Occurrence and abundance of fungus–dwelling beetles (Ciidae) in boreal forests and clearcuts: habitat associations at two spatial scales

A. Komonen & J. Kouki

Abstract

Occurrence and abundance of fungus–dwelling beetles (Ciidae) in boreal forests and clearcuts: habitat associations at two spatial scales.— Insect material (> 30,000 individuals) reared from the fruiting bodies of wood–decaying *Trametes* fungi was compared between old–growth boreal forests and adjacent clearcuts in Finland. *Sulcacis affinis* and *Cis hispidus* occurred more frequently and were, on average, more abundant in the clearcuts. Interestingly, *Octotemnus glabriculus* and *Cis boleti* had a slightly higher frequency of occurrence in the forests, despite lower resource availability. The former also showed a higher average abundance. On average, the cluster size of *Trametes* fruiting bodies occurring on woody debris was higher in the clearcuts than in the forests and had a positive effect on species occurrence and abundance in these clusters. The independent effect of the macrohabitat (forest or clearcut) underscores the importance of the macrohabitat where specific resources occur, and this may override the positive effects of resource availability.

Key words: Forest landscape, Boreal forest, Coarse woody debris, Wood–decaying fungi, *Trametes*, Ciidae.

Resumen

Presencia y abundancia de los escarabajos fungícolas (Ciidae) en los bosques y claros de tala boreales: asociaciones al hábitat según dos escalas espaciales.— Se compararon las cantidades de insectos (> 30,000 individuos) que se alimentan de los cuerpos fructíferos de los hongos desintegradores de la madera *Trametes* en los bosques boreales maduros y los claros adyacentes en Finlandia. *Sulcacis affinis* y *Cis hispidus* aparecían con mayor frecuencia, y en promedio eran más abundantes en los claros. Llama la atención la frecuencia ligeramente mayor de *Octotemnus glabriculus* y *Cis boleti* en los bosques, a pesar de una menor disponibilidad de recursos. El primero también presentaba una abundancia promedio mayor. En promedio, el tamaño de las masas de cuerpos fructíferos de *Trametes* de los restos de árboles era mayor en los claros que en los bosques, y tenía un efecto positivo en la presencia y abundancia de especies en dichas masas. El efecto independiente del macrohábitat (bosque o claro) subraya la importancia del macrohábitat cuando los recursos específicos aparecen, pudiendo anular los efectos positivos de la disponibilidad de recursos.

Palabras clave: Paisaje forestal, Bosque boreal, Restos gruesos de madera, Hongos desintegradores de la madera, *Trametes*, Ciidae.

Atte Komonen & Jari Kouki, Fac. of Forest Sciences, P. O. Box 111, FI–80101, Univ. of Joensuu, Finland.

Corresponding author: A. Komonen. E–mail: atte.komonen@joensuu.fi

Introduction

Ecological research on habitat fragmentation has often metaphorically viewed suitable habitats as "islands" in a hostile "sea" (Haila, 2002). Because there is a low degree of deforestation in the boreal forest, landscapes rarely appear simply as a black–and–white contrast between habitat and non–habitat, rather the many shades of grey reflect differential habitat suitability (Mönkkönen & Reunanen, 1999). Forestry practices in boreal forests create highly dynamic landscapes which remain forested while undergoing spatial and temporal changes in structure and dynamics (Kouki et al., 2001; Schmiegelow & Mönkkönen, 2002). The structural heterogeneity in the forest landscape is manifested in the amount and quality of living and dead wood (Siitonen, 2001), forest–stand age structure and naturalness (Uotila et al., 2002), and in the distribution of different stand types in the landscape (Löfman & Kouki, 2003).

Dead wood is a key resource for thousands of organisms in boreal forests (Esseen et al., 1997; Siitonen, 2001). Dead wood is scarce in managed forests and many dead–wood dependent organisms are consequently absent or occur in low numbers. This has contributed to the misconception that the majority of these species would require natural forests. However, many dead–wood dependent species can persist in clearcuts if critical resources are left in adequate densities and qualities in management operations (Kaila et al., 1997; Jonsell et al., 2001; Jonsson et al., 2001; Martikainen, 2001; Sverdrup–Thygeson & Ims, 2002). However, the importance of the macrohabitat and landscape context where these resources occur is poorly understood, particularly for species that have high habitat specificity and limited powers of dispersal, such as fungus–dwelling insects (Jonsell et al., 1999; Jonsson et al., 2001; Komonen et al., 2000). It is important to disentangle the large– and small–scale effects of forestry on habitat suitability to fully understand the limiting factors for species occurrences and abundances (Mönkkönen & Reunanen, 1999).

Trametes fruiting bodies occur in a variety of forest environments where deciduous dead wood is available. Nevertheless, it is not known how *Trametes*–dwelling beetles respond to the different forest surroundings. There are generally marked ecological differences among the fungus–dwelling insects in dispersal ability (Jonsell et al., 1999; Jonsson, 2003), habitat requirements (Nilsson, 1997; Guevara et al., 2000*a*; Thunes et al., 2000; Jonsell et al., 2001) and host–fungus specificity (Lawrence, 1973; Økland, 1995; Fossli & Andersen, 1998; Guevara et al., 2000b; Komonen, 2001). In this paper, the occurrence and abundance of four fungivorous beetle species (Ciidae) co–occurring in *Trametes* fruiting bodies is investigated at two spatial scales. The small–scale effects of fungal–cluster size and the large–scale effects of macrohabitat (forest–clearcut) are tested.

Table 1. Study site characteristics. Area of forest refers to the area (ha) with > 60 m³ fallen woody debris (diameter at breast height ≥ 7 cm) ha⁻¹: As. Area sampled; Af. Area of the forest; Ac. Area of the clearcut, refers to the area (ha) logged at the same time and consists of interconnected openings rather than a single large opening; CWD. Number of stumps, snags, logs and branches (diameter ≥ 10 cm) of birch and aspen ha⁻¹; Yl. Year of logging; MAI. Mean age at the time of logging, refers to the mean age of trees belonging to the dominant canopy storey; Vl. Volume at logging, refers to the volume of living spruce, pine and birch at the time of logging.

Tabla 1. Características del área de estudio. Área forestal se refiere al área (ha) con > 60 m³ de residuos de madera caída (diámetro a la altura del tórax ≥ 7 cm) ha⁻¹: As. Área muestreada; Af. Área de bosque; Ac. Área de claros, se refiere al área (ha) talada al mismo tiempo, y consiste en varios claros interconectados, más que en uno solo de mayor tamaño; CWD. Número de tocones, cepas, troncos y ramas (diámetro ≥ 10 cm) de abedules y álamos temblones ha⁻¹; Yl. Edad de talado; MAI. Edad media de talado, se refiere a la edad media de los árboles del piso dominante del dosel forestal; Vl. Volumen cuando la tala, se refiere al volumen de pinos, álamos y píceas en el momento de la tala.

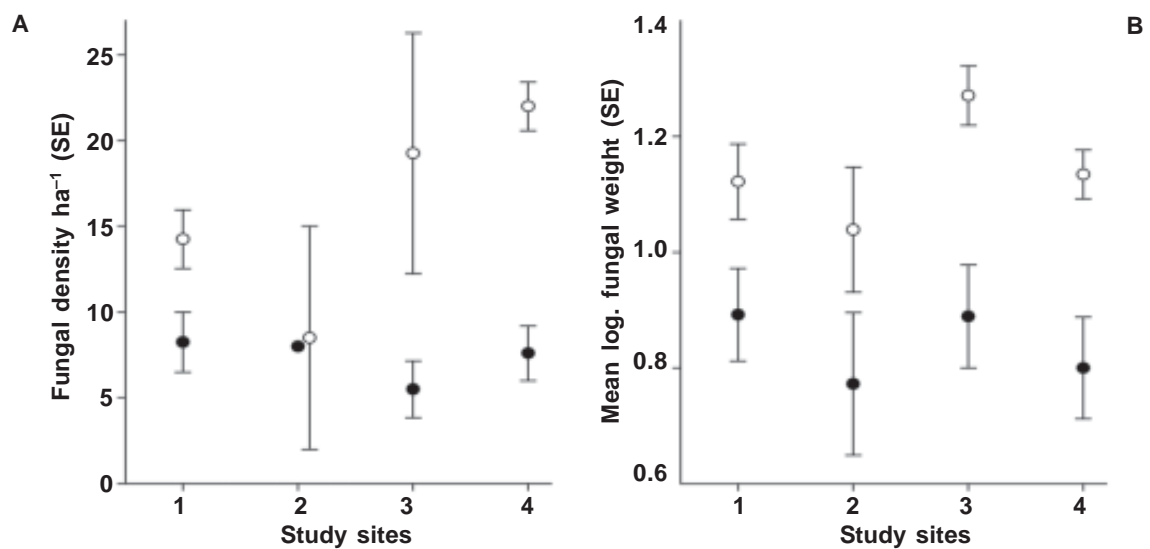| Study site | As | Forest | | Clearcut | | | | |
		Af	CWD	A	Yl	MAI	Vl	CWD
1. Ruunavaara	4.0	37	50	51	1994	155	239	48
2. Pieni Hovinvaara	2.0	19	59	54	1990/1993	145/128	226/268	55
3. Haapahasianvaara	3.5	83	54	58	1993	127	197	111
4. Vankonvaara	4.5	64	52	22	1994	132	223	52

Fig. 1. A. The mean ± SE fungal density in the study sites (density is measured as the number of occupied pieces of woody debris ha⁻¹); B. The mean ± SE fungal–cluster weight in the study sites, note that y–axis starts from 0.6: Black circles represent forests and open circles indicate clearcuts.

Fig. 1. A. Densidad fúngica media ± EE en las áreas de estudio (la densidad se mide como el número de trozos de restos de madera ocupados ha⁻¹); B. Peso medio ± EE de las masas fúngicas en las áreas de estudio; obsérvese que el eje y parte de 0,6: Círculos negros representan los bosques; círculos vacíos, los claros.

Materials and methods

Study system

Four species of *Trametes* (formerly included in *Coriolus* Quél.) occur in the study region in eastern Finland. Of these, *Trametes ochracea* (Pers.) Gilb. & Ryvarden is the most common species inhabiting dead deciduous trees, mainly aspen (*Populus tremula* L.) and birch (*Betula* spp.) (Niemelä, 2001). Over 95% of our samples were *T. ochracea* (K. Junninen det.), but as the fruiting bodies of all *Trametes* species are very similar in physical structure (Ryvarden & Gilbertson, 1993) it was impossible to identify some of the heavily–consumed samples with certainty. As far as it is documented, there are no great differences in the Ciidae fauna associated with the different species of *Trametes* found in Fennoscandian boreal forests (Fossli & Andersen, 1998; Selonen, 2004). *Trametes* fruiting bodies are annual and typically occur in a relatively early phase of decay succession (3–7 yrs; Hintikka, 1993). They are common in woody debris and stumps, and typically form clusters of fruiting bodies. Although the fruiting bodies of *Trametes* are annual, dead fruiting bodies can remain attached to wood for one to two years and become entirely consumed by insects, mainly larvae and adults of Ciidae.

Information on Ciidae life history is limited. The life history is completed within the same piece of fungus and several generations may occur before the adults emigrate to find a fresh piece of fungus (Entwistle, 1955). The adults are long–lived for an insect (up to seven months; Klopfenstein, 1971) and during the summer all life–stages may be found at the same time. Three of the species included in this study [*Sulcacis affinis* (Gyllenhal), *Octotemnus glabriculus* (Gyllenhal) and *Cis boleti* (Scopoli)] lay eggs singly. The adults copulate at intervals during the oviposition period of the female and are not monogamous (Entwistle, 1955). The latter two species, in addition to *Cis hispidus* (Paykull) encountered in this study, are specialists in *Trametes* (Fossli & Andersen, 1998; Guevara et al., 2000b; Selonen, 2004).

Study sites

The study area is located in North Karelia, eastern Finland, in the middle boreal zone (63° 00' – 30' N, 30° – 31° E). First, 12 spruce–dominated old–growth stands were visited. They were rich in aspen (Kouki et al., 2004) and thus assumed to have a sufficiently high density of *Trametes* to provide adequate sample size. Only four stands were adjacent to clearcuts and these were selected for the study: 1. Ruunavaara; 2. Pieni

Table 2. Number of individuals and percent of samples occupied by ciid beetles in this study in forests and clearcuts.

Tabla 2. Número de individuos y porcentaje de muestras ocupadas por escarabajos cíidos en este estudio, en los bosques y en los claros de tala.

	Forest		Clearcut	
Species	Indiv.	%	Indiv.	%
Sulcacis affinis	80	9	18,125	87
Octotemnus glabriculus	4,096	80	3,529	72
Cis hispidus	508	53	3,719	87
Cis boleti	239	51	570	50
Sulcacis fronticornis	0	0	254	9
Cis comptus	1	1	94	9
Cis glabratus	13	5	19	4
Ennearthron laricinum	7	1	1	0.4
Orthocis alni	1	1	6	2
Cis lineatocribratus	0	0	4	1
Cis jacquemartii	1	1	2	1
Ennearthron cornutum	2	1	1	0.4

Hovinvaara; 3. Haapahasianvaara; 4. Vankonvaara (table 1). As not all stands had large enough (≥ 2 ha) adjacent clearcuts, two of the sampling quadrats (see below) in site 4, and one in site 2 were located further from the studied forest, yet within 1–km distance and adjacent to other patches of old–growth. All the clearcut areas had once been part of the larger old–growth forest but had been logged 7 or 8 years earlier; part of the clearcut in site two had been logged 11 years earlier (data from Forest and Park Service, Lieksa). This oldest clearcut area was the only one with 2–3 m tall birch trees, the others were fully open. The small difference between the mean fungal density in site two results from this difference (fig. 1).

Sampling

Fungal samples were collected between 22 IX and 6 X 01, the optimal time given the species phenology. One hectare study quadrats were randomly positioned and marked in the field; in the forests, quadrats were at least 50 m from the forest–clearcut edge. An equal area was sampled in a given old–growth forest and the adjacent clearcut (table 1). The sampled areas varied in size among forest–clearcut pairs, because larger forest stands allowed larger sampling coverage, thus increasing sample size and statistical power. However, the area sampled does not consistently follow the area of forests due to the discrepancy between the forest area and the area and shape of the adjacent clearcuts. Due to the shape and size of the clearcut in site 4, it was

impossible to establish all the sample units as 1–ha quadrats; instead we used 200 m x 50 m strips. In sites 3 and 4, two 50 m x 50 m quadrats were used for sampling the area of 0.5 ha.

In all study quadrats we examined all woody debris (dbh ≥ 10 cm) of deciduous trees for *Trametes* fruiting bodies. As *Trametes* fruiting bodies often occur in tight clusters, insect larvae could potentially move from one fruiting body to another. Thus, all the fruiting bodies in a cluster were considered one sample and carefully removed. If the fungal clusters were located in separate parts of the same individual tree, for example in a stump and a trunk not attached to each other, these were considered separate samples. Samples were transferred to mesh–net covered plastic boxes and kept in outdoor conditions. On 8 II 02, all the samples were transferred to room temperature and weighed after two weeks, a period which was considered adequate for excess water to evaporate and make the weight of samples collected under different daily weather conditions more comparable. The fungal cluster size was determined by weighing, reflecting both the number and size (g) of fruiting bodies. All the fruiting bodies were carefully dissected and the adult insect individuals were removed and identified.

Statistical analyses

Generalized Linear Models (GLM; McCullagh & Nelder, 1989) were used to analyze the data. In all models, site was introduced as a random effect and management category (forest or clearcut) as

Table 3. GLM results on the fungal–cluster occupancy for four ciid beetles. The change in deviance indicates the model improvement when a given term is included in the model. The full model was compared to a model with only a constant term: F. Full model; Mng. Management nested within site; S. Site; W. Weight. Rd. Residual deviance

Tabla 3. Resultados GLM de la ocupación de las masas fúngicas por parte de cuatro coleópteros cíidos. El cambio de la desvianza indica la mejora del modelo cuando se incluye en éste un término dado. El modelo completo se comparó con un modelo con un único término constante: F. Modelo completo; Mng. Manejo anidado dentro del área; S. Área; W. Peso. Rd. Desvianza residual.

Ciid species	d.f.	Change in deviance χ^2	P
Sulcacis affinis			
F	8	277.86	0.000
Mng	4	185.76	0.000
S	3	2.87	0.412
W	1	47.99	0.000
Rd	276	156.74	1.000
Octotemnus glabriculus			
F	8	80.18	0.000
Mng	4	27.11	0.000
S	3	12.83	0.005
W	1	55.43	0.000
Rd	276	262.94	0.704
Cis hispidus			
F	8	111.05	0.000
Mng	4	24.12	0.000
S	3	1.66	0.647
W	1	61.30	0.000
Rd	276	225.17	0.988
Cis boleti			
F	8	99.49	0.000
Mng	4	12.57	0.014
S	3	8.11	0.044
W	1	91.53	0.000
Rd	276	315.30	0.052

Table 4. Parameter estimates ± SE give the change in the log of the odds for a ciid species occurring or not occurring in a fungal cluster sampled from forests, holding fungal–cluster weight constant. Estimates are taken from the GLM in table 3: Mng. Management; W. Weight. (* Unstable estimate as this ciid species was absent from the forest in this site.)

Tabla 4. Las estimas de los parámetros ± EE nos dan el cambio en el logaritmo de los valores predichos/observados ("odds") para cada especie de cíido, que aparece o no, en las masas fúngicas muestreadas en los bosques, siendo constante el peso de dichas masas fúngicas. Las estimas se tomaron de los valores GLM de la tabla 3: Mng. Control; W. Peso. (Estima inestable cuando esta especie de cíido estaba ausente del bosque en ese lugar.)*

Ciid species	Estimate ± SE
Sulcacis affinis	
Mng (site 1)	−1.63 ± 0.35
Mng (site 2)	−3.08 ± 0.79
Mng (site 3)	−7.28 ± 26.6*
Mng (site 4)	−2.10 ± 0.35
W	2.88 ± 0.48
Octotemnus glabriculus	
Mng (site 1)	1.25 ± 0.30
Mng (site 2)	0.31 ± 0.45
Mng (site 3)	0.20 ± 0.30
Mng (site 4)	0.82 ± 0.32
W	2.38 ± 0.36
Cis hispidus	
Mng (site 1)	−0.68 ± 0.29
Mng (site 2)	−1.34 ± 0.62
Mng (site 3)	−0.35 ± 0.31
Mng (site 4)	−0.85 ± 0.26
W	2.63 ± 0.38
Cis boleti	
Mng (site 1)	0.79 ± 0.28
Mng (site 2)	0.30 ± 0.41
Mng (site 3)	0.54 ± 0.29
Mng (site 4)	0.17 ± 0.24
W	2.74 ± 0.34

a fixed effect nested within site. Fungal–cluster weight was included as a continuous covariate. For the distribution of a species (i.e. the presence or absence of a species in a cluster; a binary response) a binomial error distribution and a logit link–function were assumed. For the abundance of a species (the average number of individuals per cluster) an identity link–function and normally dis-
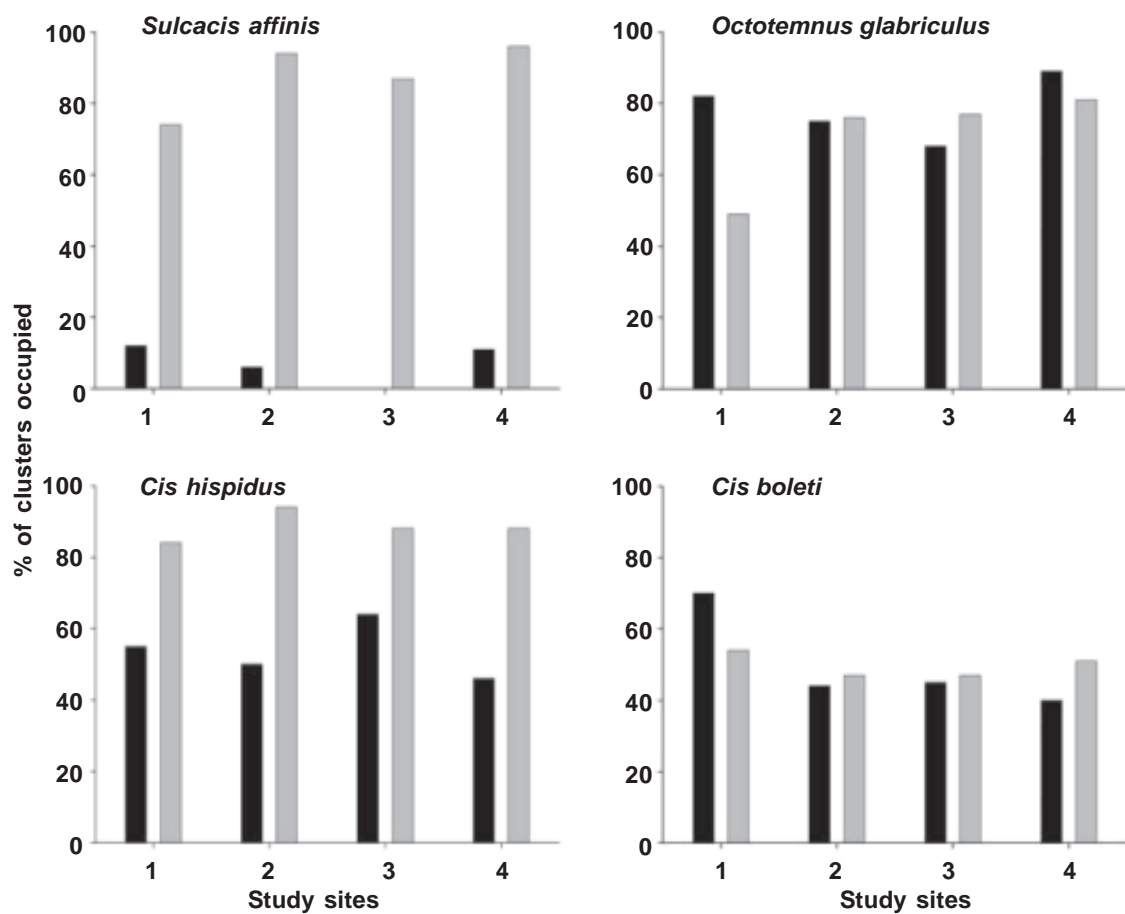
Fig. 2. Percent of fungal clusters occupied by ciid species in the four study sites; black bars represent forests and grey bars show clearcuts.

Fig. 2. Porcentaje de masas fúngicas ocupadas por especies de cíidos en las cuatro áreas estdiadas; las barras negras representan los bosques, y las grises los claros.

tributed errors were assumed. The significance of each term was evaluated based on the increase in deviance when the term was dropped from the full model containing all explanatory parameters. Fungal–cluster weight and the number of individuals were $\log_{10}(x+1)$–transformed in all analyses, unless otherwise stated.

Results

Host availability

Altogether, 106 and 245 pieces of woody debris occupied by dead fruiting bodies of *Trametes* were recorded and sampled from forests and clearcuts, respectively. The density of woody debris occupied by *Trametes* was consistently lower in the forest sites (mean ha^{-1} ± SE = 7.34 ± 0.63) than in the clearcut sites (16.00 ± 2.97; fig. 1A).

The average fungal–cluster weight was also consistently lower in the forest than in the clearcut sites (fig. 1B; change in deviance = 1.760, $F_{4, 343} = 8.560$, $P < 0.000$).

Patterns of beetle occupancy

A total of 32,193 insect individuals were removed from the sampled fruiting bodies. These included 12 species of Ciidae, the four most common species of which (96% of all insect individuals) were used in the analyses (table 2). Fungal–cluster weight had a positive effect of similar magnitude on the probability of a cluster being occupied for all four species (tables 3, 4). *Sulcacis affinis* and *Cis hispidus* had a very consistent pattern of occurrence in all sites, in comparison with *Octotemnus glabriculus* and *Cis boleti*, in that they were more frequent in clearcuts (fig. 2, table 4). Interestingly, *O. glabriculus* and *C. boleti* were
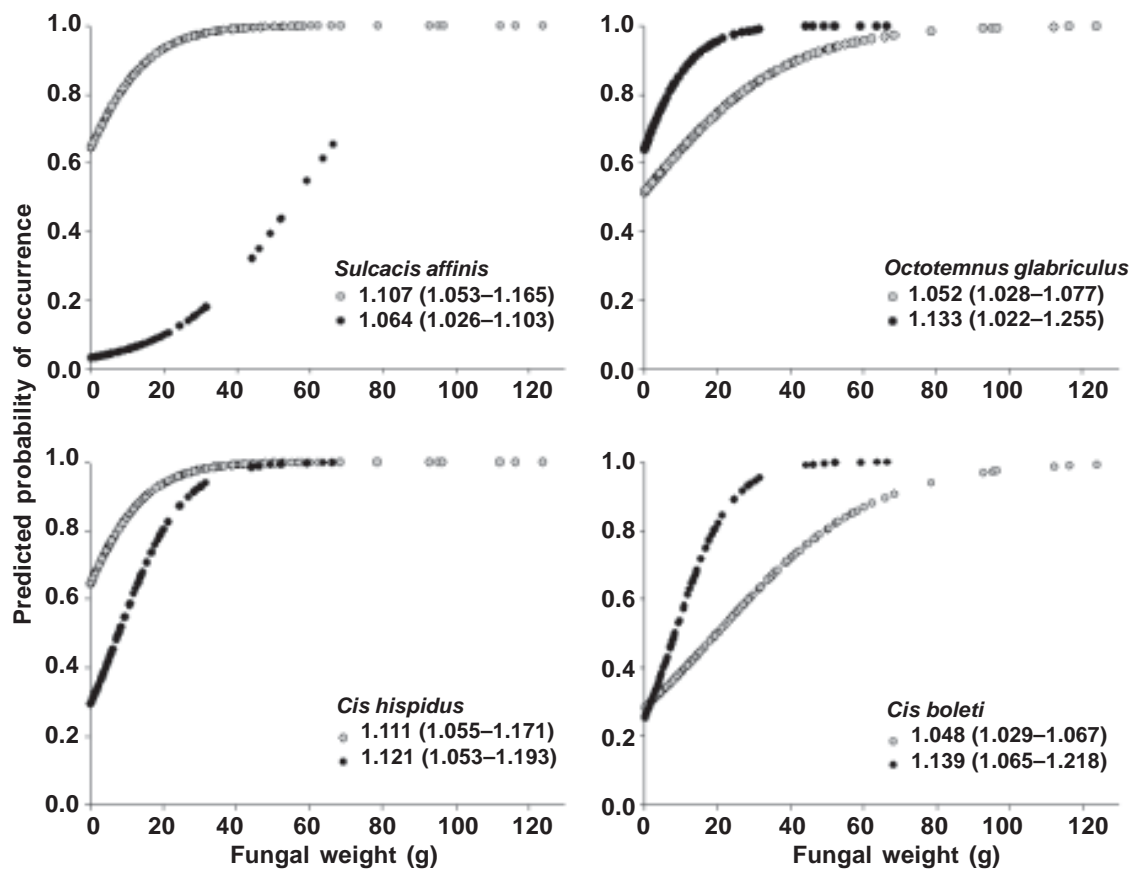
Fig. 3. The predicted probability of occurrence of the four ciid species in the fungal clusters as a function of cluster weight (untransformed), based on a logistic regression model. Figures give the estimated odds ratios and 95% CIs; black dots represent forests, grey dots clearcuts.

Fig. 3. Probabilidad predicha de la presencia de las cuatro especies de cíidos en las masas fúngicas, como función del peso de dichas masas (no transformado), basada en un modelo logístico de regresión. Las cifras se refieren a la estima de la razón entre los valores predichos y observados ("odds ratio") y los CIs 95%; los círculos negros representan los bosques, y los grises los claros.

more likely to be found from forests, as indicated by signs of parameter estimates (table 4), despite lower fungal availability (fig. 1). For the two "forest species", the predicted probability of occurrence increased more slowly as a function of fungal–cluster weight in the clearcut clusters than in the forest clusters (fig. 3). The opposite pattern was observed for the two "clearcut species".

Patterns of beetle abundance

Sulcacis affinis and *C. hispidus* were more abundant on average in the clearcut than in the forest clusters, and *O. glabriculus* was more abundant in the forest clusters, after controlling for fungal weight (table 5; fig. 4). *Cis boleti* did not show significant difference in abundance between a forest and a clearcut. It was further tested whether there were interspecific differ-

ences in average abundances in forest and clearcut clusters. In the forests, *O. glabriculus* had a larger mean population size in the clusters than *S. affinis*, *C. hispidus* and *C. boleti* ($F_{3, 200} = 35.273$, $r^2 = 0.346$, $P < 0.05$; Dunnett's C for pairwise comparisons). In the clearcuts, *S. affinis* had a significantly larger population size than the other three species and *C. boleti* population size was significantly smaller ($F_{3, 722} = 112.343$, $r^2 = 0.318$, $P < 0.05$; Dunnett's C for pairwise comparisons).

Discussion

Findings from this study demonstrate that the macrohabitat where specific resources occur is important for ciid beetles in *Trametes* fruiting bodies (c.f. Thunes & Willassen, 1997; Jonsell et al., 2001;

Table 5. GLM results on the mean abundance of ciid beetles in fungal clusters. The change in deviance indicates the model improvement when a given term is included in the model. The interaction term between management category and weight was non–significant for each species (F < 2.63, *P* > 0.1), and thus it was excluded from the final models: η^2. Proportion of explained variance; Mng. Management nested within site; W. Weight; Rd. Residual deviance; * d.f. is only 3 because one site did not include any occupied fungal clusters).

*Tabla 5. Resultados GLM de la abundancia media de coleópteros cíidos en las masas fúngicas. El cambio de la desvianza indica la mejora del modelo cuando se incluye en éste un término dado. El término de interacción entre la categoría de gestión y el peso para cada especie (F < 2,63, P > 0,1) no fue significativo, por lo que se excluyó de los modelos finales: η^2. Proporción de varianza explicada; Mng. Manejo anidado dentro del área; W. Peso; Rd. Desvianza residual; * d.f. es sólo de 3 debido a que uno de los lugares no incluía ninguna masa fúngica ocupada).*

Species					
Source	d.f.	Change in deviance	F	P	η^2
Sulcacis affinis					
Mng	3*	3.775	17.113	0.000	0.193
Site	3	3.064	0.376	0.779	0.287
W	1	27.736	125.723	0.000	0.370
Rd	214	0.221			
Octotemnus glabriculus					
Mng	4	3.405	16.415	0.000	0.207
Site	3	0.263	0.080	0.968	0.056
W	1	14.665	70.686	0.000	0.219
Residual deviance	252	0.207			
Cis hispidus					
Mng	4	0.552	4.525	0.001	0.065
Site	3	0.383	0.705	0.597	0.344
W	1	16.675	136.666	0.000	0.344
Residual deviance	261	0.122			
Cis boleti					
Mng	4	0.128	1.568	0.185	0.036
Site	3	0.207	1.634	0.311	0.539
W	1	2.443	29.815	0.000	0.151
Residual deviance	168	0.082			

Jonsson et al., 2001). Most interestingly, some ciids seem to prefer forests over clearcuts despite lower fungal density and smaller size of fungal clusters in the former. In the absence of experiments, however, we cannot make explicit causal inferences. We therefore discuss two potential ecological factors that could contribute to the difference observed in beetle species occurrence and abundance between forests and clearcuts.

Small–scale effects of fungal cluster

For all ciid species of the present study, fungal–cluster weight contributed positively to the probability of a sample being occupied, both in the forest and clearcut (see also Midtgaard et al., 1998). The higher frequency of occurrence of ciids can be explained by the greater probability of detecting larger fungal clusters (actively or by chance only), as well as by a longer expected persistence time of the local beetle population in larger clusters. There is evidence that both walking and flying ciids are attracted to the volatile compounds of their host fungus rather than finding the fungi accidentally (Jonsell & Nordlander, 1995; Guevara et al., 2000a, 2000b). If larger fungal clusters emit greater amounts of volatile compounds, then they would also attract more
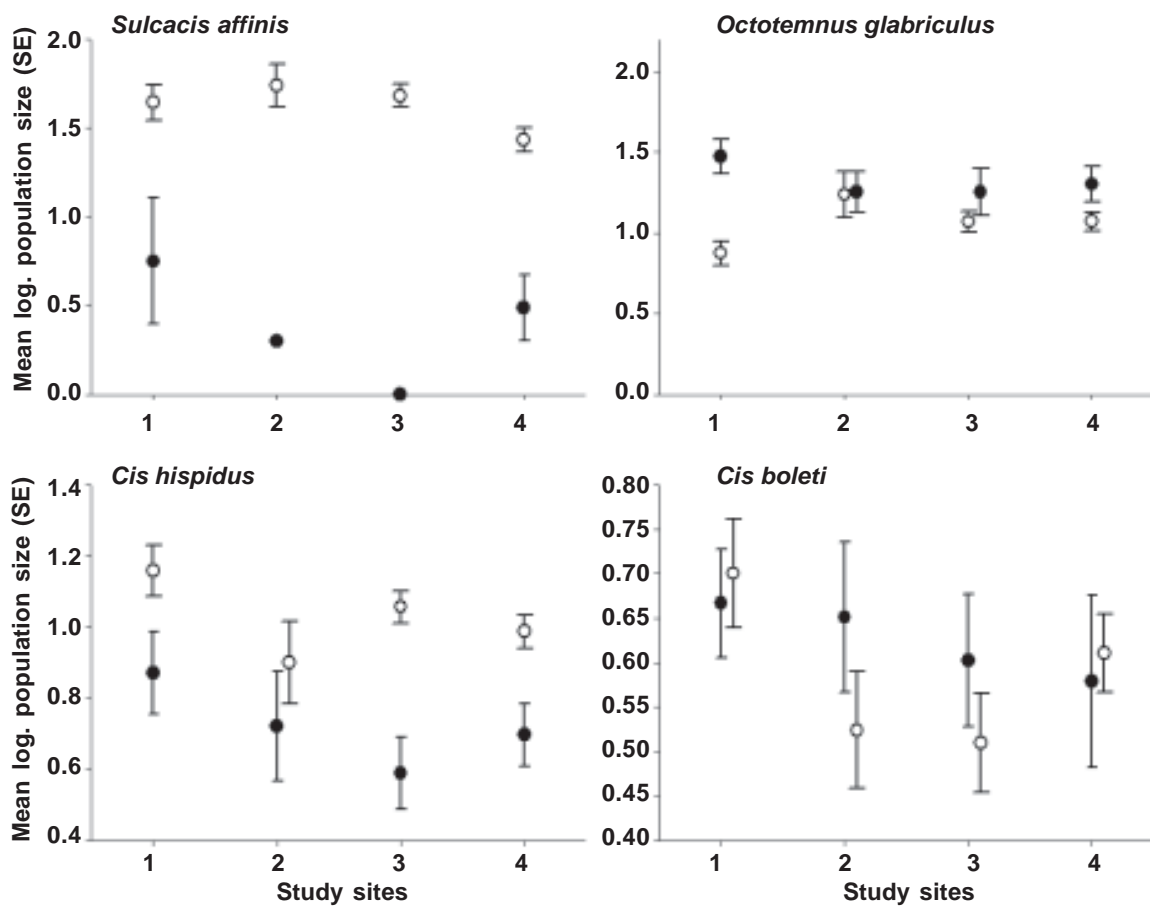
Fig. 4. The mean ± SE population size per fungal cluster occupied by a given ciid species in the study sites; black circles represent forests and open circles clearcuts.

Fig. 4. Tamaño medio ± EE de la población por masa fúngica ocupada por una especie dada de cíido en las áreas de estudio; los círculos negros representan los bosques, y los vacíos los claros.

ciids, partly explaining the positive effect of fungal weight on the probability of occurrence.

In this study it is shown that "forest species" have a higher probability of occurrence in a fungal cluster of a given size in forests (optimal macrohabitat) vs clearcuts (suboptimal macrohabitat), and "clearcut species" show an opposite pattern. These results suggest that species may compensate for adverse environmental conditions in the suboptimal macrohabitat by utilizing larger fungal clusters. As the measure of fungal cluster weight used here incorporates both the number and the weight of fruiting bodies, it is difficult to say much about the possible mechanisms that cause the observed difference in species incidence. The observed pattern may result from a higher colonization rate or from a longer ciid population persistence time in larger fungal clusters. Besides, larger clusters probably have greater variation in the quality of fruiting bodies, thus increasing the likelihood that a given beetle species meets its

specific ecological requirements. In larger clusters there is also more potential for resource partitioning, which could facilitate coexistence by reducing interspecific competition between ciid species (Guevara et al., 2000a). Of the species recorded in this study, only *S. affinis* is known to inhabit —in great numbers— fruiting bodies of fungal species other than *Trametes*, namely *Pycnoporus cinnabarinus* (Jacq.: Fr.) P. Karsten (Økland, 1995). The fruiting bodies of this fungus occur exclusively in warm, open areas (Niemelä, 2001) and were also abundant in the clearcuts of this study. This supplementary host fungus could contribute to the very high frequency of occurrence of *S. affinis* in the clearcuts.

Larger fungal clusters inherently support larger ciid populations (Midtgaard et al., 1998), which in turn could affect local occurrence patterns via increased number of dispersing individuals. Evidence on the dispersal ability of ciid beetles is scarce and indirect, making it impossible to assess the dispersal rate

between fungal clusters. Jonsell et al. (1999) demonstrated that some ciid species were absent from fruiting bodies placed out in forest fragments 350–2,000 m from the natural forest. Similarly, Rukke (2000) found out that the incidence of ciid species in fruiting bodies was negatively affected by increased isolation at the scale of individual trees, 15 to over 500 m depending on the species. Given the high density of *Trametes* fruiting bodies it seems unlikely there would have been great difficulties for ciids in moving between clusters in clearcuts. However, restricted movement between clusters in forests and between adjacent forests and clearcuts is possible.

Large scale effects of macrohabitat

The forest management category had an independent effect on species frequency of occurrence, even less so than fungal–cluster weight. Similarly, the management category contributed positively to the abundance of *S. affinis* and *C. hispidus* in the clearcuts and *O. glabriculus* in the forests. In this study, it is difficult to explicitly distinguish between the effect of fungal cluster density and management category on the frequency of occurrence of the ciid beetles in the clusters, as the density was consistently higher in the clearcuts. The apparent inconsistent response of the two "forest species" to the management category may be due to opposing forces of microclimate and resource availability (Jonsell et al., 2001; Jonsson et al., 2001). However, a larger sample of forest and clearcut sites is needed to clarify whether such trade–off exists, or if the inconsistency results from inadequate sampling.

Microclimatic conditions are one of the most important abiotic differences between forests and clearcuts. Therefore, varying interspecific responses of ciid species to forest management may result from different microclimatic optima. Other studies have documented that increased sun–exposure and dryness of fruiting bodies increase the probability of occurrence of some fungus–dwelling insect species (Midtgaard et al., 1998; Rukke & Midtgaard, 1998), whilst other species occur more frequently in moist fruiting bodies or in shady conditions (Økland, 1996; Jonsell et al., 2001; Thunes et al., 2000). Sverdrup–Thygeson & Ims (2002) showed that among the beetle species in dead aspen there are clear preferences concerning the degree of sun–exposure. Their window–trap material also included *O. glabriculus* and, as in the present study, the species preferred shady conditions being more abundant in traps on shady aspen logs. Fossli & Andersen (1998) collected *Trametes* fruiting bodies from forests and, again, *S. affinis* was very rare. In Germany, *S. affinis* occurs readily in clearcuts, whereas *O. glabriculus* and *C. boleti* manage well in more shady conditions (Reibnitz, 1999). Microclimate can affect the abundance of ciids directly by speeding up the individual development and indirectly by affecting the quality of fruiting bodies. However, there are no studies linking population growth to the quality of fruiting bodies.

Conclusions

Many dead–wood dependent organisms can successfully occur in clearcuts if critical resources are left in adequate densities and qualities (Jonsell et al., 2001; Jonsson et al., 2001; Martikainen, 2001; Sverdrup–Thygeson & Ims, 2002). Prior to the extensive fire suppression in Finnish forests in the 1900s, many of these species may have favored open areas created by forest fires. Nevertheless, sweeping generalizations about species responses should be avoided even for common species, as demonstrated here. Despite higher *Trametes* density, clearcuts are more ephemeral environments for *Trametes*–dwelling insects in comparison with old–growth forests. The rationale is that most woody debris becomes unsuitable for *Trametes* over the course of years (3–7 years; Hintikka, 1993), after which it takes decades before new woody debris is available. Retaining green and dead deciduous trees in clear–cutting makes woody debris available for *Trametes* and many other more demanding species after the logging residues have become unsuitable.

Acknowledgements

References

Entwistle, H. M., 1955. The biology and morphology of the fungus beetles of the family Ciidae and their parasites. MSc thesis, Univ. of London.

Esseen, P.–A., Ehnström, B., Ericson, L. & Sjöberg, K., 1997. Boreal forests. *Ecol. Bull.*, 46: 16–47.

Fossli, T.–E. & Andersen, J., 1998. Host preference of Ciidae (Coleoptera) on tree–inhabiting fungi in northern Norway. *Entomol. Fennica*, 9: 65–78.

Guevara, R., Hutcheson, K. A., Mee, A. C., Rayner, A. D. M. & Reynolds, S. E., 2000a. Resource partitioning of the host fungus *Coriolus versicolor* by two ciid beetles: the role of odour compounds and host ageing. *Oikos*, 91: 184–194.

Guevara, R., Rayner, A. D. M. & Reynolds, S. E., 2000b. Orientation of specialist and generalist fungivorous ciid beetles to host and non–host odours. *Physiol. Entomol.*, 25: 288–295.

Haila, Y., 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecol. Appl.*, 12: 321–334.

Hintikka, V., 1993. Occurrence of edible fungi and other macromycetes on tree stumps over a sixteen–year period. *Acta Bot. Fenn.*, 149: 11–17.

Jonsell, M. & Nordlander, G., 1995. Field attraction of Coleoptera to odours of the wood–decaying polypores *Fomitopsis pinicola* and *Fomes*

fomentarius. *Ann. Zool. Fenn.*, 32: 391–402.

Jonsell, M., Nordlander, G. & Ehnström, B., 2001. Substrate associations of insects breeding in fruiting bodies of wood–decaying fungi. *Ecol. Bull.*, 49: 173–194.

Jonsell, M., Nordlander, G. & Jonsson, M., 1999. Colonization patterns of insects breeding in wood–decaying fungi. *J. Insect Conserv.*, 3: 145–161.

Jonsson, M., 2003. Colonization ability of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. *Ecol. Entomol.*, 28: 159–167.

Jonsson, M., Jonsell, M. & Nordlander, G., 2001. Priorities in conservation biology: a comparison between two polypore–inhabiting beetles. *Ecol. Bull.*, 49: 195–204.

Kaila, L., Martikainen, P. & Punttila, P., 1997. Dead trees left in clear–cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodivers. Conserv.*, 6: 1–18.

Klopfenstein, P. C., 1971. The ecology, behavior, and life cycle of the mycetophilous beetle, *Hadreule blaisdelli* (Casey) (Insecta: Coleoptera: Ciidae). Thesis, Bowling Green State Univ., Ohio.

Komonen, A., 2001. Structure of insect communities inhabiting two old–growth forest specialist bracket fungi. *Ecol. Entomol.*, 26: 63–75.

Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I., 2000. Forest fragmentation truncates a food chain based on an old–growth forest bracket fungus. *Oikos*, 90: 119–126.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A., 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood–associated threatened species to landscape and habitat changes. *Scand. J. Forest Res. Suppl.*, 3: 27–37.

Kouki, J., Arnold, K. & Martikainen, P., 2004. Long–term persistence of aspen –a key host for many threatened species– is endangered in old–growth conservation areas in Finland. *Journal for Nature Conservation*, 12: 41–52.

Lawrence, J. F., 1973. Host preference in Ciid beetles (Coleoptera: Ciidae) inhabiting the fruiting bodies of basidiomycetes in North America. *Bull. Mus. Comp. Zool.*, 145: 163–212.

Löfman, S. & Kouki, J., 2003. Scale and dynamics of transforming forest landscape. *For. Ecol. Manage.*, 175: 247–252.

Martikainen, P., 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. *Ecol. Bull.*, 49: 205–218.

McCullagh, P. & Nelder, J. A., 1989. *Generalized linear models.* 2nd ed. Chapman & Hall, New York.

Midgaard, F., Rukke, B. A. & Sverdrup–Thygeson, A., 1998. Habitat use of the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera: Tenebrionidae): effects of basidiocarp size, humidity and competitors. *Eur. J. Entomol.*, 95: 559–570.

Mönkkönen, M. & Reunanen, P., 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos*, 84: 302–305.

Niemelä, T., 2001. *Guide to the polypores of Finland*. 13th ed. Botanical Bulletins of the Univ. of Helsinki 179.

Nilsson, T., 1997. Survival and habitat preferences of adult *Bolitophagus reticulatus. Ecol. Entomol.*, 22: 82–89.

Økland, B., 1995. Insect fauna compared between six polypore species in a southern Norwegian spruce forest. *Fauna Norv. Ser. B*, 42: 21–26.

– 1996. Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). *Biol. Conserv.*, 76: 297–310.

Reibnitz, J., 1999. Verbreitung und Lebensräume der Baumschwammfresser Südwestdeutschlands (Coleoptera: Cisidae). *Mitt. Ent. Stuttgart*, 34: 1–76.

Rukke, B. A., 2000. Effects of habitat fragmentation: increased isolation and reduced habitat size reduces the incidence of dead wood fungi beetles in a fragmented forest landscape. *Ecography*, 23: 492–502.

Rukke, B. A. & Midtgaard, F., 1998. The importance of scale and spatial variables for the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae) in a fragmented forest landscape. *Ecography*, 21: 561–572.

Ryvarden, L. & Gilbertson, R. L., 1993. *European Polypores 1. Abortiporus–Lindtneria*. Synopsis Fungorum 6. Fungiflora A/S, Oslo.

Schmiegelow, F. K. A. & Mönkkönen, M., 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecol. Appl.*, 12: 375–389.

Selonen, V. A. O., 2004. Polypores and associated beetles in a forest–clearcut ecotone. MSc thesis, Univ. of Jyväskylä.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.*, 49: 11–41.

Sverdrup–Thygeson, A. & Ims, R. A., 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biol. Conserv.*, 106: 347–357.

Thunes, K. H. & Willassen, E., 1997. Species composition of beetles (Coleoptera) in the bracket fungi *Piptoporus betulinus* and *Fomes fomentarius* (Aphyllophorales: Polyporaceae): an explorative approach with canonical correspondence analysis. *J. Nat. Hist.*, 31: 471–486.

Thunes, K. H., Midtgaard, F. & Gjerde, I., 2000. Diversity of coleoptera of the bracket fungus *Fomitopsis pinicola* in a Norwegian spruce forest. *Biodivers. Conserv.*, 9: 833–852.

Uotila, A., Kouki, J., Kontkanen, H. & Pulkkinen, P., 2002. Assessing the naturalness of boreal forests in eastern Fennoscandia. *For. Ecol. Manage.*, 161: 257–277.