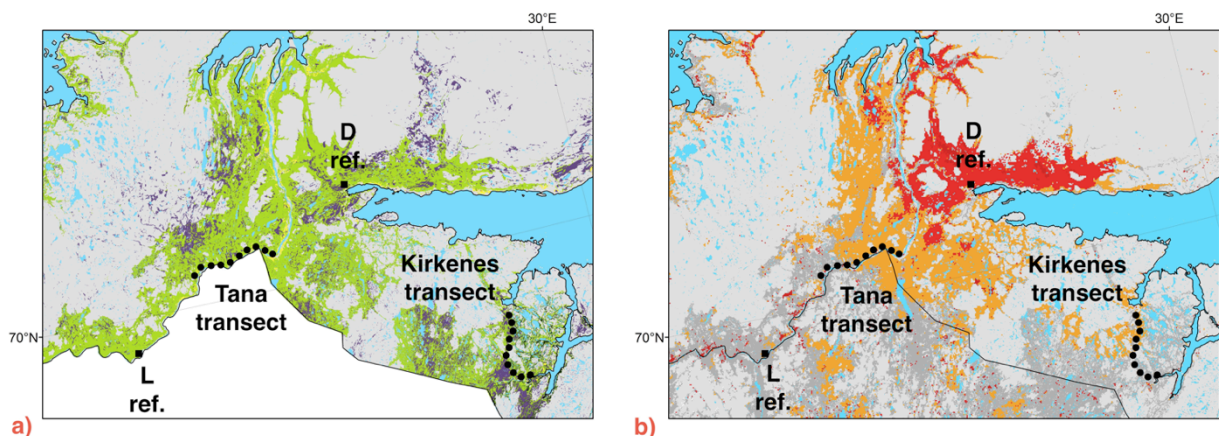

Fig. 2: a) **Vegetation map** of the study area with birch forest (light green), mixed coniferous forest (dark green), mires (lilac) and agricultural area (yellow) with added locations of the transects and reference stations (L ref.=live wood reference, D ref.=dead wood reference). Map reclassified from Johansen (2009).
b) **Moth outbreak areas** of 2002-2004 (red) and 2005- 2008 (orange) in relation to the transects and reference stations. Map reclassified from Jepsen *et al.* (2009a)

At each station, three window-traps were mounted. All three traps were set up in a line, with a minimum of 50 m between each. The traps were mounted between two adjacent trees, at a height of approx. 1.5 - 2 m, and attached to the ground with a rope to reduce

movement by wind. The window traps consisted of two plexi-glass panels fixed to one another in a rectangular fashion ["crosstraps" see: Menke (2006)], so that insects from all directions could be trapped (fig. 3). The panels were fastened to a funnel, which ended in a plastic bottle filled with glycol and one drop of dishwashing detergent to reduce surface tension. Several small holes were drilled into the upper part of the bottle, to prevent the bottle from overflowing in rain.

The traps were mounted in the first week of June (4-9 June). Samples were retrieved after one month, in the beginning July (5-6 July), and again in the beginning of August (8-13 August) when the traps were dismounted. The samples were stored in glycol until sorting and the individual insects were then transferred into ethanol. Identification of the beetle species was done by a specialist. Information on the biology of the beetle species was derived from the following sources: Hansen (1964), Eivind (1996), Anderson (1997), Ehnström and Axelsson (2002), Dahlberg and Stokland (2004), Böhme (2005), Krasutskii (2006), Menke (2006). Not all species could be found in the literature. For detailed information on the classification of trophic groups and saproxylic species, see appendix 1.

Fig. 3: Arrangement of a **window crosstrap** between two birch trees

Wood vitality scores

To be able to relate the community composition and abundance of the beetles to forest vitality, the vitality of birch trees was scored at each station. For this, two transects were established within all stations, each transect starting from the central trap and running 50m towards one of the two outer traps. Every seven meters along each transect, the closest standing or lying birch above 1.3 m height was selected. The vitality of the three thickest stems (above a min. height of 1.3 m) within each tree was classified according to the criteria in table 1. The stem-based vitality scores were then used to calculate an average vitality score for each station.

Table 1: Categories for vitality classification of birch stems

Vitality	Classification	Definition	Vitality score
L	live undamaged	Stem retains most of its leaves Overall healthy appearance	1
LD1	lightly damaged	Overall leaf-crown of the stem is reduced, but it retains more than 50% of its leaves	2
LD2	severely damaged	Overall leaf-crown of the stem is strongly reduced, it retains less than 50% of its leaves	3
D	dead	No live leaves remain No live basal shoots are present	4

The average wood vitality score calculated for each station varied from the maximum value 4.0 (all encountered trees were dead) in some parts of the moth outbreak areas to a minimum value of 1.5 (undamaged forest with only background levels of dead wood) in the unaffected areas (fig. 4). The wood vitality scores did not change in a gradual manner along the transects, but shifted very abruptly between two adjacent stations [Kirkenes: station four (wood vitality: 4.0) and five (1.7), Tana: station six (3.2) and seven (1.5)] (fig. 4). On this basis, two wood categories were established: The first four stations in Kirkenes, with average values between 4.0 and 3.8, were classified as "dead wood", while stations five to ten, varying between 1.5 and 2.1, were classified as "live wood". For Tana the first six stations, with values between 4.0 and 3.2, were classified as "dead wood", while station seven to ten, varying between 1.5 and 2.0, were classified as "live wood". This classification fits well with the wood vitality values of the two reference stations. The dead wood reference had a wood vitality value of 3.8, while the live wood reference had a wood vitality value of 2.1.
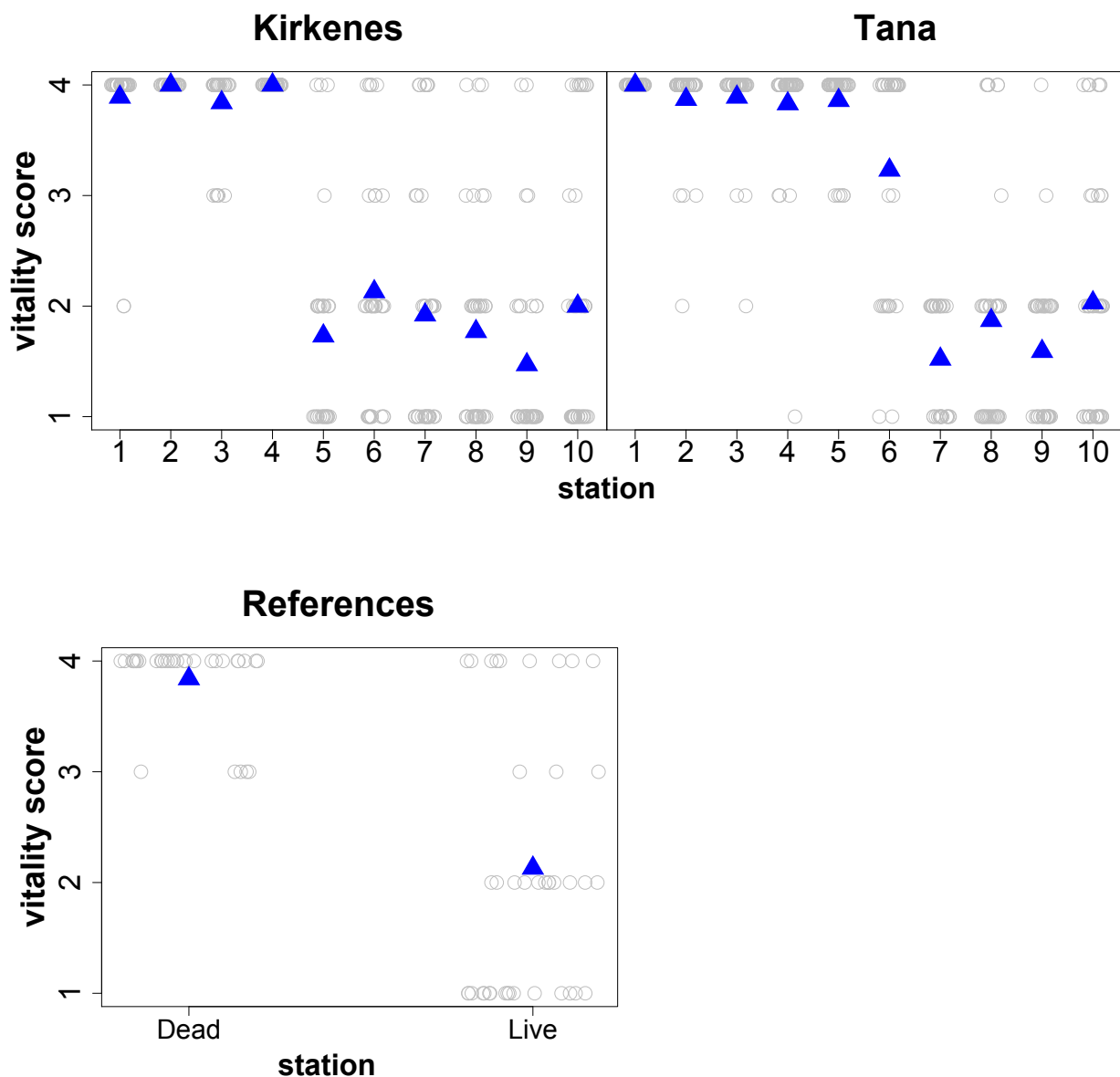
Fig. 4: **Dead wood vitality score** per stem (open dots: with jitter function) and as average per station (blue triangle) at the Kirkenes and Tana transect and the reference stations (average value of 1 signifies: only live healthy stems, 4: only dead stems, 2 and 3: mix out of dead, damaged and live stems in varying proportions).

Data analysis

Because the primary intention of this study was to investigate large-scale spatial community patterns across an entire sampling season, all inferences were based on pooled beetle samples across sampling periods and traps (the sum of six samples per station: three traps with two sample retrievals each). Beetle abundance data was analysed using generalized linear models (GLMs) with Poisson error distribution and log link-function (I.e. log-linear models). Wood vitality (dead or alive) and transect (Tana or Kirkenes) were used as categorical predictor variables in the models, while abundance per station was the response variable. Wood vitality was treated as a categorical variable, due to the clear separation of our sampling stations into a dead wood and a live wood

8

group (see study design and sampling) (fig. 4). Interactions were tested and excluded from the models if they were not significant. Models were fitted for overall beetle abundance (all species pooled) and for the individual beetle species that were common enough to be modeled separately. Beetles were also grouped and modeled according to saproxylic properties (saproxylic and non saproxylic) and trophic groups (see appendix 1 for grouping). Some of the groups were strongly dominated by single species and in these cases, models were also fitted without these dominant species, in order see if the groups showed any responses without their most common members. The carnivorous trophic group included a high number of both saproxylic and non saproxylic species. Therefore, in addition to fitting a single overall model for carnivorous species, separate models were also fitted for the saproxylic and non saproxylic fractions of this trophic group. Beetle species richness was also analysed using the model structure described above. Richness was modelled for all beetle species collectively, for the saproxylic and non saproxylic groups and for the trophic groups (again with separate models for saproxylic and non saproxylic carnivores). For the species richness analysis, one influential station (Kirkenes station two) was excluded whenever diagnostic plots showed that this station had a disproportionately large influence on the models (appendix 3). All models showed a significant degree of overdispersion and, thus, a quasi-likelihood correction was implemented to correct for the unexplained variation in the response.

The structure of the beetle community was investigated using correspondance analysis (CA, R-library 'vegan') for each of the transect localities separately.

All analyses were done using R 2.14.0 (R Development Core Team, 2011).

Results

Overall community structure

A total of 148 beetle species with a total of 2322 individuals (Kirkenes: 1395 ind.; Tana: 659 ind; dead wood reference: 215 ind.; live wood reference: 53 ind.) were trapped. Most species were represented by a very low number of individuals in the material. For only 7 species more than 50 individuals per species were caught. Only these species were subjected to species-specific statistical analyses of spatial abundance patterns. More than half (55.4%) of the species were represented by only one (58 species) or two (24 species)

individuals. The frequency distribution of the number of individuals caught per species was very similar between the two transects (fig. 5).
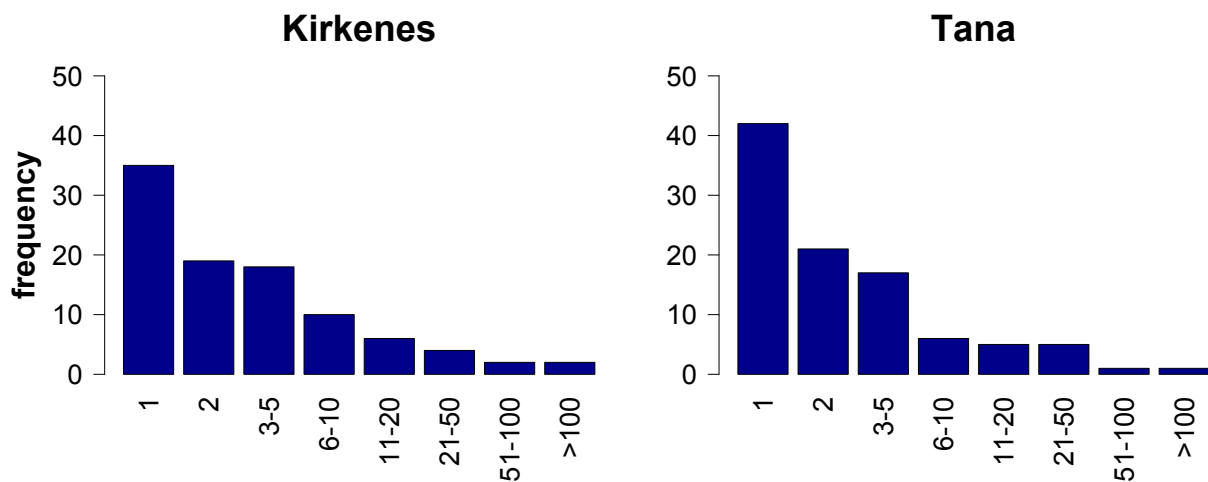

Fig. 5: Frequency distribution for the number of individuals caught per species in the two transects

The patterning of overall beetle abundance with regard to wood vitality differed markedly between the two transects (fig. 6). While beetle abundance in the Kirkenes transect was significantly higher in the dead wood section than in the live wood section of the transect, the opposite pattern was true for the Tana transect (transect × wood vitality interaction: p = 0.0086; appendix 3). The two transects also differed greatly with regard to the total number of beetles caught, with the Kirkenes transect having a higher total number of trapped individuals as well as a high variation between stations and traps (fig. 6; fig. app. 5-1 for among trap variation). The Tana transect, in contrast, had altogether lower numbers of trapped beetle individuals and abundance was considerably more stable between stations and traps. The dead wood reference station had a considerably higher abundance of beetle individuals than the live wood reference station. However both values were well within range of the variation observed in the transects (fig. 6, fig. app. 5-1).
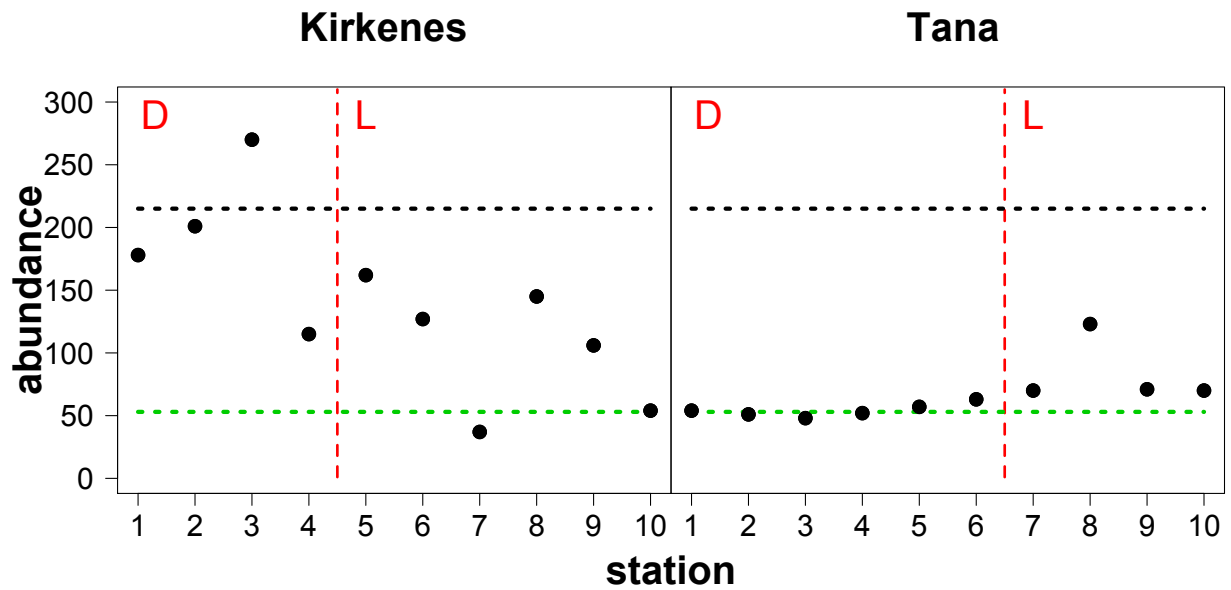
Fig. 6: **Number of beetle individuals** trapped in the two transects according to stations and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The abundance of the beetles at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.

Overall species richness, expressed as the total number of species caught, was higher in the dead wood than in the live wood sections of the transects (main effect of wood vitality after exclusion of outlier Kirkenes station two: p= 0.0002, appendix 3; fig. 7). Station two in the Kirkenes transect had an exceptionally high species richness with more than twice the number of species as the average station.

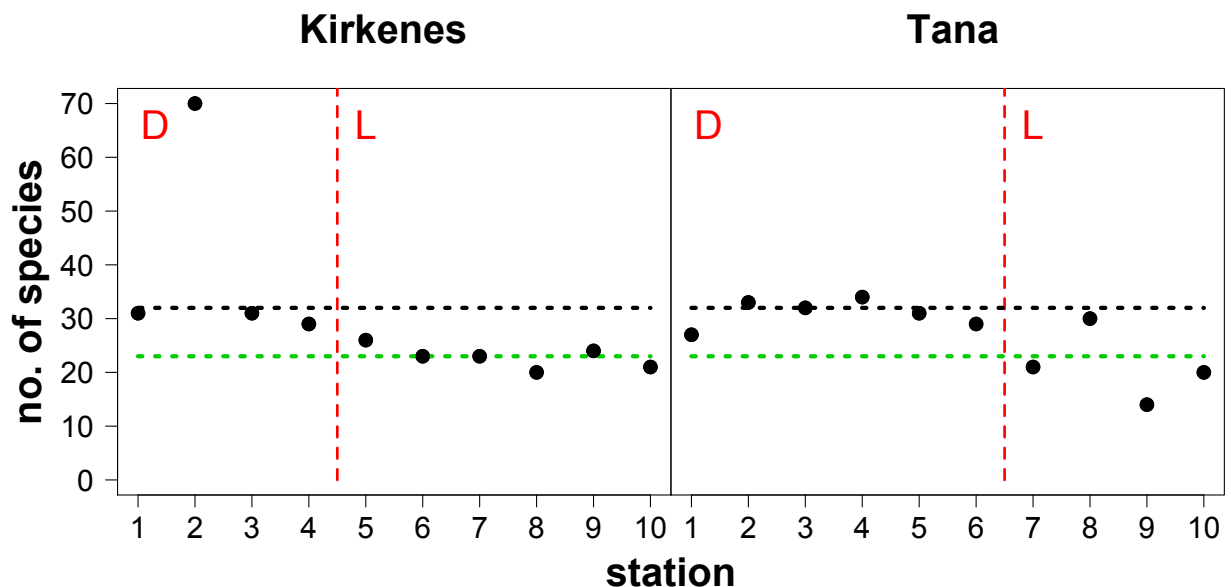**Fig. 7**: **Species richness** (total number of species caught) in the two transects according to station and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The species richness at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.

Saproxylic beetle community

Altogether 68 (46.0%) of the species and 787 (33.9%) of the individuals (Kirkenes 25.2% of the individuals; Tana: 39.3%; dead wood reference: 65.1%; live wood reference: 69.8%) were categorized as saproxylic (appendix 1). This group includes individuals of different trophic groups and different dead wood successional stages (appendix 1).

The saproxylic group had a higher abundance in the dead wood section in Kirkenes and the live wood section in Tana (fig. 8) (transect × wood vitality interaction: $p = 0.0189$; appendix 3), but neither effect remained significant upon the exclusion of the dominant saproxylic species *Hylecoetus dermestoides*. The species richness of the saproxylic group, after exclusion of outlier Kirkenes station two, was not significantly different between the two wood vitality classes or transects (fig. 9, appendix 3). While abundance of saproxylic species was considerably higher at the dead wood reference station (140 individuals) than at the life wood reference station (37 individuals), the species richness of saproxylics was quite similar at the dead- and live wood reference (fig. 9). The Correspondance analysis plot (fig. 10) showed no clear separation between saproxylic and non saproxylic group, nor any subgrouping within the groups. There was also no strong patterning of the species along any axis, meaning that the dead wood resource had no consistently clear structuring influence on the community. It also became apparent that except for Kirkenes station seven, the stations were quite similar in the species composition they harboured. Station seven in Kirkenes differed from other stations in the sense that all species, even generally common ones, showed low abundances at this station.

Non saproxylic beetles were more abundant in the dead wood section than in the live wood section of the Kirkenes transect, but were more abundant in the live wood section in the Tana transect (transect × wood vitality interaction: $p = 0.0292$; appendix 3, fig. app. 5-2). The species richness of non saproxylic beetles was significantly higher in the dead wood sections of the transects (main effect of wood vitality after exclusion of outlier Kirkenes station two: $p = 0.0031$; appendix 3, fig. app. 5-3).

Fig. 8: **Number of saproxylic individuals** trapped in the two transects according to stations and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The abundance of the species at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.

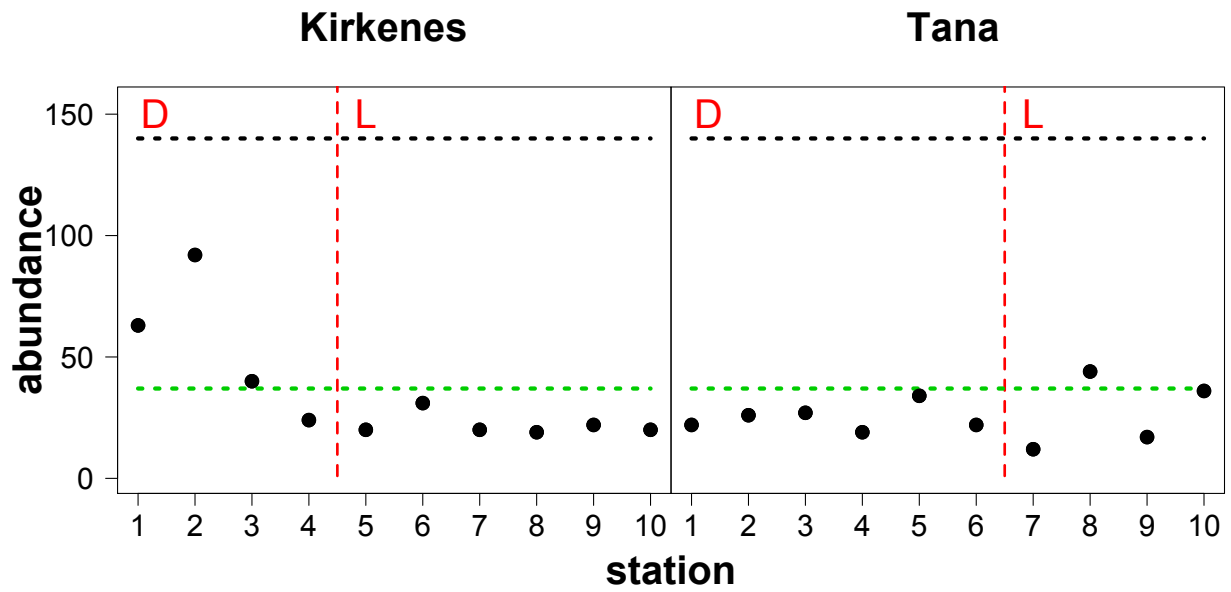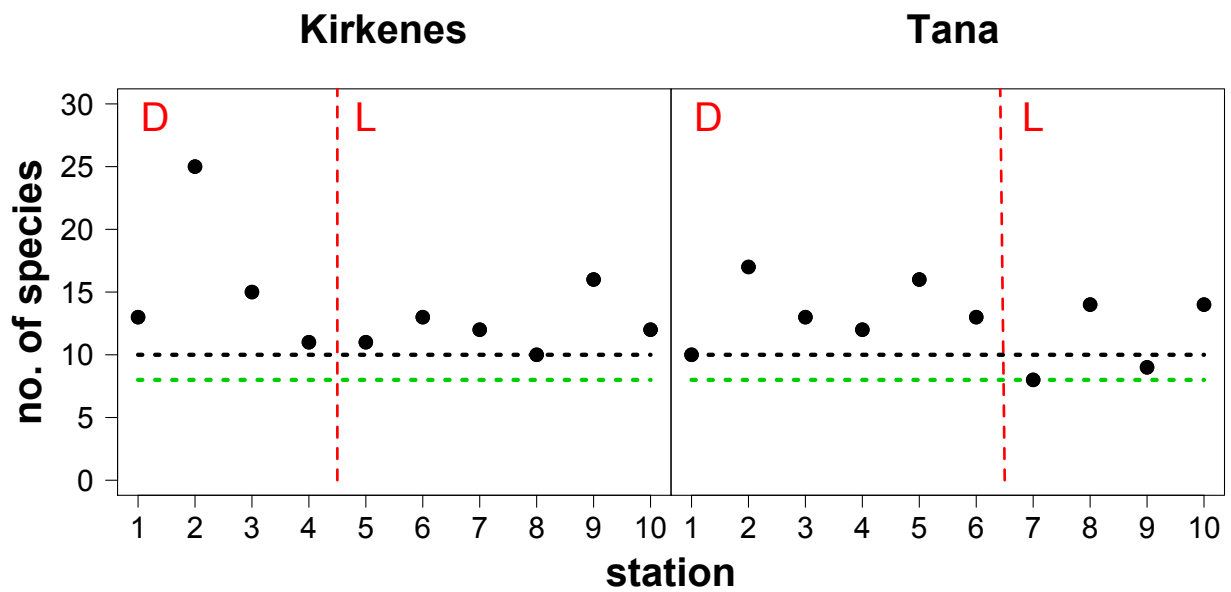**Fig. 9**: **Species richness** of **saproxylic species** in the two transects according to stations and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The species richness at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.
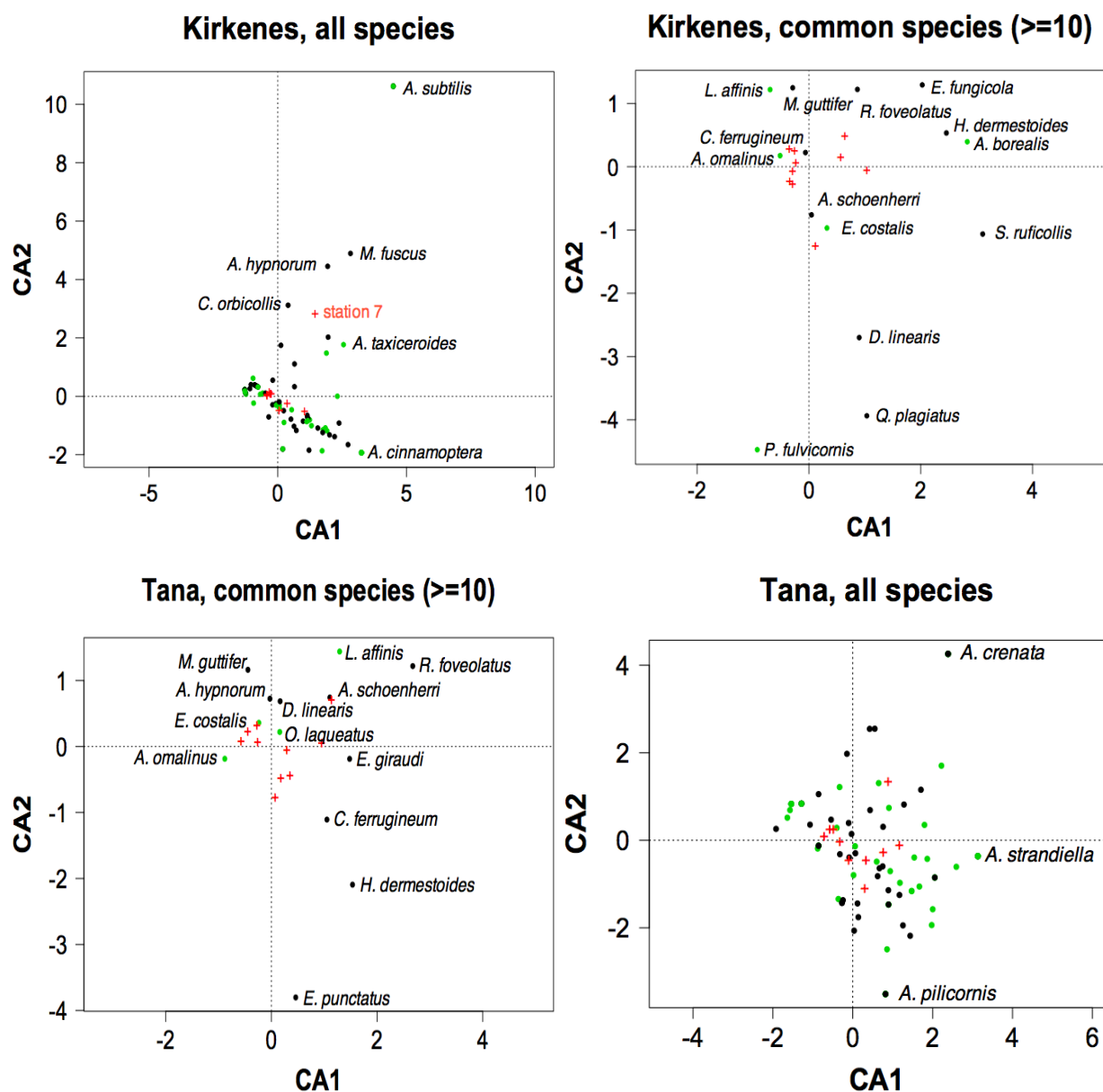
Fig. 10: **Correspondance analysis plot plot of saproxylic** (black) and **non saproxylic/uncertain** (green) beetles for all (a) and the ten most common species (b) of the Kirkenes and Tana transects in relation to stations (red crosses).

Trophic groups

Carnivores constituted the most common trophic group with regard to abundance. In the Kirkenes transect, an average of 66.0% of all individuals were classified as carnivores, while in Tana the carnivorous group constituted 65.6% of all individuals. Mycetophages constituted 9.7% of total abundance in the Tana transect and 10.0% in Kirkenes. Phytophags were less common in both transects (Kirkenes: 7.2%, Tana: 5.2%) and xylophages, coprophages and saprophages were only marginally represented. 13.6% and 14.7% of the beetles in Kirkenes and Tana, respectively, were unknown or uncertain with respect to their trophic classification. Similarly to the transects, the live wood reference was dominated by carnivorous species (50.9%), followed by mycetophages (20.8%). The

abundance of phytophages constituted 9.4% at the live wood reference. At the dead wood reference station, however, mycetophagous beetles predominated (49.3%), followed by carnivorous beetles (44.2%) and phytophagous (0.9%) ones. Among the trophic groups, only carnivores, mycetophages and phytophages were abundant enough to be subjected to statistical analysis of spatial patterns in abundance and species richness.

The carnivorous group (fig. 11a, b) had a higher abundance in the dead wood section of the Kirkenes transect, while in the Tana transect abundance was higher in the live wood section (transect × wood vitality interaction: p = 0.0367; appendix 3). However this pattern was strongly driven by the two most abundant carnivorous species, *Anthophagus omalinus* and to a lesser degree *Rabocerus foveolatus*, and upon statistical exclusion of these two species from the trophic group, no significant effects of transect nor wood vitality could be shown. While the saproxylic subgroup of the carnivores had a higher abundance in the dead wood section in Kirkenes, in Tana the abundance was higher in the live wood section (transect × wood vitality interaction: p = 0. 0517: this interactions was retained because it borders closely on significance; appendix 3; fig. app. 5-4). The non saproxylic carnivores subgroup did not show a significantly different abundance between the wood vitality sections (appendix 3, fig. app. 5-5), but the subgroup had a significantly lower abundance in the Tana transect than in the Kirkenes transect (main effect of transect p = 0.0059; appendix 3, fig. app. 5-5). The mycetophagous trophic group (fig. 11c, d) had a significantly lower abundance in the live wood sections than the dead wood sections (main effect of wood vitality: p = 0.0173; appendix 3), and an overall lower abundance in the Tana transect than the Kirkenes transect (main effect of transect: p = 0.0256; appendix 3). This group was strongly dominated by the single species *H. dermestoides*, and upon exclusion of this species, no significant effects and only very few individuals remained. The abundance of the phytophagous trophic group (fig. 11e, f) did not differ significantly between the wood vitality sections, but was significantly lower in the Tana transect (main effect of transect p = 0.0243; appendix 3).

Fig. 11: Number of carnivorous (a,b) **mycetophagous** (c,d) and **phytophagous** (e,f) **individuals** in the two transects according to stations and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The abundance of the species at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.
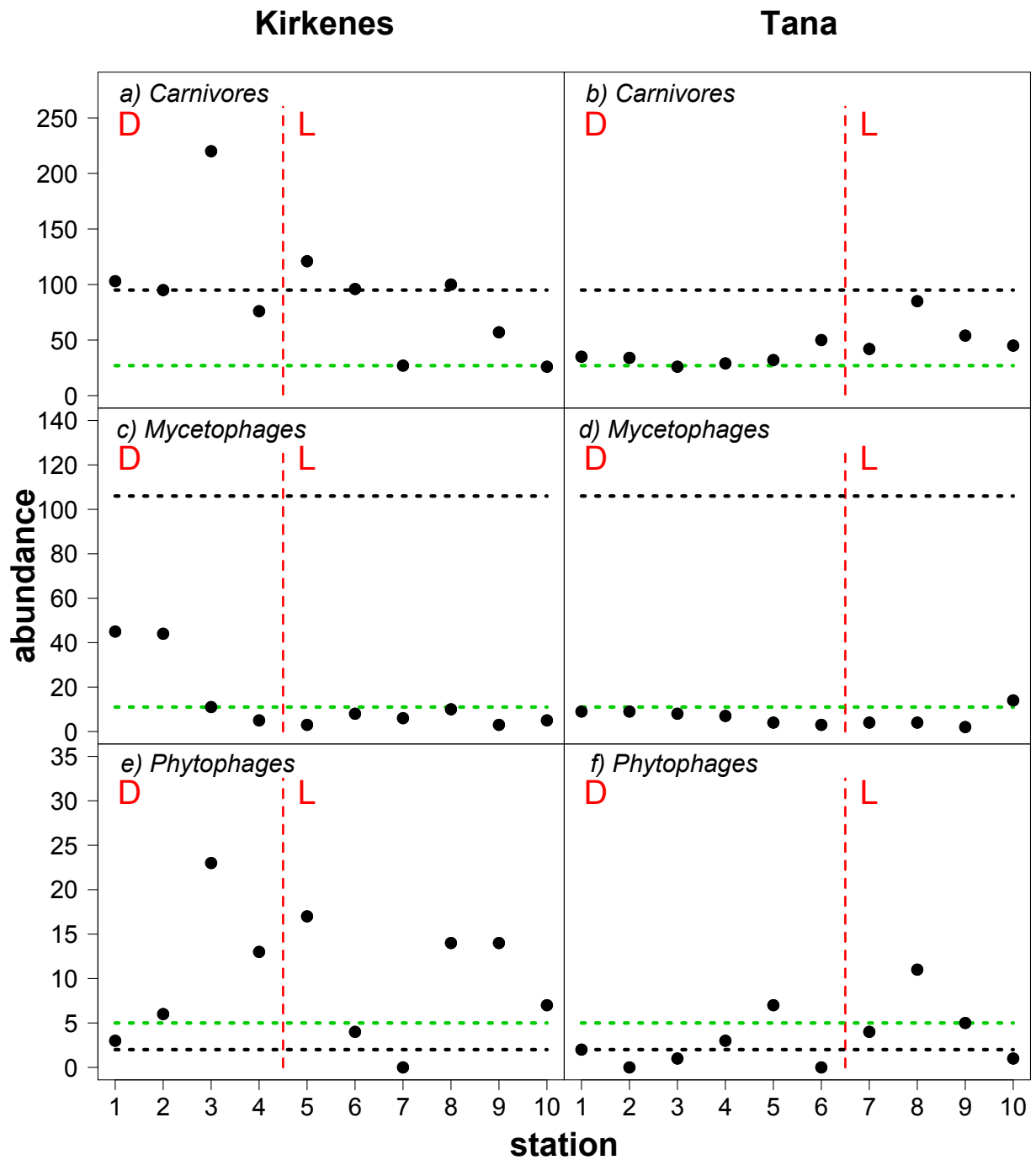
The most species rich trophic group were the carnivores (65 species), followed by mycetophages (29 species), xylophages (7 species), phytophages (5 species), coprophages (3 species) and saprophages (2). 37 species could not clearly be assigned to the above stated trophic groups, or had no trophic information available. Of the trophic groups, the carnivores had a higher species richness in the dead wood than in the live wood sections of the transects (main effect of wood vitality after exclusion of the outlier Kirkenes station two: $p = 0.0051$; appendix 3, fig 12a, b). Among the carnivores, the species richness of the saproxylic subgroup was not significantly affected by either wood vitality nor transect. (fig. app. 5-6, appendix 3). The non saproxylic carnivores, however, had a significantly higher species richness in dead wood than in live wood and higher overall species richness in Tana (after exclusion of the outlier Kirkenes station two; main effect of wood vitality: $p = 0.0020$; main effect of transect: $p = 0.0085$; appendix 3; fig. app. 5-7). The species richness of the mycetophagous group was not significantly different between neither transects nor wood vitality sections (fig. 12c, d; appendix 3). The phytophagous group (fig. 12e, f) had a significantly higher species richness in the Kirkenes transect (main effect of transect: $p = 0.0259$; appendix 3), but showed no significant difference in richness between the wood vitality sections of the transects (appendix 3).
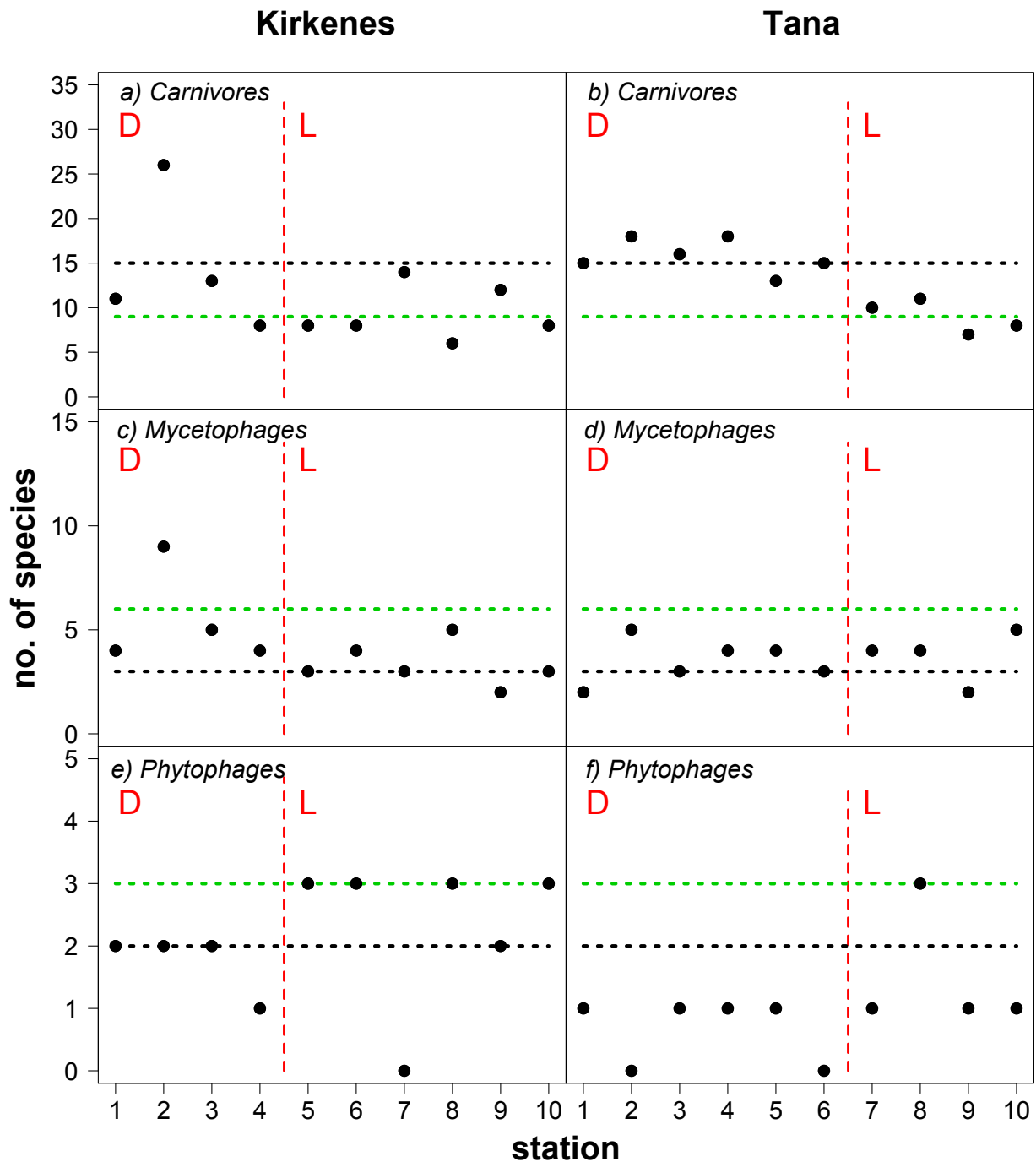
Fig. 12: Species richness of the **carnivorous** (a,b) **mycetophagous** (c,d) and **phytophagous** (e,f) trophic groups in the two transects according to stations and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The species richness at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.

Single species

Anthophagus omalinus (Zetterstedt 1828, family: Staphylinidae, fig. 13a, b) is a carnivorous species living in herbs and flowers (appendix 1). This was overall the most common species found in the traps, which was present with 957 individuals in all samples. The species fluctuated strongly among the stations of the Kirkenes transect

(around mean: 69.7, fig. 13a), while showing a lower, more stable abundance level (around mean: 19.9) in the Tana transect (fig. 13b). *A. omalinus* was significantly more abundant in the Kirkenes (fig. 13a) than the Tana transect (fig. 13b) (main effect of transect: p = 0.0083; appendix 3), while abundance did not differ significantly between wood vitality sections (appendix 3). *A. omalinus* was considerably more abundant in the dead wood reference than in the live wood reference (fig. 13a, b).

Hylecoetus dermestoides (Linnaeus 1761, family: Lymexylidae, fig. 13c, d) is a mycetophagous early successional obligate saproxylic species occurring in the wood under the bark of dead, dying or damaged trees (Veit (2003), Dahlberg and Stokland (2004); appendix 1). The species was present with 223 individuals in all samples. It was overall more common in the Kirkenes transect (mean: 8.4, fig. 13c) than in the Tana transects (mean: 3.2, fig. 13d), but its abundance was mainly restricted to rather few stations in both transects. The species showed a high abundance in dead wood stations one, two and partially three of the Kirkenes transect (fig. 13c), and a virtual absence (0-3 ind.) at the other stations. In the Tana transect (fig. 13d), the pattern was not so clear: A few individuals were present in dead wood stations one to four, almost none were present in live wood stations five to nine, and nine individuals were present in live wood station ten. The species showed significant main effect of wood vitality (p = 0.0377, appendix 3), but not of transect. While the live wood reference contained only six individuals, the dead-wood reference contained a total of 101 individuals (fig. 13c, d), which is considerably more than was found in any of the transect stations.

For ***Eanus costalis*** (Paykull 1800, family: Elateridae, fig. 13e, f) no information on species biology could be obtained. *E. costalis* occured 209 times in all samples. On average, more individuals were caught in the Kirkenes transect (mean: 13.9, fig. 13e), than in the Tana transect (mean: 5.9, fig. 13f). While the abundance in Kirkenes fluctuated in similar ways for both live and dead wood stations (fig. 13e), in Tana, higher abundances were restricted to two stations in the live wood section (fig. 13f). The species showed a significant interaction between transect and wood vitality (p= 0.0105; appendix 3), with a higher abundance in the dead wood section in Kirkenes and a higher abundance in the live wood section in Tana. The abundance of *E. costalis* was similarly low for both reference stations (fig. 13e, f).

Liotrichus affinis (Paykull 1800, family: Elateridae, fig. 13g, h) is a phytophagous species occurring in trees (appendix 1). *L. affinis* occurred 91 times in total in the samples and was caught more often in the Kirkenes transect (mean: 6.6, fig. 13g) than in the Tana transect (mean: 2.3, fig. 13h) (main effect of transect: p = 0.0425; appendix 3). There was no significant difference between the wood vitality sections for this species (appendix 3). The two reference stations had equally low abundances (fig. 13g, h).

Absidia schoenherri (Dejean 1837, family: Cantharidae, fig. 14i, j) is a carnivorous and obligate saproxylic species of mid to late successional stage (Dahlberg and Stokland (2004); appendix 1). *A. schoenherri* was caught 69 times in total, with on average 2.7 individuals per station in the Kirkenes transect (fig. 13i) and 4.0 individuals per station in the Tana transect (fig. 13j). For this species, there was no significant effect of neither wood vitality nor transect (appendix 3). While *A. schoenherri* was present with 2 individuals in the live wood reference, it was entirely absent at the dead wood reference (fig. 13i, j).

Malthodes guttifer (Kiesenwetter 1852, family Cantharidae: fig. 13k, l) is an obligate saproxylic carnivorous species hunting in wood detritus. The successional stage of this species is uncertain (Dahlberg and Stokland (2004); appendix 1). *M. guttifer* occurred 66 times in all samples with an average of 3.6 individuals in the Kirkenes transect (fig. 13k) and 2.7 in the Tana transect (fig. 13l). For this species there was a significant interaction between wood vitality and transect (p = 0.0120; appendix 3). While in the Kirkenes transect the species was more abundant in the dead wood section, the opposite was true for the Tana transect (appendix 3). Both reference stations showed relatively low numbers of *M. guttifer* individuals (fig. 13k, l).

Rabocerus foveolatus (Ljungh 1824, family: Salpingidae: fig. 13m, n) is an early successional obligate saproxylic species (Dahlberg and Stokland (2004); appendix 1). *R. foveolatus* is coleopterophagous and hunts underneath the bark of dead or dying trees (appendix 1). *R. foveolatus* occurred 64 times in all samples, with an average of 3.0 individuals in the Kirkenes transect (fig. 13m) and 1.5 in the Tana transect (fig. 13n). There was a higher abundance of *R. foveolatus* in the dead wood sections of both transects (main effect of wood vitality: p = 0.0008; appendix 3), and a higher abundance in the Kirkenes transect than the Tana transect (main effect of transect: p = 0.0092; appendix 3).

At the reference stations (fig. 13m, n) *R. foveolatus* was clearly most abundant at the dead wood station, with 19 individuals caught at that one station. *R. foveolatus* was entirely absent at the live wood reference station (fig. 13m, n).

Kirkenes

Tana
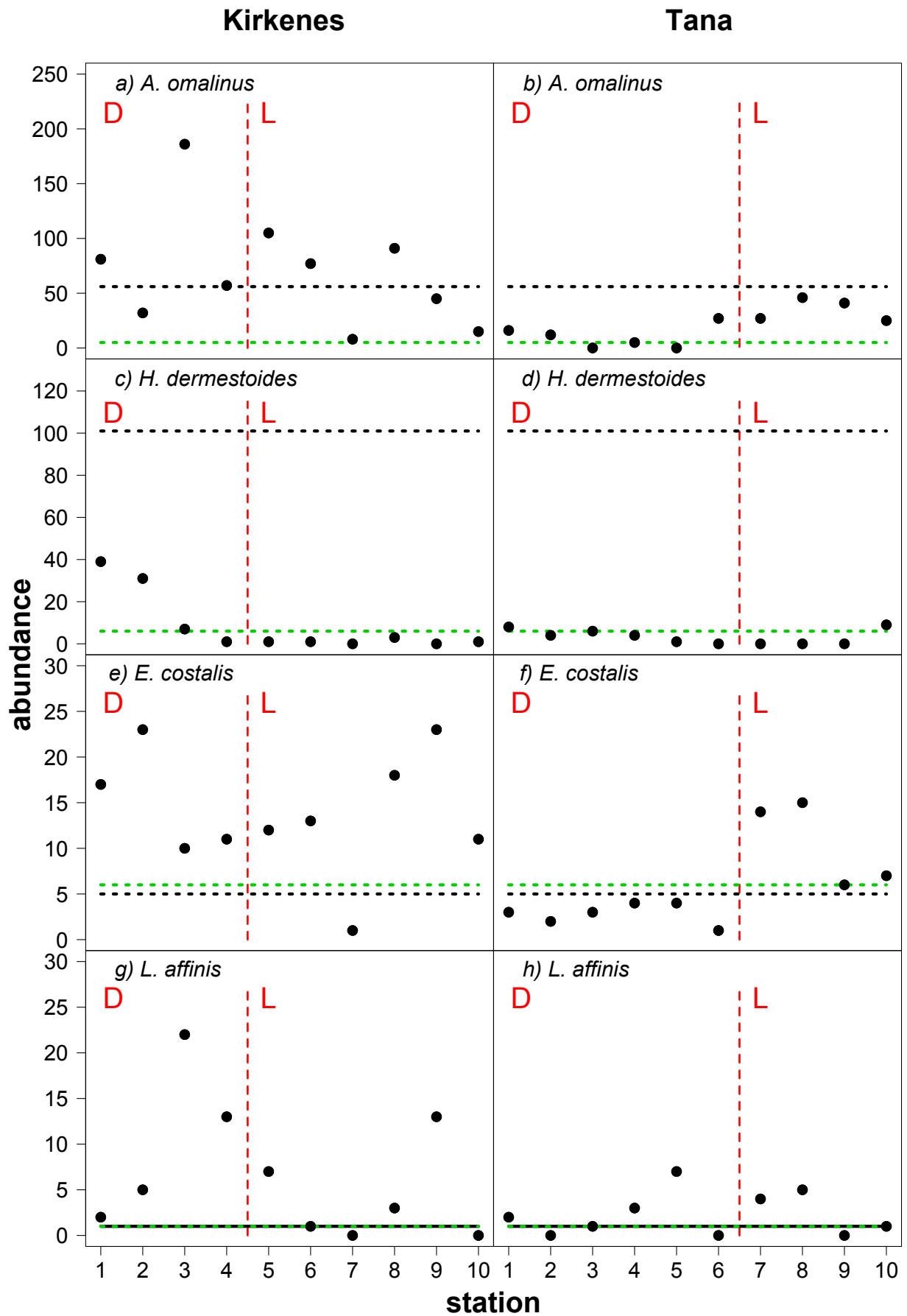
Fig. 13: to be continued on the next page
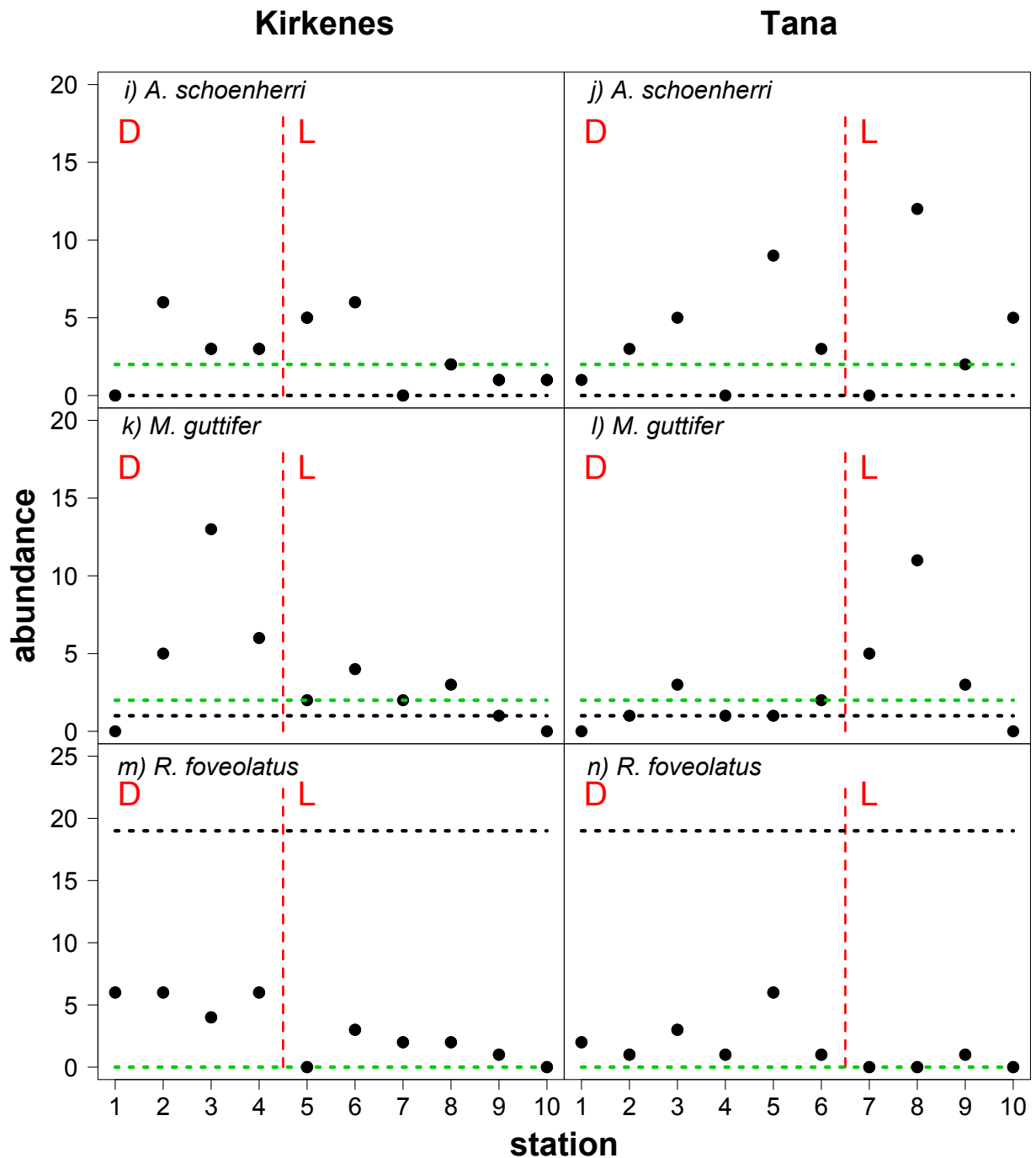
Fig. 13: **Abundance** patterns of ***Anthophagus omalinus** (a,b),* ***Hylecoetus dermestoides** (c,d),* ***Eanus costal****is (e,f),* ***Liotrichus affinis** (g,h)* ***Absidia schoenherri** (i,j),* ***Malthodes guttifer** (k,l)* **and *Rabocerus foveolatus** (m,n)* in the two transects according to stations and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The abundance of the species at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.

Discussion

The major dead wood resource pulse following the moth outbreaks in the Varanger area between 2003 and 2009 would be expected to have a considerable impact on the structure of the local beetle community. This is especially so for the dead wood associated

saproxylic community, which in theory should benefit greatly from a major dead wood input and would be expected to react with a clear increase in the abundance and diversity of species. Surprisingly, our results in the present study matched this expectation only to a very limited extent. The overall abundance and diversity of saproxylic beetles did not differ consistently between the wood vitality sections of the transects (although saproxylic species were more abundant in the dead wood section in Kirkenes), and no clear changes in favour of dead wood dependent trophic groups could be detected. Xylophages (which are almost exclusively saproxylic) showed very low overall abundance and diversity in the whole study area. Mycetophages (mostly saproxylic species in this study) tended to be more abundant (but not more species-rich) in the dead wood sections of the transects, but carnivores (to a large degree non-saproxylic species) were still by far the most abundant and diverse trophic group at all transect stations, regardless of wood vitality. The only exception was the dead wood reference, where the total number of saproxylic individuals, driven mainly by the mycetophagous trophic group, was considerably higher than anywhere in the transects. Among the single species analysed separately, only two out of four saproxylic species (*H. dermestoides* and *R. foveolatus)* had a consistently higher abundance in the dead wood sections of either transect. In addition *H. dermestoides* was also the main driver of the dead wood responses found in the saproxylic and mycetophagous groups. Notably, the two species with a clear dead wood response are also both early successional saproxylics. The fact that only two early successional saproxylic beetle species showed a clear response to the dead wood availability along the transects, may suggest that the beetle community in Varanger is still in an initial stage of responding to the recent dead wood input. This conclusion is supported by the pattern at the dead wood reference, which is the oldest (i.e. longest time since the outbreak) dead wood location in our study: The predominance of dead wood-dependent mycetophagous species at this location may suggest that larger shifts in community composition are under way in the transects, but still need more time to occur. Patterns from a single station need to be interpreted cautiously though, and the above prediction will have to be validated by further monitoring of the beetle community in the transects.

The saproxylic community in the north
Any possible response of a community to a resource pulse strongly depends on the overall accessible species pool in the area. Insect species diversity is generally reduced

towards the Arctic (Strathdee and Bale 1998, Martikainen *et al.* 2000) and saproxylic beetles may be particularly strongly affected, since saproxylic species have been shown to be considerably more sensitive with regard to habitat quality than non saproxylic ones (Martikainen *et al.* 2000). Several studies suggested that saproxylic diversity is strongly dependent on a) the tree species diversity b) the amount of available dead wood c) the size of the available litter d) the continuity in space and time from other dead wood sites (Siitonen 2001, Grove 2002). In the sub-arctic environment saproxylic species diversity and abundance will therefore likely be strongly reduced due to climate induced reduction in plant diversity and tree abundance and size (Siitonen 2001).

As Martikainen (2004) pointed out, even a small-scale one year window trap based study can give an appropriate overview of the most common beetle species at one location. In our study located in subarctic Finnmark overall 148 beetle species and a total of 2322 individuals were caught in the traps. Approximately 46% of the species and 34% of the individuals were categorized as saproxylic (see appendix 1). While the number of trapped individuals and species (both overall abundance and species richness as well as saproxylic abundance and species richness) was indeed considerably lower than compared to the results of studies with comparable sampling effort per year in other systems (Menke, 2006), the overall percentage of saproxylic species in the community is well within the range of other studies (see Grove (2002) for a detailed list). While a reduced saproxylic diversity and abundance in the subarctic area might affect the intensity and timing of a response, as well as the exact course of dead wood succession, a clear response of saproxylics to the dead wood pulse is nonetheless expected.

Community and group responses

Saproxylic species

Pulsed resource superabundance in general benefits local generalist consumers, highly mobile specialist consumers and the detritus community the most (Yang *et al.* 2008). A dead wood resource pulse will initially be most attractive for specialist species, due to the barrier function of the bark and still active plant defences. While this may in the beginning exclude many generalist consumers, saproxylic species diversity tend to increase progressively in early dead wood succession after initial colonization (Maser and Trappe 1984, Hammond *et al.* 2001). Behavioural aggregation and reproductive response of these consumers (Yang *et al.* 2008) would be expected to lead to clear differences in species

abundance and composition between live and dead wood sections already after a short time, with saproxylic species clearly favouring the dead wood sections.

Although several years have passed since initial defoliation in the dead wood sections of all our study areas, no changes in saproxylic diversity were visible between live and dead wood sections. While the diversity of the saproxylic species, most of which were mid to late successional, was moderate in relation to overall species diversity in the area, most had very low abundances. Thus, the majority of the saproxylic group apparently still remains unaffected by the new dead wood input. Any increase in the abundance of the saproxylic group in the dead wood sections was very strongly mediated by the single species *H. dermestoides* and, to a lesser degree, by *R. foveolatus.* The correspondance analysis displaying saproxylic and non saproxylic species did not allow for a clear separation between saproxylic and non saproxylic species or dead and live wood areas and did not show any strong grouping tendency according to stations. A clear subgrouping of saproxylic species of a similar successional stage and differences between dead and live wood areas would, however, be expected to be visible if saproxylic succession had progressed past an initial stage to a point where community structure was starting to become strongly affected. Although the grouping into non saproxylic and saproxylic species presented several difficulties (see appendix 1 b for further elaborations), altogether the results for the saproxylic community structure suggests that saproxylic succession has not progressed far.

Trophic groups

In early dead wood succession, a predominance of early successional wood-boring beetles (including bark beetles, other early successional xylem and phloem feeders (here collectively referred to as "xylophages") and early successional mycetophagous species that bore their terraces in fresh wood) of the xylophagous or mycetophagous trophic groups and to a lesser degree their associated specialist predators is expected (Hammond *et al.* 2001, Vanderwel *et al.* 2006). In contrast, the live-wood community should overall be characterised by a more balanced trophic composition depending on the forest type [see: Menke (2006)]. However, in my study area in Varanger carnivores strongly dominated the samples in terms of both individual abundance and species richness, regardless of wood vitality and to similar degree in both transects. The carnivores were followed to a considerably lesser degree by mycetophages, while the typically early

successional group of xylophages only contributed very little to total abundance at the community level. The only exception to these patterns was the dead wood reference, where mycetophagous species, driven by the single species *H. dermestoides,* predominated.

While window trap samples are strongly affected by beetle activity levels and therefore favour active carnivorous species to a certain degree (Alinvi *et al.* 2007), this alone is unlikely to lead to such a strong dominance of carnivores as observed in this study. In a window trap based three year study in a senescent wood in middle Europe, Menke (2006) found a dominance of mycetophagous individuals (average 39.2%, with strong variability between the years), followed by only 24.7% carnivorous individuals. While the study area and ecological circumstances differed considerably from the present study, the results of Menke (2006) would nevertheless suggest that the high percentage of carnivorous species in my samples is unlikely to be explained by trapping method alone. A strong dominance of carnivorous species at the first stage in dead wood succession was also reported by Vanderwel *et al.* (2006), but that was directly associated with a very high abundance of primary wood boring prey species in the study. The proportion of carnivorous to non-carnivorous species in the present study did not differ markedly between the wood vitality sections of the transect. Nor did the abundance of the carnivore group show an increase in dead wood sections, which would have been expected if the high percentage of carnivorous species was based on the establishing saproxylic wood boring community. It is also noteworthy that the higher species diversity of the carnivorous group observed in the dead wood sections of both transects was entirely due to non saproxylic carnivores. Furthermore, the dead wood reference, being the oldest dead wood site in the study, had a unique trophic composition, with a strong dominance of mycetophagous species, in contrast to the live wood reference, which was more similar to the transects. It is therefore likely that the high percentage of carnivorous species was quite unrelated to the recent dead wood resource pulse.

Among the primary wood boring beetles found in this study, only one single species (*H. dermestoides* of the mycetophagous trophic group) was common in the samples. However, abundance levels of this prevalent species in the dead wood sections of the transects were still low compared to abundance levels at the dead wood reference. The low abundance and diversity of early successional specialist wood boring species in my samples was

unexpected, since this functional group is usually highly prevalent in a multitude of forest types (Martikainen *et al.* 1999, Grove 2002, Wermelinger *et al.* 2002, Menke 2006), and has been shown to respond rapidly, in great numbers and considerable diversity, to a new dead wood resource pulse (Wermelinger *et al.* 2002, McHugh *et al.* 2003, Bouget and Duelli 2004). It is likely that the dominant birch forest vegetation in subarctic areas is only attractive for a small number of birch specialist early successional wood borers. Moreover, the diversity of such species may be further reduced by subarctic climate conditions and lower overall dead wood availability in the region. For instance, Brattli *et al.* (1998) showed that the number of species attracted to birch dead wood was somewhat higher in a region further west (Tromsø area) with similar birch dominated forest types, but a more oceanic climate. It is also of notice that the early successional mycetophagous ambrosia beetle *Trypodendron signatum* (Fabricius 1787), which is quite similar in its biology to *H. dermestoides*, attracted to birch dead wood and prevalent in the Tromsø area (Brattli *et al.* 1998), was found in very low numbers in my samples. However, beetle individual abundances can fluctuate very strongly over time (Martikainen 2004, Menke 2006), and a large portion of a population may be present under the bark and thus non accessible for window trapping. It is also possible that the temporal flight window of some species has been missed in the two month trapping period.

Altogether, the lack of major changes in the abundance and relative prevalence of trophic groups along the transects suggests that there is of yet little community response to the dead wood input. The only exception to this was the dead wood reference, where a dominance of mycetophagous species (driven by *H. dermestoides*) was apparent.

Single species

The two major trophic groups in this study, carnivores and mycetophages, were strongly dominated by single abundant species, which affected the group-specific abundance patterns along the transects considerably (appendix 3). Of the seven single species analysed, two species are reportedly non saproxylic (*A. omalinus* and *L. affinis*), two species are early successional saproxylic (*H. dermestoides* and *R. foveolatus*), one species is mid to late successional saproxylic (*A. schoenherri*) and one saproxylic species remains uncertain with regard to the preferred successional stage (*M. guttifer*) [appendix 3; Dahlberg and Stokland (2004)]. The classification of one species, *E. costalis*, remains

entirely uncertain. Of these species, only the two early successional saproxylic species *H. dermestoides* and *R. foveolatus* showed a uniformly higher abundance in areas of similar wood vitality (namely the dead wood sections) in both transects. This tendency was strengthened by the high abundance of these species in the dead wood reference.

Pioneer wood boring saproxylic beetles have the potential to act as catalysts in the colonization of dead wood, by opening up dead trunks and thereby making them more accessible for other saproxylic species. *H. dermestoides* appears to be the only wood boring species in the study area that is abundant enough to be ecologically important in this respect. Therefore the distribution pattern of this single species could have important implications for local dead wood decay rates. The abundance pattern of *H. dermestoides* was characterized by a relatively focused occurrence in the dead wood areas of the transects (except for a single live wood station in Tana), as might be expected for an early successional saproxylic species. Some of the small scale variation in the abundance of the species may be explained by its specific micro-habitat demands, such as the dependency on a high water content of the trunks [between 30% and 120% of dry-wood weight (Veit 2003)], which is essential for the successful growth of the mutualistic ambrosia fungi [*Ascoidea hylecoeti* (Neger, 1909)] of *H. dermestoides* in the under-bark corridors (Egger 1974, Ehnström and Axelsson 2002).

The other common species besides *H. dermestoides* and *R. foveolatus* did not react in a consistent numerical fashion to the wood vitality of the transects. Moreover, their overall abundance often differed strongly between the transects. These tendencies were also apparent for overall beetle abundance and for some of the trophic groups. In general, differences in beetle catch rates among and within species may either be due to actual diverging abundances in the environment or due to variation in trapping efficiency. While the actual beetle abundances may indeed differ strongly between the two transects (e.g. due to different habitat quality), it is also possible that the observed differences, at least partially, are explained by divergent trapping efficiency between the transects. Catchment rates of window traps reflect individual beetle flight activity level at a certain height, which is partially dependent on the species (e.g. dispersal ability and overall activity) but also on the local environment (e.g. wind conditions and microclimate) (Martikainen *et al.* 1999). Since local variation in microhabitat-conditions, such as shading and temperature, are already suspected to have considerable influence on beetle activity and thus on

trapping efficiency (Martikainen *et al.* 1999, Ranius and Janssons 2002, Lindhe *et al.* 2005), large scale differences in environment and terrain also seem likely to affect trapping efficiency considerably. Although the terrain variables analysed showed that the Kirkenes transect had an overall more variable terrain, too little information was gathered to allow a clear picture of whether any large scale factors exist with the potential to explain the strongly diverging abundances of the two transects. Altogether, the abundance patterns suggest that spatial variation in abundance, for most species, was mainly driven by other factors than wood vitality.

While this study revealed only a snapshot of the beetle community in the study area, the strong presences of *H. dermestoides* and the lack of reaction by later successional species suggests that four to eight years after initial defoliation of the dead wood areas, the dead wood succession in the Varanger area is still in an initial phase. The high abundance of *H. dermestoides* and *R. foveolatus* at the dead wood reference (the oldest dead wood station) may also indicate that a future population build-up will occur in at least some of the transect dead wood areas, although this tendency based on a single station must be considered with caution. A system still remaining in very early dead wood succession four to eight years after defoliation, stands in strong contrast to the results of studies in temperate areas, where dead wood succession has been shown to have progressed considerably further in a similar timeframe (Hammond *et al.* 2001, Wermelinger *et al.* 2002). The time differences in saproxylic succession between these studies and the present one may have several causes: For one, as a result of the death of the birch trees by defoliation, the actual dying process of the trees might have taken some time and since some saproxylic species are primarily attracted to wood decay molecules (Brattli *et al.* 1998, Veit 2003) the onset of saproxylic beetle attraction to the trees may have been later than in cases where trees died of other causes (eg. windthrow). In addition almost all trees remained standing after their death. This is a factor which has been shown to slow down decay rates considerably, since the water content of standing trunks is on average considerably lower than the water content of lying trunks (Maser and Trappe 1984). This in turn is of high importance for many wood decaying fungi species and in turn for associated beetle species (Maser and Trappe 1984, Veit 2003). Furthermore, the pace of dead wood succession in Varanger may be influenced by several factors inherent to the subarctic ecosystem, such as climate effects on the time window of insect activity, and the high density of the wood of the mountain birch trees (Repola 2006). The high amount of

bound precipitation in subartic areas (long seasons with snow cover) may also affect wood decay to a certain degree, since it is likely to affect the water content of the trunks. Generally slow wood decay rates in the subarctic study area may also explain why no successional differences could be found in the dead wood section of the two transects, although the sections differ in time since defoliation to a degree, that a clear successional difference could have been expected [see: Hammond *et al.* (2001), Wermelinger *et al.* (2002)]

Conclusion:

Although between four to eight years have passed since initial defoliation at the time of the study, the dead wood succession at the study sites in Finnmark is apparently still in its initial phase. Two specialist early successional species, *H. dermestoides* and *R. foveolatus*, were the only species that showed a clear increase in abundance in dead wood areas. Without these two species, the saproxylic community as a whole, including many species of later successional stages, showed no reaction to the dead wood resource pulse. The overall beetle community seemed to be more strongly governed by some large-scale factor(s) at the level of the transects than by the variable wood vitality within the transects.

To get a better understanding of the study system, it is essential to continue to investigate the saproxylic beetle community in Finnmark over the next several years. It would also be beneficial to lengthen the sampling season, to ensure that no beetle species stay undetected because of their flight phenology (see Martikainen (2004) for the importance of long sampling seasons). Furthermore, since dead wood decay is a highly dynamic community process, it is, in my opinion, essential to include other insect orders, microorganism and especially fungi in further investigations of saproxylic communities.

Acknowledgements:

References:

Alinvi, O., J. Ball, K. Danell, J. Hjältén, and R. Pettersson. 2007. Sampling saproxylic beetle assemblages in dead wood logs: comparing window and eclector traps to traditional bark sieving and a refinement. Journal of Insect Conservation **11**:99-112.

Anderson, R. 1997. Species inventory for Northern Ireland Rove beetles (Coleoptera: staphylinidae). Environment and Heritage Service, Belfast (United Kingdom)

Böhme, J. 2005. Die Käfer Mitteleuropas, Katalog (Faunistische Übersicht). 2 edition. Elsevier, München.

Bouget, C. and P. Duelli. 2004. The effects of windthrow on forest insect communities: a literature review. Biological Conservation **118**:281-299.

Brattli, J. G., J. Andersen, and A. C. Nilssen. 1998. Primary attraction and host tree selection in deciduous and conifer living Coleoptera: Scolytidae, Curculionidae, Cerambycidae and LymexyIidae. Journal of Applied Entomology **122**.

Bylund, H. 1999. Climate and the Population Dynamics of Two Insect Outbreak Species in the North. Ecological Bulletins:54-62.

Dahlberg, A. and J. N. Stokland. 2004. Vedlevande arters krav på substrat - sammanställning och analys av 3600 arter. Skogsstyrelsen, Jönköping.

Egger, A. 1974. Beiträge zur Morphologie und Biologie von Hylecoetus dermestoides L. (Col.,Lymexylonidae). Anzeiger für Schädlingskunde **47**:7-11.

Ehnström, B. and R. Axelsson. 2002. Insektgnag i bark och ved. SLU, Uppsala.

Eivind, P. 1996. Nordeuropas snudebiller, 1, de kortsnudede arter (Coleoptera: Curculionidae) med særlig henblik på den danske fauna / Eivind Palm. Stenstrup : Apollo books.

Grove, S. J. 2002. Saproxylic Insect Ecology and the Sustainable Management of Forests. Annual Review of Ecology and Systematics **33**:1-23.

Hammond, H. E. J., D. W. Langor, and J. R. Spence. 2001. Early colonization of Populus wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research **31**:1175-1183.

Hansen, V. 1964. Danmarks biller (Coleoptera). Entomologiske meddeleser, København.

Jepsen, J. U., S. B. Hagen, K. A. Høgda, R. A. Ims, S. R. Karlsen, H. Tømmervik, and N. G. Yoccoz. 2009b. Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch forest using MODIS-NDVI data. Remote Sensing of Environment **113**:1939-1947.

Jepsen, J. U., S. B. Hagen, R. A. Ims, and N. G. Yoccoz. 2008. Climate change and outbreaks of the geometrids Operophtera brumata and Epirrita autumnata in subarctic birch forest: evidence of a recent outbreak range expansion. Journal of Animal Ecology **77**:257-264.

Jepsen, J. U., S. B. Hagen, S. R. Karlsen, and R. A. Ims. 2009a. Phase-dependent outbreak dynamics of geometrid moth linked to host plant phenology. Proc Biol Sci **276**:4119-4128.

Johansen, B. E. 2009. Vegetasjonskart for Norge basert på Landsat TM/ETM+ data. Direktoratet for Naturforvaltning, Norsk Romsenter.

Kamata, N. 2002. Outbreak of forest defoliating insects in Japan, 1950-2000. Bulletin of Entomological Research **92**:109-117.

Klemola, T., T. Andersson, and K. Ruohomaki. 2008. Fecundity of the autumnal moth depends on pooled geometrid abundance without a time lag: implications for cyclic population dynamics. J Anim Ecol **77**:597-604.

Köhler, F. 1995. Neue Untersuchungen zur Totholzkäferfauna (Coleoptera) des Waldnaturschutzgebietes Geldenberg bei Kleve. Mitt. Arb. gem. Rhein. Koleopterologen (Bonn) **12**:71-111.

Krasutskii, B. 2006. Beetles (Coleoptera) associated with the birch fungus <i>Piptoporus betulinus (Bull.: Fr.) P. Karst. (Basidiomycetes, Aphyllophorales) in forests of the Urals and Transurals. Entomological Review **86**:889-900.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature **452**:987-990.

Liebhold, A., J. Elkinton, D. Williams, and R. M. Muzika. 2000. What causes outbreaks of the gypsy moth in North America? Population Ecology **42**:257-266.

Lindhe, A., Å. Lindelöw, and N. Åsenblad. 2005. Saproxylic Beetles in Standing Dead Wood Density in Relation to Substrate Sun-exposure and Diameter. Biodiversity and Conservation **14**:3033-3053.

Lovett, G. M., L. M. Christenson, P. M. Groffman, C. G. Jones, J. E. Hart, and M. J. Mitchell. 2002. Insect Defoliation and Nitrogen Cycling in Forests. BioScience **52**:335-341.

Lovett, G. M. and A. E. Ruesink. 1995. Carbon and Nitrogen Mineralization from Decomposing Gypsy Moth Frass. Oecologia **104**:133-138.

Martikainen, P. 2004. Sampling saproxylic beetles: lessons from a 10-year monitoring study. Biological Conservation **120**:171-181.

Martikainen, P., J. Siitonen, L. Kaila, P. Punttila, and J. Rauh. 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.

Martikainen, P., J. Siitonen, P. Punttila, L. Kaila, and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation **94**:199-209.

Maser, C. and J. Trappe. 1984. The seen and unseen world of a fallen tree. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. General Technical Report: PNW-164.

McHugh, C. W., T. E. Kolb, and J. L. Wilson. 2003. Bark Beetle Attacks on Ponderosa Pine Following Fire in Northern Arizona. Environmental Entomology **32**:510-522.

Menke, N. 2006. Untersuchungen zur Struktur und Sukzession der saproxylen Käferfauna (Coleoptera) an Eichen- und Buchentotholz. Georg-August-University of Göttingen.

Moen, A., A. Lillethun, and A. Odland. 1999. National atlas of Norway: vegetation. Norwegian Mapping Authority.

Myers, J. H. 1998. Synchrony in Outbreaks of Forest Lepidoptera: A Possible Example of the Moran Effect. Ecology **79**:1111-1117.

Ranius, T. and N. Janssons. 2002. A comparison of three methods to survey saproxylic beetles in hollow oaks. Biodiversity and Conservation **11**.

Repola, J. 2006. Models for Vertical Wood Density of Scots Pine, Norway Spruce and Birch Stems, and Their Application to Determine Average Wood Density. Silva Fennica **40**.

Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying Landscape Ruggedness for Animal Habitat Analysis: A Case Study Using Bighorn Sheep in the Mojave Desert. The Journal of Wildlife Management **71**:1419-1426.

Siitonen, J. 1994. Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. Annales Entomologici Fennici **31**.

Siitonen, J. 2001. Forest Management, Coarse Woody Debris and Saproxylic Organisms: Fennoscandian Boreal Forests as an Example. Ecological Bulletins:11-41.

Speight, M. C. D. 1989. Saproxylic invertebrates and their conservation. Nature and Environment Series.

Strathdee, A. T. and J. S. Bale. 1998. Life on the edge: insect ecology in arctic environments. Annu Rev Entomol **43**:85-106.

Sverdrup-Thygeson, A. and R. A. Ims. 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. Biological Conservation **106**:347-357.

Tenow, O. 1972. The outbreaks of Oporinia autumnata Bkh. and Operophtera spp. (Lep., Geometridae) in the Scandinavian mountain chain and northern Finland 1862-1968. Zoologiska bidrag från Uppsala, Supplement, 2, 1-107.

Ulyshen, M. D. and J. L. Hanula. 2010. Patterns of saproxylic beetle succession in loblolly pine. Agricultural and Forest Entomology **12**:187-194.

Väisänen, R., O. Biström, and K. Heliövaara. 1993. Sub-cortical Coleoptera in dead pines and spruces: is primeval species composition maintained in managed forests? Biodiversity and Conservation **2**:95-113.

Vanderwel, M., J. Malcolm, S. Smith, and N. Islam. 2006. Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. Forest Ecology and Management **225**:190-199.

Veit, H. 2003. Waldschutz Info 1/2003 Säghörniger Werftkäfer (Hylecoetus dermestoides L.). Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg, Abteilung Waldschutz.

Wermelinger, B., P. Duelli , and M. K. Obrist. 2002. Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. For. Snow. Landsc. Res **77**:133-148.

Weslien, J., L. B. Djupstrom, M. Schroeder, and O. Widenfalk. 2011. Long-term priority effects among insects and fungi colonizing decaying wood. J Anim Ecol **80**:1155-1162.

Wood, S. N. 2006. Generalized Additive Models: An Introduction with

R. Chapman and Hall/CRC. Boca Raton, Florida.

Yang, L. H. 2004. Periodical Cicadas as Resource Pulses in North American Forests. Science **306**:1565-1567.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. WHAT CAN WE LEARN FROM RESOURCE PULSES. Ecology **89**:621-634.

Appendix 1:

List of beetles species

Table app. 1: List of beetle species caught in the study, with total abundance across all traps, trophic and habitat information (with sources in brackets), assigned trophic group and information on saproxylic status (further information on the classification of the beetles and further sources at the end of this table).

Keys:
Trophic groups: 1 = xylophagous (inc. phloeophagous), 2 = mycetophagous, 3 = carnivorous, 4 = saprophagous,
5 = phytophagous, 6 = coprophagous, 7 = other, 8 = uncertain, 9 = no information

Saproxylic groups: 1 = saproxylic, 2 = non saproxylic or uncertain

Sources for habitat and trophic information (in brackets):
1 = Böhme (2005); 2 = Menke (2006); 3 = Ehnström & Axelsson (2002); 4 = Hansen (1964) (only habitat preferences);
5 = Anderson (1997); 6 = Krasutskii (2006); 7 = Eivind (1996)

Species	Family	Total abundance	trophic and habitat information	assigned to trophic group	saproxylic
Bembidion grapii	Carabidae	1	?	9	0
Agonum consimile	Carabidae	1	?	9	0
Amara apricaria	Carabidae	1	phytophagous, carnivorous (1)	8	0
Dromius agilis	Carabidae	5	carnivorous (1)	3	1
Cercyon lateralis	Hydrophilidae	2	coprophagous, phytophagous (1), saprophagous (2)	8	0
Cercyon melanocephalus	Hydrophilidae	2	coprophagous, phytophagous (1), saprophagous (2)	8	0
Megasternum concinnum	Hydrophilidae	1	?	9	0
Acrotrichis cognata	Ptiliidae	5	mycetophagous (in detritus) (1)	2	0
Acrotrichis intermedia	Ptiliidae	1	mycetophagous (in humus) (1;2)	2	0
Acrotrichis sericans	Ptiliidae	3	mycetophagous (in detritus) (1;2)	2	0
Acrotrichis strandi	Ptiliidae	2	mycetophagous (in detritus) (1)	2	0
Hydnobius septentrionalis	Leiodidae	1	?	9	0
Leiodes inordinata	Leiodidae	1	?	9	0
Leiodes obesa	Leiodidae	1	mycetophagous (in grass) (1)	2	0
Agathidium confusum	Leiodidae	1	mycetophagous (in detritus) (1;2)	2	1
Agathidium rotundatum	Leiodidae	3	mycetophagous (in detritus) (1;2)	2	1
Catops alpinus	Leiodidae	1	(4)	9	0
Stenichnus bicolor	Scydmaenidae	8	carnivorous (in humus) (1)	3	1
Nicrophorus vespilloides	Silphidae	2	(4)	7	0
Euplectus karsteni	Staphylinidae	3	carnivorous (in detritus (1), in wood-detritus (2))	3	1
Euplectus punctatus	Staphylinidae	21	carnivorous (in wood-detritus) (1;2)	3	1
Acrulia inflata	Staphylinidae	1	carnivorous, mycetophgous (in humus) (1)	8	1
Omalium septentrionis	Staphylinidae	1	carnivorous, saprophagous (in detritus) (1)	8	0

Species	Family	Total abundance	trophic and habitat information	assigned to trophic group	saproxylic
Eucnecosum brachypterum	Staphylinidae	1	carnivorous (in humus) (1)	3	0
Acidota crenata	Staphylinidae	5	carnivorous (in humus) (1)	3	1
Anthophagus alpinus	Staphylinidae	8	carnivorous (in herbs and flowers) (1)	3	0
Anthophagus omalinus	Staphylinidae	957	carnivorous (in herbs and flowers) (1)	3	0
Eudectus giraudi	Staphylinidae	21	carnivorous (in humus) (1)	3	1
Megarthrus nigrinus	Staphylinidae	2	?	9	0
Megarthrus depressus	Staphylinidae	1	carnivorous (in detritus) (1) ; saprophagous (2)	8	0
Olisthaerus megacephalus	Staphylinidae	1	mycetophagous (?) (under bark) (1)	2	1
Mycetoporus baudueri	Staphylinidae	1	carnivorous (in humus) (1)	3	0
Mycetoporus lepidus	Staphylinidae	2	carnivorous (in humus, detritus) (1;2)	3	1
Mycetoporus tenuis	Staphylinidae	2	carnivorous (in humus) (1)	3	0
Mycetoporus punctus	Staphylinidae	4	carnivorous (in humus) (1)	3	1
Bryoporus cernuus	Staphylinidae	3	carnivorous (in humus) (1)	3	0
Bryophacis rugipennis	Staphylinidae	13	carnivorous (in humus) (1)	3	0
Lordithon speciosus	Staphylinidae	1	carnivorous (on polypore wood-fungi) (1)	3	1
Lordithon trinotatus	Staphylinidae	1	mycetophagous(?) (in humus) (1); carnivorous (on fungi) (2)	8	0
Tachinus elongatus	Staphylinidae	3	carnivorous (in humus) (1;2)	3	0
Tachinus laticollis	Staphylinidae	5	carnivorous (in detritus), phytophagous (?) (1)	8	0
Tachinus pallipes	Staphylinidae	1	carnivorous (in detritus) (1)	3	0
Aleochara brundini	Staphylinidae	1	carnivorous (in grass dominated areas) (1)	3	0
Oxypoda haemorrhoa	Staphylinidae	1	carnivorous (in detritus) (1)	3	0
Oxypoda brevicornis	Staphylinidae	2	carnivorous (1;2) (in detritus (1))	3	0
Acrostiba borealis	Staphylinidae	22	?	9	0
Ischnoglossa prolixa	Staphylinidae	2	carnivorous (in wood-detritus (1); under bark (2))	3	1
Mniusa incrassata	Staphylinidae	1	carnivorous (in humus) (1;2)	3	1
Phloeopora corticalis	Staphylinidae	4	carnivorous (1;2) - coleopterophagous (1) (under bark (1;2))	3	1
Liogluta alpestris	Staphylinidae	2	carnivorous (in humus, detritus) (1)	3	0
Dadobia immersa	Staphylinidae	3	carnivorous (1;2) (under bark (2))	3	1
Philhygra debilis	Staphylinidae	2	(4)	9	0
Philhygra elongatula	Staphylinidae	1	(4)	9	0
Atheta allocera	Staphylinidae	5	carnivorous (1)	3	0
Atheta altaica	Staphylinidae	1	?	9	0
Atheta brunneipennis	Staphylinidae	3	carnivorous (in detritus) (1)	3	1
Atheta cinnamoptera	Staphylinidae	8	carnivorous (in detritus) (1)	3	0

Species	Family	Total abundance	trophic and habitat information	assigned to trophic group	saproxylic
Atheta diversa	Staphylinidae	1	carnivorous (in detritus) (1)	3	0
Atheta excellens	Staphylinidae	4	carnivorous (in detritus) (1)	3	0
Atheta flavipes	Staphylinidae	1	carnivorous (1)	3	0
Atheta fungi	Staphylinidae	10	carnivorous (in detritus, humus) (1;2)	3	0
Atheta graminicola	Staphylinidae	4	carnivorous (in detritus) (1)	3	0
Atheta hypnorum	Staphylinidae	31	carnivorous (in detritus) (1)	3	1
Atheta islandica	Staphylinidae	5	?	9	0
Atheta lateralis	Staphylinidae	1	?	9	0
Atheta laticollis	Staphylinidae	2	carnivorous (in detritus) (1;2)	3	0
Atheta orbata	Staphylinidae	1	carnivorous (in detritus) (1)	3	0
Atheta picipennis	Staphylinidae	2	carnivorous (1)	3	1
Atheta pilicornis	Staphylinidae	1	carnivorous (1;2) (in dead-wood fungi (2))	3	1
Atheta procera	Staphylinidae	5	?	9	0
Atheta strandiella	Staphylinidae	1	carnivorous (in detritus (1)); carrion-feeder in association with Cortinarius spec. (mycorrhizza fungi (5))	3	0
Atheta subtilis	Staphylinidae	7	carnivorous (in detritus) (1)	3	0
Atheta taxiceroides	Staphylinidae	6	carnivorous (1)	3	0
Dinaraea aequata	Staphylinidae	1	carnivorous (in wood-detritus (1); under bark (2))	3	1
Encephalus complicans	Staphylinidae	1	carnivorous (in detritus, humus) (1)	3	1
Autalia puncticollis	Staphylinidae	1	carnivorous (on excrements) (1)	3	0
Oxytelus laqueatus	Staphylinidae	18	carnivorous (in detritus) (1), saprophagous (2)	3	0
Stenus geniculatus	Staphylinidae	2	carnivorous (in humus) (1)	3	0
Atrecus pilicornis	Staphylinidae	1	carnivorous (under bark) (1)	3	1
Bisnius puella	Staphylinidae	2	carnivorous (in detritus) (1)	3	0
Philonthus albipes	Staphylinidae	1	carnivorous (in detritus) (1)	3	0
Quedius plagiatus	Staphylinidae	11	carnivorous - coleopterophagous (in humus) (1)	3	1
Aphodius lapponum	Scarabaeidae	8	coprophagous (1)	6	0
Aphodius piceus	Scarabaeidae	15	coprophagous (1)	6	0
Aphodius uliginosus	Scarabaeidae	4	coprophagous (1)	6	0
Potosia cuprea	Scarabaeidae	1	phytophagous (1)	5	0
Cyphon variabilis	Scirtidae	1	phytophagous (1)	5	0
Byrrhus fasciatus	Byrrhidae	3	phytophagous, muscophagous (1)	8	0
Limonius aeneoniger	Elateridae	2	xylophagous (on *Fagus sylvatica*; in wood detritus) (1)	1	1
Harminius undulatus	Elateridae	2	xylophagous (in wood detritus) , phytophagous (1)	8	1

Table app. 1: continued

Species	Family	Total abundance	trophic and habitat information	assigned to trophic group	saproxylic
Denticollis linearis	Elateridae	**25**	xylophagous (in wood detritus (1); carnivorous (in flowers) (1) , xylophagous (in wood) (2)	1	1
Liotrichus affinis	Elateridae	**91**	phytophagous (in trees and bushes) (1)	5	0
Orithales serraticornis	Elateridae	**2**	phytophagous (in trees and bushes) (1)	5	0
Selatosomus impressus	Elateridae	**4**	phytophagous (in trees and bushes) (1)	5	0
Eanus costalis	Elateridae	**209**	?	9	0
Neohypdonus arcticus	Elateridae	**1**	?	9	0
Ampedus nigrinus	Elateridae	**6**	xylophagous (in wood detritus; in trees and bushes) (1)	1	1
Sericus brunneus	Elateridae	**12**	xylophagous (in trees and bushes, in herbs) (1)	1	1
Podabrus alpinus	Cantharidae	**1**	carnivorous (1;2)	3	0
Podabrus lapponicus	Cantharidae	**2**	?	9	0
Rhagonycha elongata	Cantharidae	**2**	carnivorous (1)	3	0
Rhagonycha limbata	Cantharidae	**1**	carnivorous (1)	3	0
Absidia schoenherri	Cantharidae	**69**	carnivorous (1)	3	1
Malthodes brevicollis	Cantharidae	**8**	carnivorous (in wood detritus) (1;2)	3	1
Malthodes fuscus	Cantharidae	**3**	carnivorous (in wood detritus) (1)	3	1
Malthodes guttifer	Cantharidae	**66**	carnivorous (in wood detritus (1;2); in trees and bushes (1))	3	1
Hylecoetus dermestoides	Lymexylidae	**223**	mycetophagous (under bark (1); on lignified wood(2); on ambrosia fungi *Endomyces hylecoeti* (3))	2	1
Aplocnemus tarsalis	Melyridae	**2**	carnivorous (on *Pinaceae spp.*; in trees and bushes; in wood detritus) (1)	3	1
Dasytes obscurus	Melyridae	**1**	carnivorous (in wood-detritus) (1)	3	1
Epuraea aestiva	Nitidulidae	**9**	saprophagous, (in nests and dens, in flowers and herb (1)), carnivorous (in nests, also nests in dead-wood)(2)	8	1
Epuraea boreella	Nitidulidae	**1**	saprophagous (under bark) (1)	4	1
Epuraea melina	Nitidulidae	**1**	saprophagous, (in nests and dens; in flowers and herbs) (1)	4	0
Epuraea rufomarginata	Nitidulidae	**1**	saprophagous, mycetophagous (under bark) (1)	2	1
Omosita depressa	Nitidulidae	**1**	omnivorous, necrophagous (1)	7	0
Glischrochilus quadripunctatus	Nitidulidae	**1**	saprophagous, mycetophagous (under bark) (1)	2	1
Phalacrus substriatus	Phalacridae	**1**	mycetophagous (in grass) (1)	2	0
Cryptophagus lapponicus	Cryptophagidae	**7**	saprophagous (1), mycetophagous (living in bird nests) (1;2)	2	1
Cryptophagus tuberculosus	Cryptophagidae	**1**	associated with birch fungus *Piptoporus betulinus* (6)	8	1
Atomaria peltataeformis	Cryptophagidae	**1**	mycetophagous, saprophagous (1)	2	0
Triplax scutellaris	Erotylidae	**5**	mycetophagous (on polypore fungi) (1)	2	1

Species	Family	Total abundance	trophic and habitat information	assigned to trophic group	saproxylic
Cerylon ferrugineum	Cerylonidae	**28**	carnivorous (1;2) (in wood detritus (2)), mycetophagous (under bark) (1)	3	1
Coccinella trifasciata	Coccinellidae	**2**	carnivorous - aphidophag (on *Pinus cembra;* in trees and bushes), in grass- dominated areas (1)	3	0
Latridius anthracinus	Latridiidae	**3**	mycetophagous (eurytopic; in association with humans) (1)	2	1
Latridius consimilis	Latridiidae	**3**	mycetophagous (eurytopic; in association with humans) (1)	2	1
Enicmus apicalis	Latridiidae	**2**	?	9	1
Enicmus fungicola	Latridiidae	**19**	mycetophagous (in wood detritus(1), on dead-wood fungi (2))	2	1
Dienerella filum	Latridiidae	**1**	mycetophagous (eurytopic; in association with humans) (1)	2	1
Corticaria ferruginea	Latridiidae	**8**	mycetophagous (eurytopic, in association with humans) (1)	2	1
Corticaria orbicollis	Latridiidae	**9**	mycetophagous (1)	2	1
Corticaria rubripes	Latridiidae	**5**	?	9	1
Cis boleti	Ciidae	**1**	mycetophagous (on polypore fungi) (1;2)	2	1
Cis comptus	Ciidae	**1**	mycetophagous (on polypore fungi) (1)	2	1
Cis jacquemarti	Ciidae	**1**	mycetophagous (on polypore fungi) (1)	2	1
Orthocis alni	Ciidae	**6**	mycetophagous (on polypore fungi) (1;2)	2	1
Tetratoma ancora	Tetratomidae	**7**	mycetophagous (on trees and bushes (1), on fungi (1), on polypore fungi(2))	2	1
Orchesia micans	Melandryidae	**3**	mycetophagous (on polypore fungi) (1)	2	1
Orchesia minor	Melandryidae	**1**	mycetophagous (on polypore fungi (1), in wood (2))	2	1
Schizotus pectinicornis	Pyrochroidae	**1**	xylophagous (on bushes and trees) (1) , carnivorous (on flowers (1); under bark (2))	3	1
Rabocerus foveolatus	Salpingidae	**64**	carnivorous - coleopterophagous (under bark) (1)	3	1
Salpingus ruficollis	Salpingidae	**27**	carnivorous (1;2) - coleopterophagous (1) (under bark (1;2))	3	1
Anaspis arctica	Scraptiidae	**5**	carnivorous, phytophagous (1)	8	1
Rhagium mordax	Cerambycidae	**7**	polyphagous (in wood detritus) (1), xylophagous (1,2) (under bark (2))	1	1
Gonioctena intermedia	Chrysomelidae	**1**	on *Prunus pardos, Sorbus aucuparia* (1)	7	0
Polydrusus fulvicornis	Curculionidae	**37**	polyphagous on *Alnus spp., Betula spp.* (7)	7	0
Coeliodes rubicundus	Curculionidae	**5**	on *Betula spp.* (1)	7	0
Hylastes brunneus	Scolytidae	**1**	xylophagous on *Pinus spp, Picea abies* (under bark) (1)	1	1
Pityogenes bidentatus	Scolytidae	**1**	xylophagous on *Pinus spp* (1)	1	1
Trypodendron signatum	Scolytidae	**2**	mycetophagous (on ambrosia fungi (1); on *Betula spp., Alnus spp.*(1) ; on wood (2))	2	1

Information on classification of beetles in table app. 1:

a) Trophic groups:

The definition of trophic groups was based on trophic information from several sources (see trophic and habitat information in table app. 1). If more than one trophic information was available for a species, and the information diverged, the species was defined as "uncertain". If three pieces of information were available, and two were similar, while one diverged, the one mentioned twice was used. If "saprophagous" was combined with "mycetophagous", the species was assigned to the group mycetophagous under the assumption that the beetles likely feed on fungi on top of decaying material. Most of the sources did not provide separate trophic information for adult and juvenile and male and female beetles. Thus, some of the diverging trophic information for single beetle species may very well result from different feeding habits of juveniles and adults or males and females. However this could not be taken into account since no meta- information was available for trophic information.

b) Saproxylic species:

Information on dead wood association (saproxylic species) was derived primarily from the database of the Dahlberg and Stokland (2004) report. For species not contained in this list, definitions were made based on a combination of habitat information and trophic information. Beetle species were defined as saproxylic when they were either listed as (1) tree-xylem feeders, (2) carnivores or mycetophages associated with polypore fungi, (3) mycetophages associated with wood-detritus, or (4) mycetophages associated with nests and dens in dead wood trunks. While some species of tree xylem feeder may attack live trees, they were here defined entirely as saproxylic species. Through their boring activity, tree xylem feeder initiate (or facilitate) wood decay in the damaged or dying tree (Maser and Trappe 1984) and including them in the saproxylic group is common practice (Wermelinger *et al.* 2002, Menke 2006). The definition of saproxylic species is aimed at being inclusive (meaning those species fitting the categories are indeed very likely saproxylic), but not exclusive. Especially predators and detritus/humus associates not fitting the above definition may still be saproxylic in a broader sense, but were not included. However, due to the scarcity of available information, a more precise categorization was not possible. The saproxylic group thus includes a mixture of species that all have in common that they are dependent on, or associated with, dead wood of any successional stage at certain point(s) in their lifecycles [see definitions of obligate and

facultative saproxylic in Dahlberg and Stokland (2004)]. The different members of this group can have a very diverse biology and preferences for different successional stages. Moreover the non saproxylic group is an outgroup, including species that are certain to be non saproxylic and those which are of unknown or uncertain biology. The grouping in saproxylic and non saproxylic species is therefore only aimed at investigating general community tendencies and need to be interpreted with care.

Appendix 2:

Number of individuals of less common trophic groups per sampling station and transect

Table app. 2: Number of beetle individuals of the trophic group not analysed statistically (see fig. 11 for the abundance patterns of the major trophic groups) at the separate stations in Kirkenes and Tana as well as the respective reference stations.

Kirkenes

Trophic group	Station									
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
xylophagous	3	8	3	3	1	4	0	2	4	2
saprophagous	0	0	0	0	0	0	0	0	0	0
coprophagous	3	3	2	1	3	1	0	0	1	0
other	0	1	0	0	0	0	0	0	0	0
uncertain	0	7	0	1	1	1	0	0	4	3
no information	21	37	11	16	16	13	4	19	23	11

Tana

Trophic group	Station									
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
xylophagous	1	1	3	1	3	4	0	3	2	0
saprophagous	0	0	0	0	0	0	0	2	0	0
coprophagous	1	0	0	2	3	1	2	1	1	1
other	0	1	0	0	0	0	0	0	0	0
uncertain	1	2	4	3	1	2	0	1	1	2
no information	5	4	6	7	7	3	18	16	6	7

References

Trophic group	Dead wood ref.	Live wood ref.
xylophagous	2	4
saprophagous	0	0
coprophagous	1	0
other	1	0
uncertain	0	0
no information	8	6

Appendix 3:

Coefficients of log linear models

Table app. 3: Coefficients of the log linear models relating wood vitality (Dead (D) and Live (L)) and transect (Kirkenes and Tana) to abundance and species richness of all beetles caught, to abundance and species richness of saproxylic and trophic groups and to the abundance of single species. The intercept is the predicted value of the models with wood vitality "dead wood "at the Kirkenes transect.

Parameter	Estimate	95% confidence interval		p-value
All beetles:				
	Abundance			
Intercept (Kirkenes, D)	5.25	5.52	4.99	
Vitality: L	-0.60	-0.21	-0.99	0.0076
Transect: Tana	-1.26	-0.78	-1.74	0.0001
Vitality L* Transect Tana	1.03	1.72	0.34	0.0086
	Species richness (excl. outlier KI st. 2)			
Intercept (Kirkenes, D)	3.44	3.57	3.32	
Vitality: L	-0.33	-0.20	-0.47	0.0002
Transect: Tana	-0.02	0.11	-0.16	0.7553
Saproxylic group:				
	Abundance			
Intercept (Kirkenes, D)	4.00	4.31	3.69	
Vitality: L	-0.91	-0.41	-1.42	0.0023
Transect: Tana	-0.78	-0.30	-1.27	0.0052
Vitality L* Transect Tana	1.00	1.76	0.23	0.0189
	Species richness (excl. outlier KI st. 2)			
Intercept (Kirkenes, D)	2.61	2.79	2.43	
Vitality: L	-0.12	0.07	-0.31	0.2120
Transect: Tana	-0.03	0.16	-0.22	0.7610
Non saproxylic group:				
	Abundance			
Intercept (Kirkenes, D)	4.91	5.26	4.57	
Vitality: L	-0.49	0.01	-1.00	0.0673
Transect: Tana	-1.54	-0.84	-2.25	0.0005
Vitality L* Transect Tana	1.15	2.11	0.19	0.0292
	Species richness (excl. outlier KI st. 2)			
Intercept (Kirkenes, D)	2.45	2.71	2.20	
Vitality: L	-0.48	-0.20	-0.75	0.0031
Transect: Tana	0.19	0.46	-0.08	0.1854

Parameter	Estimate	95% confidence interval		p-value
Trophic groups:				
	Abundance			
	a) Mycetophages			
Intercept (Kirkenes, D)	3.14	3.67	2.62	
Vitality: L	-1.08	-0.26	-1.90	0.0173
Transect: Tana	-0.98	-0.18	-1.78	0.0256
	b) Carnivores			
Intercept (Kirkenes, D)	4.82	5.17	4.46	
Vitality: L	-0.55	-0.03	-1.07	0.0503
Transect: Tana	-1.28	-0.63	-1.93	0.0012
Vitality L* Transect Tana	1.05	1.97	0.13	0.0367
	Carnivores subgroup: saproxylic			
Intercept (Kirkenes, D)	3.22	3.60	2.84	
Vitality: L	-0.64	-0.07	-1.21	0.0380
Transect: Tana	-0.49	0.06	-1.03	0.0912
Vitality L* Transect Tana	0.86	1.67	0.04	0.0517
	Carnivores subgroup: non saproxylic			
Intercept (Kirkenes, D)	4.43	4.91	3.95	
Vitality: L	-0.22	0.39	-0.82	0.4808
Transect: Tana	-1.08	-0.39	-1.76	0.0059
	c) Phytophages			
Intercept (Kirkenes, D)	2.26	2.90	1.62	
Vitality: L	0.09	0.85	-0.67	0.8220
Transect: Tana	-1.07	-0.20	-1.94	0.0243
	Species richness			
	a) Mycetophages (excl. outlier KI st. 2)			
Intercept (Kirkenes, D)	1.36	1.62	1.09	
Vitality: L	-0.09	0.19	-0.37	0.5400
Transect: Tana	-0.04	0.24	-0.32	0.7690
	b) Carnivores (excl. outlier KI st. 2)			
Intercept (Kirkenes, D)	2.52	2.74	2.29	
Vitality: L	-0.38	-0.14	-0.61	0.0051
Transect: Tana	0.19	0.43	-0.04	0.1207
	Carnivores subgroup: saproxylic			
Intercept (Kirkenes, D)	2.18	2.42	1.94	
Vitality: L	-0.22	0.06	-0.50	0.1280
Transect: Tana	-0.15	0.12	-0.43	0.2830

Parameter	Estimate	95% confidence interval		p-value
Trophic groups:				
	Species richness *Carnivores subgroup: non saproxylic (excl. outlier KI st.2)*			
Intercept (Kirkenes, D)	1.39	1.81	0.98	
Vitality: L	-0.80	-0.37	-1.23	0.0020
Transect: Tana	0.66	1.10	0.22	0.0085
	c) Phytophages			
Intercept (Kirkenes, D)	0.43	0.91	-0.04	
Vitality: L	0.47	0.99	-0.05	0.0869
Transect: Tana	-0.65	-0.12	-1.18	0.0259
Single species:				
	a) *A .omalinus*			
Intercept (Kirkenes, D)	4.29	4.86	3.72	
Vitality: L	-0.08	0.63	-0.79	0.8187
Transect: Tana	-1.27	-0.42	-2.12	0.0083
	b) *H. dermestoides*			
Intercept (Kirkenes, D)	2.88	3.68	2.09	
Vitality: L	-2.13	-0.24	-4.03	0.0377
Transect: Tana	-1.28	0.14	-2.71	0.0889
	c) *E. costalis*			
Intercept (Kirkenes, D)	2.72	3.11	2.34	
Vitality: L	-0.16	0.36	-0.68	0.5467
Transect: Tana	-1.68	-0.85	-2.52	0.0009
Vitality L* Transect Tana	1.47	2.48	0.46	0.0105
	d) *L. affinis*			
Intercept (Kirkenes, D)	2.24	2.93	1.56	
Vitality: L	-0.69	0.28	-1.67	0.1725
Transect: Tana	-1.19	-0.10	-2.27	0.0425
	e) *A. schoenherri*			
Intercept (Kirkenes, D)	0.92	1.79	0.06	
Vitality: L	0.11	0.98	-0.76	0.7995
Transect: Tana	0.42	1.30	-0.47	0.3602

Parameter	Estimate	95% confidence interval		p-value
Single species:				
f) M. guttifer				
Intercept (Kirkenes, D)	1.79	2.41	1.17	
Vitality: L	-1.10	-0.02	-2.17	0.0577
Transect: Tana	-1.50	-0.26	-2.75	0.0276
Vitality L* Transect Tana	2.37	4.04	0.70	0.0120
g) R. foveolatus				
Intercept (Kirkenes, D)	1.74	2.16	1.33	
Vitality: L	-1.56	-0.80	-2.33	0.0008
Transect: Tana	-0.96	-0.31	-1.61	0.0092

Appendix 4:

Terrain variables

The terrain information is based on data digital terrain model with 20 m pixel size and was extracted as means over 200 m surroundings area at each site. The terrain variables used include elevation, slope, aspect of slope and VRM [Vector Ruggedness measure see: Sappington *et al.* (2007)]. VRM – indices combine both the ruggedness of a terrain and the steepness of the slope to obtain a measure of overall terrain roughness (Sappington *et al.* 2007). The aspects of a slope are divided into cos_asp ("northness": 1 denotes areas facing north; -1 area facing south) and sin_asp ("eastness": 1=east, -1=west). In combining the two aspects, all 360° of a slope can be fully described.

I had no prior expectations about the shape of the spatial variation in the terrain variables along the transects. Therefore, I used generalized additive models (GAMs)(Wood 2006) to achieve a flexible characterization of the along-transect variation in these variables. Each terrain variable was taken as the response in a separate GAM for each transect. All GAMs used the Euclidian distance from the first sampling station as a smoothed non-parametric predictor variable and assumed a normal error distribution. The smooth terms were fitted by means of thin plate regression splines in all cases. In order to emphasise large-scale spatial trends in the terrain variables without obscuring all small-scale variation, I aimed for a moderate degree of smoothing in all GAMs. This was achieved by manually setting the smoothing parameter (λ) to 0.05 in all of the models.
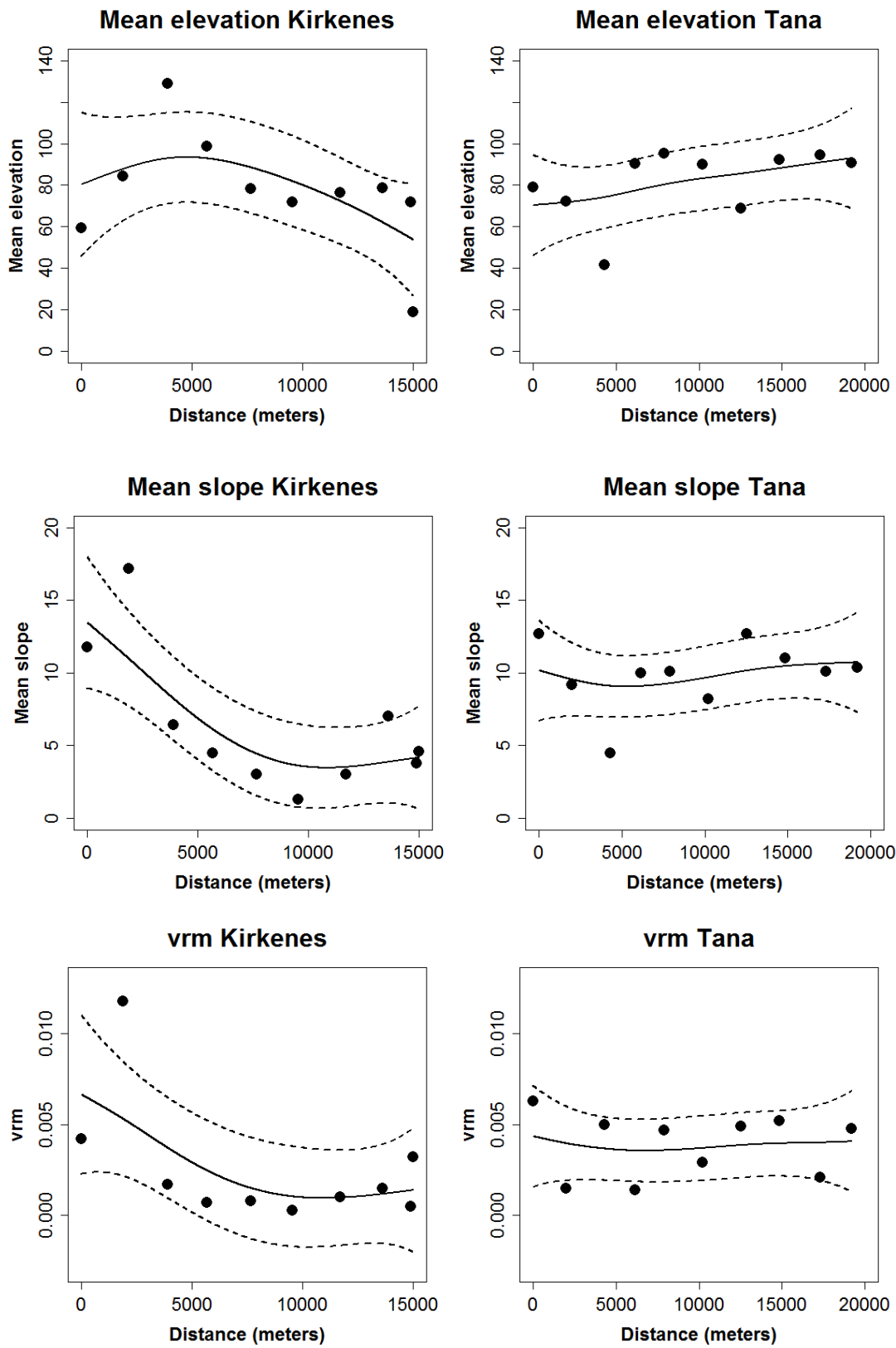
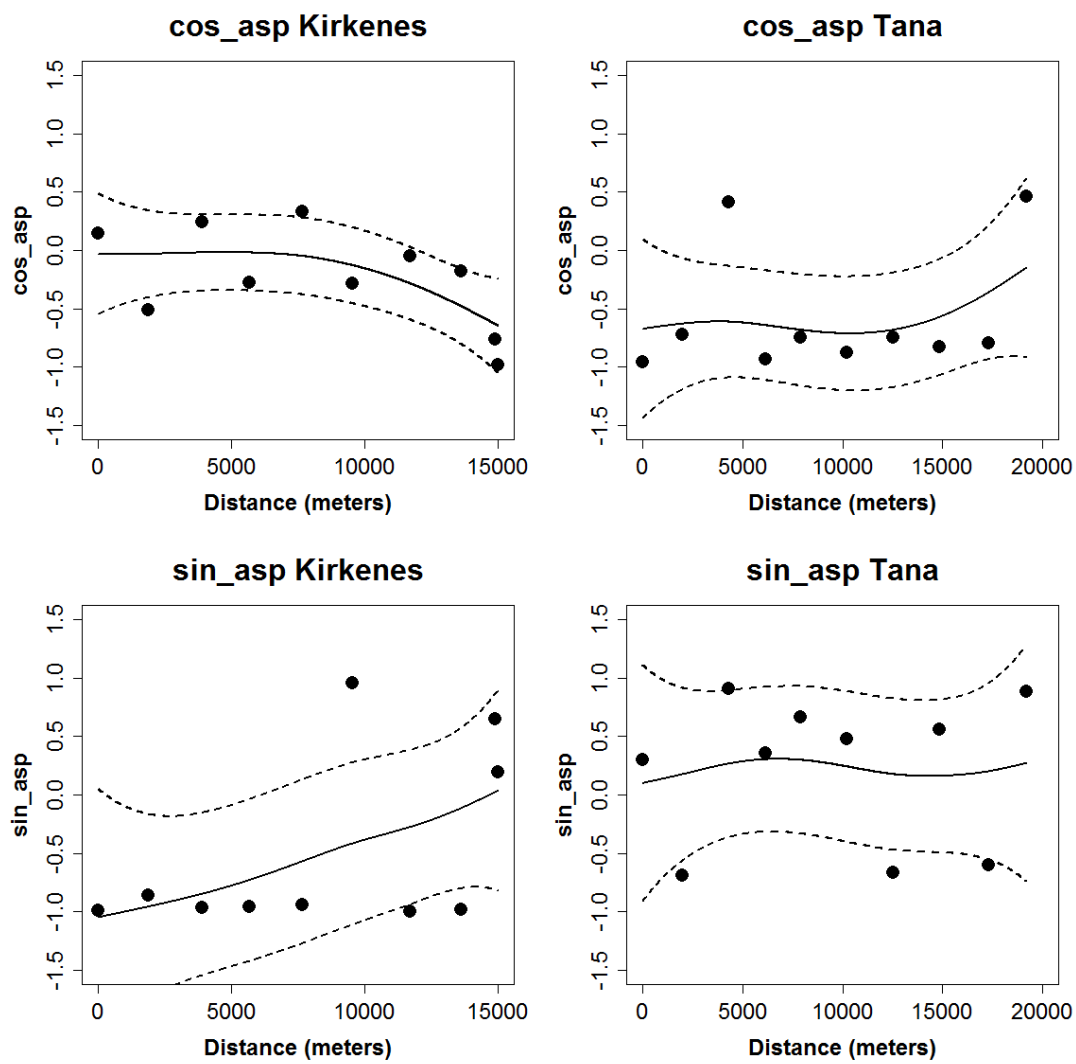**Fig. app. 4**: to be continued on the next page

Fig. app. 4: Predicted values (solid lines) ± 2 SE (dashed lines) from GAMs relating variation in selected terrain variables to the Euclidian distance from sampling station 1 in each transect. Black dots represent original datapoints.
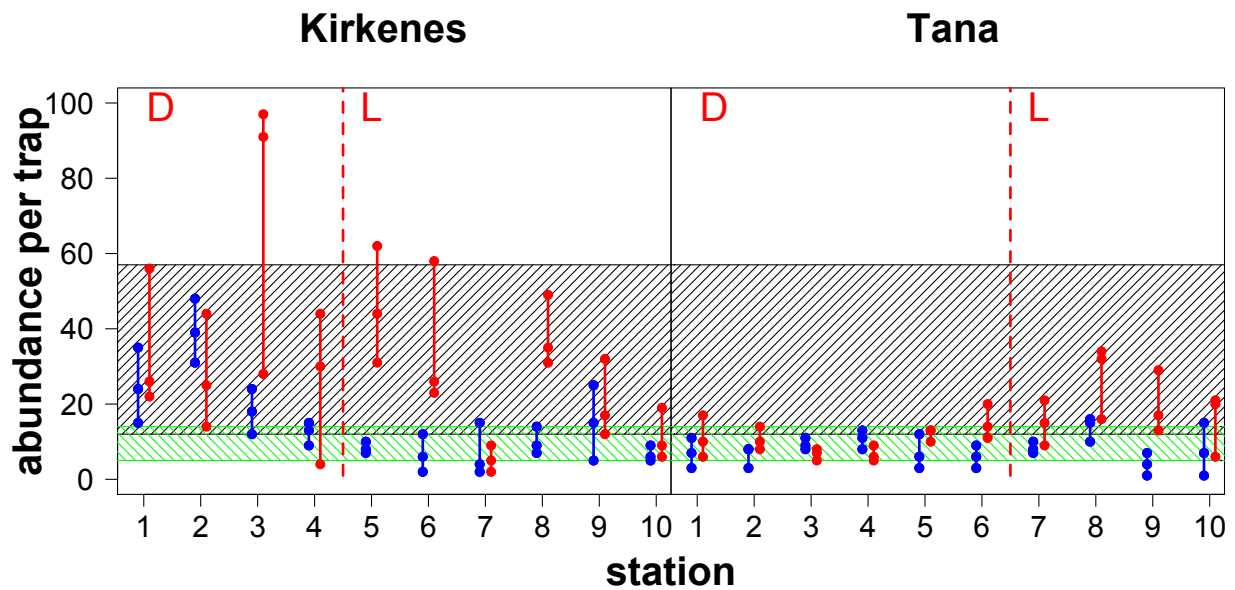
Appendix 5:

Additional plots

Fig. app. 5-1: **Number of beetles caught per trap** at each station in July (blue points) and August (red points) in each transect. The grey shaded area shows the range of per-trap abundances in the dead wood reference and the green shaded area shows the range of per-trap abundances in the live wood reference [Exemplary for total abundance plot (corresponding to fig. 6 in the main text)].
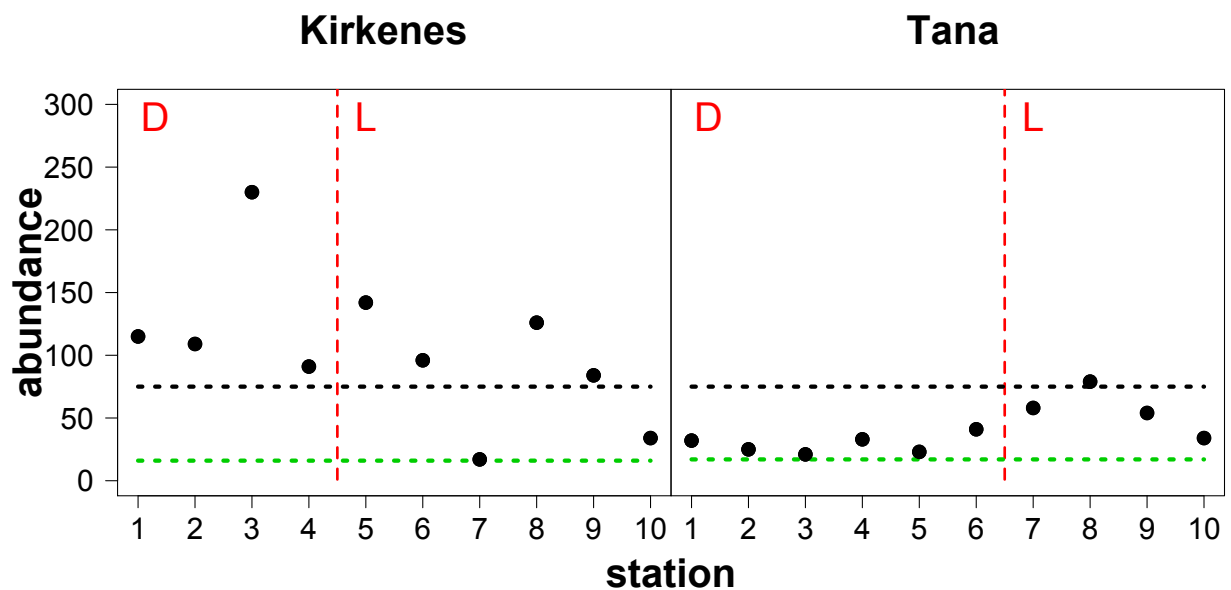
Fig. app. 5-2: Number of **non saproxylic individuals** trapped in the two transects according to station and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The abundance at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.
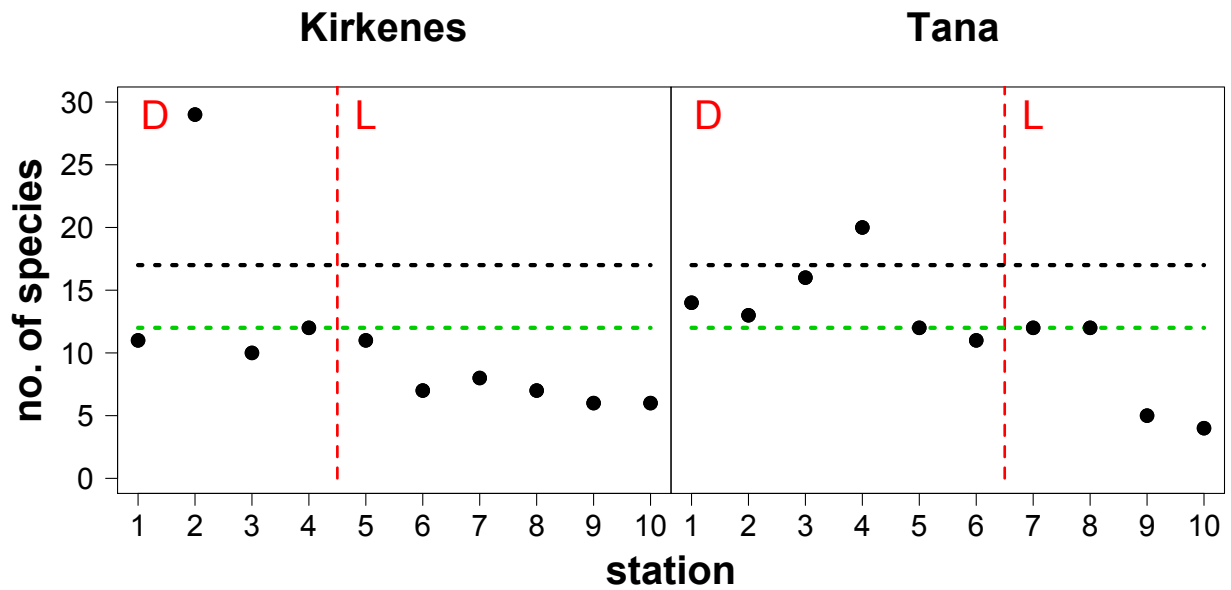
Fig. app. 5-3: Species richness of **non saproxylic species** in the two transects according to station and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The species richness at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.
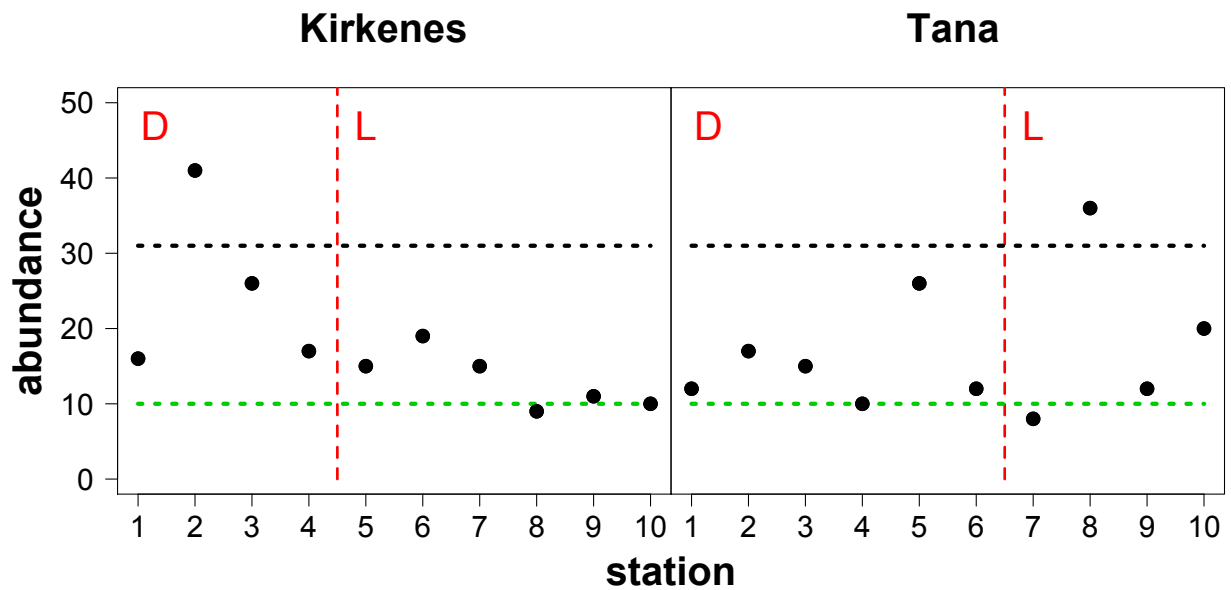

Fig. app. 5-4: Number of **carnivorous saproxylic individuals** trapped in the two transects according to station and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The abundance at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.
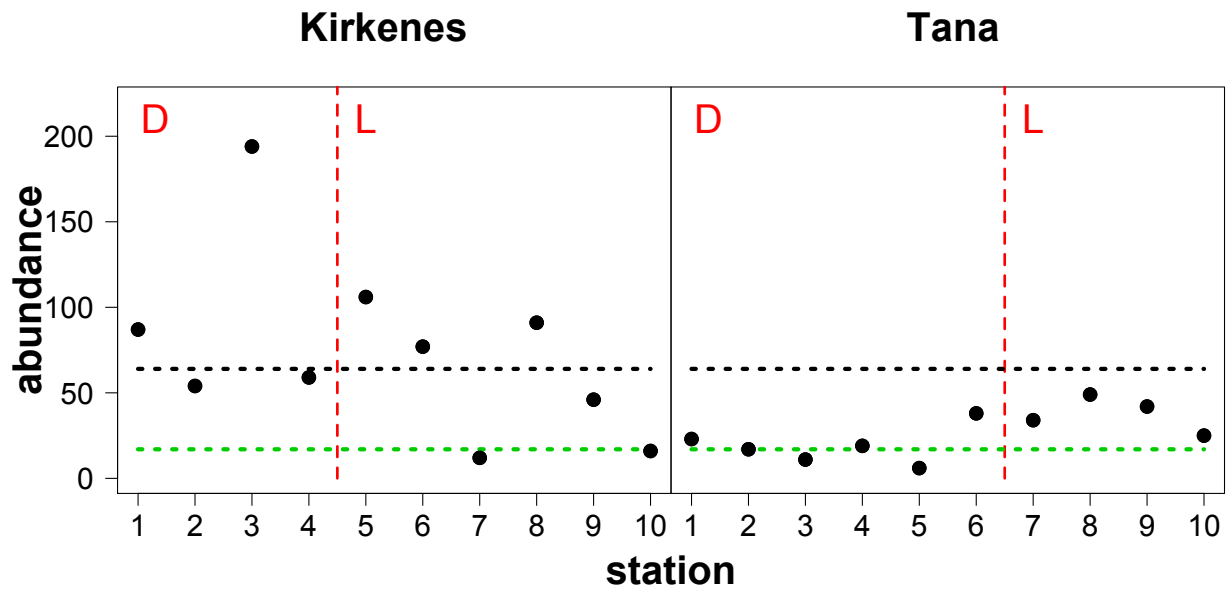
Kirkenes   Tana

Fig. app. 5-5: Number of **carnivorous non saproxylic individuals** trapped in the two transects according to station and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The abundance at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.
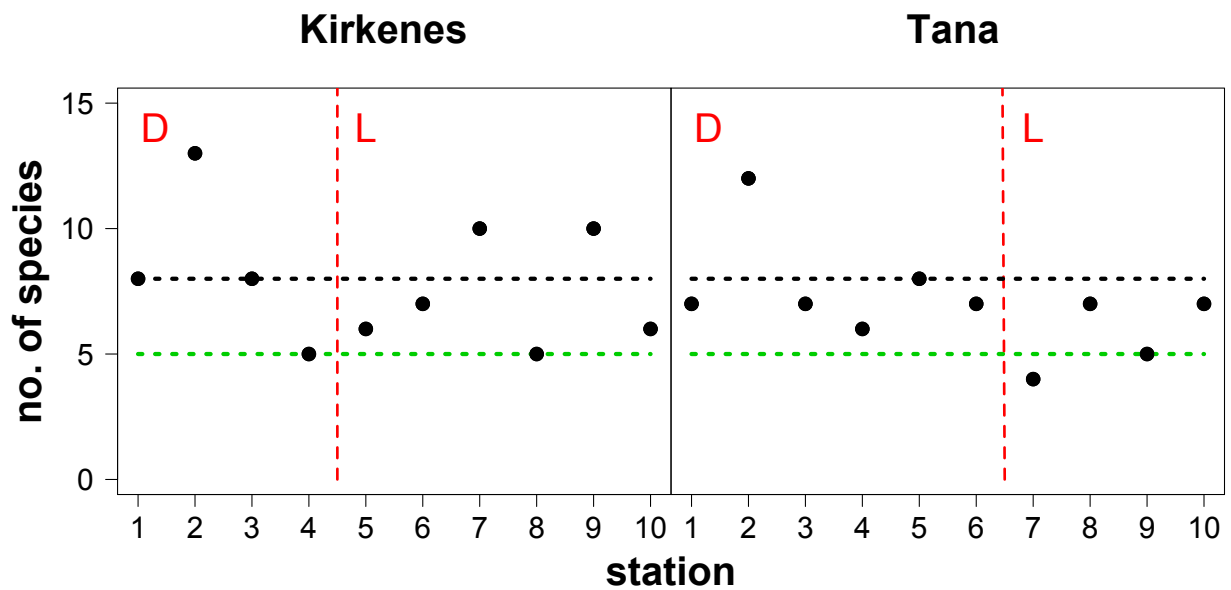
Kirkenes   Tana

Fig. app. 5-6: Species richness of **saproxylic carnivores** in the two transects according to station and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The species richness at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.
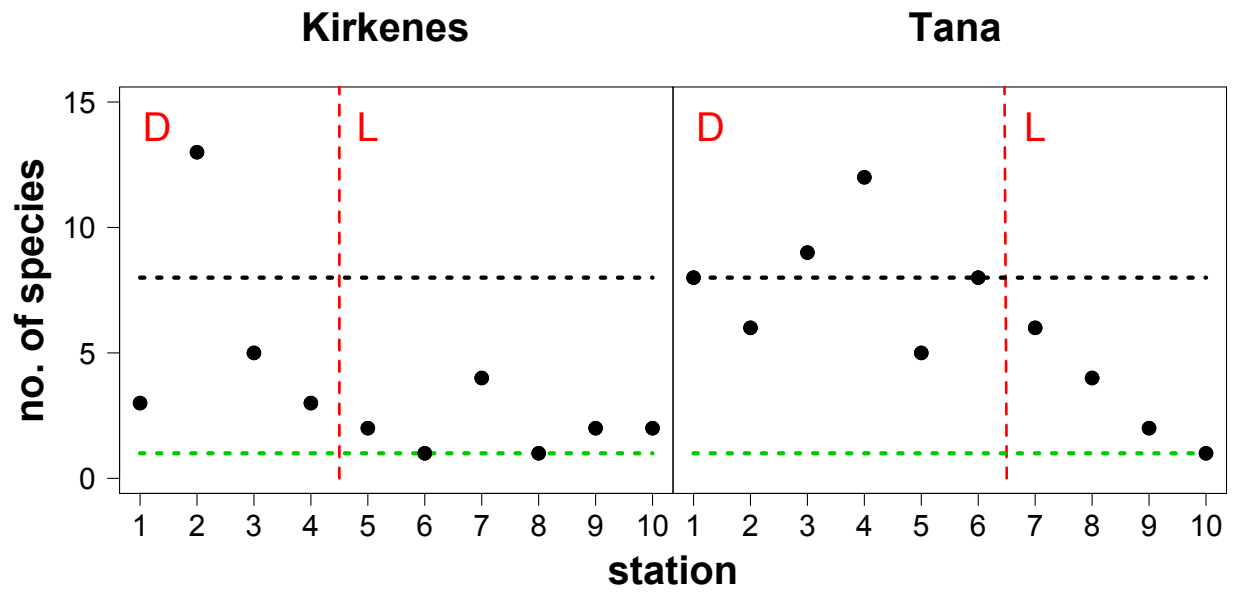
Fig. app. 5-7: **Species richness** of **non saproxylic carnivores** in the two transects according to station and wood vitality (separated by red vertical line: D= dead wood stations, L=live wood stations). The species richness at the reference stations is represented by a black (dead wood reference) and green (live wood reference) horizontal line.