

Fungivorous beetles in basidiocarps of *Fomes fomentarius* respond differently to microhabitat variables

BJØRN ARNE RUKKE*

Division of Zoology, Department of Biology, University of Oslo, P.O. Box 1050 Blindern, N-0316 Oslo, Norway
e-mail: bjorn.arne.rukke@forsvarsbygg.no

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Abstract. This study investigates the influence of microhabitat on the presence of several species of fungivorous beetles in basidiocarps of *Fomes fomentarius* (L.) Kickx. All dead basidiocarps of *F. fomentarius* from fragments of forest in an agricultural landscape in Norway were sampled and dissected, and their content of *Cis jacquemarti* Mellié, 1848/*C. alter* (Silvferberg, 1991) (did not distinguish between individuals of these two species), *C. bidentatus* (Olivier, 1790), *C. lineatocribratus* Mellié, 1848, *Ennearthron cornutum* (Gyllenhal, 1827) (Ciidae) and *Dorcatoma dresdensis* Herbst, 1792 (Anobiidae) were identified. Multiple logistic regression models revealed that these species responded differently to the microhabitat variables. The incidence of these beetles was associated with the size (volume), position (height above ground) and moisture content of the basidiocarps. The analyses also indicated possible interspecific interactions between some of the beetles. The presence of some of the species mainly in basidiocarps at particular stages of degradation indicates a successional pattern of occurrence of these species. Together these results indicate that basidiocarps of *F. fomentarius* are a heterogeneous resource for fungivorous beetles. This has implications for conservation: To preserve the diversity of fungivores, sufficient dead wood has to be left in forests to assure an adequate supply of *F. fomentarius* basidiocarps of different quality.

INTRODUCTION

Many species live in patchily distributed habitats, and these environmental discontinuities affect the distribution of organisms (Wiens, 1976). At larger scales, landscape variables like isolation and habitat size may strongly affect species occurrence (e.g. Kindvall & Ahlén, 1992), while more locally, microhabitat conditions may determine their spatial distribution (e.g. Midtgaard et al., 1998). Therefore, a multiple scale approach to habitat requirements is more likely to increase our knowledge of species distribution than a single-scale approach.

Both landscape and microhabitat variables affect the occurrence of beetles in basidiocarps of fungi growing on dead wood. The basidiocarp habitat is an example of a spatial hierarchy with more or less clearly defined patches at several nested scales. Basidiocarps are nested within trees, trees within groups of trees and groups of trees within forests. Incidence studies (Rukke & Midtgaard, 1998; Sverdrup-Thygeson & Midtgaard, 1998), a mark-recapture study (Nilsson, 1997) and a genetic survey (Knutsen et al., 2000) have revealed effects of the large-scale variables isolation and habitat size on the population dynamics of *Bolitophagus reticulatus* (Linnaeus, 1767) (Tenebrionidae), which is monophagous on basidiocarps of *Fomes fomentarius* (L.) Kickx. Another large-scale study showed that several other species inhabiting basidiocarps of *F. fomentarius* are also affected by changes in degree of habitat isolation and habitat size. Like *B. reticulatus*, the incidence of *Cis jacquemarti* Mel-

lié, 1848/*C. alter* (Silvferberg, 1991) (individuals of these two species were not distinguished), *C. bidentatus* (Olivier, 1790), *C. lineatocribratus* Mellié, 1848, *Ennearthron cornutum* (Gyllenhal, 1827) (Ciidae) and *Dorcatoma dresdensis* Herbst, 1792 (Anobiidae) decreases with increased habitat isolation and reduced habitat size (Rukke, 2000 - in this paper *C. alter* = *C. nitidius* (Fabricius, 1792)). Additionally, an incidence study at a lower scale has shown the effect of several microhabitat variables on the presence of *B. reticulatus* in basidiocarps (Midtgaard et al., 1998).

Since dead wood and its associated fungi are greatly reduced in quantity in today's forests due to forestry practices (Haila et al., 1994; Bader et al., 1995; Esseen et al., 1997), information on the habitat requirements of the beetles associated with such habitats is particularly interesting for conservation purposes. To prevent habitat depletion and subsequent population decline, a better knowledge of a species' habitat requirements, at all relevant scales, is required.

The present study aims to add information about small-scale habitat requirements of beetles associated with fungi living on dead wood. The effects of several microhabitat variables on the presence of *C. jacquemarti*/*C. alter*, *C. bidentatus*, *C. lineatocribratus*, *E. cornutum* and *D. dresdensis* in the basidiocarps of *F. fomentarius* were investigated in an attempt to reveal whether the species have particular habitat preferences.

* Current address: Kranveien 4, 0684 Oslo, Norway.

TABLE 1. Species of Coleoptera found in the dead basidiocarps of *Fomes fomentarius* (n = 587) from the study area. Included are number of specimens (S) and number of occurrences (O).

Species	Family	S	O	Species	Family	S	O
<i>Cis jacquemarti/alter</i>	Ciidae	6783	386	<i>Phyllotreta striolata</i>	Chrysomelidae	1	1
<i>Bolitophagus reticulatus</i>	Tenebrionidae	2153	134	<i>Phyllotreta undulata</i>	Chrysomelidae	1	1
<i>Dorcatoma dresdensis</i>	Anobiidae	181	40	<i>Atomaria fuscata</i>	Cryptophagidae	1	1
<i>Cis bidentatus</i>	Ciidae	168	46	<i>Atomaria impressa</i>	Cryptophagidae	1	1
<i>Ennearthron cornutum</i>	Ciidae	122	55	<i>Dalopius marginatus</i>	Elateridae	1	1
<i>Cis lineatocribratus</i>	Ciidae	110	32	<i>Selatosomus aeneus</i>	Elateridae	1	1
<i>Cis quadridens</i>	Ciidae	58	7	<i>Liestes seminigra</i>	Endomychidae	1	1
<i>Ropalodontus perforatus</i>	Ciidae	20	3	<i>Xylophilus corticalis</i>	Eucnemidae	1	1
<i>Leptusa fumida</i>	Staphylinidae	12	9	<i>Cyphon sp.</i>	Helodidae	1	1
<i>Rhizophagus dispar</i>	Rhizophagidae	9	8	<i>Agathidium badium</i>	Leiodidae	1	1
<i>Leptusa pulchella</i>	Staphylinidae	6	6	<i>Malachius bipustulatus</i>	Malachiidae	1	1
<i>Acrulia inflata</i>	Staphylinidae	5	4	<i>Rhizophagus bipustulatus</i>	Rhizophagidae	1	1
<i>Dinaraea aequata</i>	Staphylinidae	3	3	<i>Rhizophagus nitidulus</i>	Rhizophagidae	1	1
<i>Dryocoetes alni</i>	Scolytidae	3	2	<i>Atheta fungi</i>	Staphylinidae	1	1
<i>Ennearthron laricinum</i>	Ciidae	2	1	<i>Atheta nigricornis</i>	Staphylinidae	1	1
<i>Agonum micans</i>	Carabidae	1	1	<i>Gabrius sp.</i>	Staphylinidae	1	1
<i>Pterostichus oblongopunctatus</i>	Carabidae	1	1	<i>Quedius xanthopus</i>	Staphylinidae	1	1
<i>Cerylon histeroides</i>	Cerylonidae	1	1				

MATERIAL AND METHODS

The study area consisted of 58 forest patches ("forest islands") in an agricultural area (1585 ha) in the Lier municipality (59°48'N, 10°16'E), Norway. The size of the forest islands varied from 729 to 63386 m². Data was collected from April to mid June 1993. In the study area all 587 dead basidiocarps of *F. fomentarius* (as defined by Matthewman & Pielou (1971) were collected from 185 trees (125 birches (*Betula pubescens*) and 60 grey alder (*Alnus incana*)) and dissected to reveal their content of beetles. Boreal deciduous trees were the dominant tree species in the forest islands, and *F. fomentarius* basidiocarps were by far the most common basidiocarps on dead wood in the study area (pers. obs.).

All adult beetles in the basidiocarps were recorded (Table 1). In the identification of the beetles, it was difficult to separate individuals of the species *C. glabratus* Mellié, 1848, *C. jacquemarti* and *C. alter* because they were desiccated (Sindre Ligaard, pers. comm.). Since *C. glabratus* is rarely found in basidiocarps of *F. fomentarius* (e.g. Økland, 1995; Fossli & Andersen, 1998; Jonsell, 1999), all these individuals were treated as an assemblage of the two species *C. jacquemarti* and *C. alter*, which is abbreviated to *C. jacquemarti/alter*. Only *C. jacquemarti/alter* and the four species *C. bidentatus*, *C. lineatocribratus*, *E. cornutum* and *D. dresdensis* were common enough for further analyses (except for *B. reticulatus*, which is treated in Midtgaard et al. (1998)).

These species are found in central Europe (Lucht, 1987) and Scandinavia (Lindroth, 1960; Vik, 1991). They may inhabit several species of dead wood fungi (Paviour-Smith, 1960; Kaila et al., 1994; Thunes, 1994; Økland, 1995; Fossli & Andersen, 1998; Jonsell, 1999), but *F. fomentarius* is probably their most important host in the study area as it is the dominant dead wood fungus. Little is known about the life history of the study species, but one generation is probably completed within two years. Therefore, larger dead basidiocarps of *F. fomentarius*, which may persist for several years before disintegrating totally, may support several generations of the beetles. In addition, most

trees harbour several basidiocarps, which usually do not die simultaneously, sometimes making a tree bearing basidiocarps a suitable habitat patch for more than a decade.

The basidiocarps in this study were earlier used to study the effect of habitat and landscape variables on the presence of the same beetle species at higher spatial scales, i.e. at the level of individual trees with basidiocarps (the tree level) and the level of forest islands (see Rukke, 2000). At the tree level, both habitat isolation and habitat size were found to influence the presence of each of the beetle species on a tree. To reduce the influence of these tree-related variables in the present study, only basidiocarps from trees having a certain minimum probability of beetle presence were included in the analyses. These probabilities were estimated for each of the beetle species from their respective multiple logistic regression model at the tree level. For *C. jacquemarti/alter* the criterion was set to 70%, whilst it was set to 50% for the four other species in order to include a sufficient number of basidiocarps in the analyses. Additionally, all dead basidiocarps from trees having at least one basidiocarp inhabited by the respective species were included. Being able to colonise a tree, a beetle species also has the possibility to inhabit all the other basidiocarps on that tree, and consequently be tested for microhabitat preferences there.

Univariate and forward, stepwise, multiple logistic regressions (enter- and check-back-criteria were $p < 0,05$ and $p < 0,06$ respectively) (see Hosmer & Lemeshow, 1989) were used to reveal effects of microhabitat variables on the binary response variable presence/absence of each beetle species in the basidiocarps. Presence of a beetle species was defined as at least one adult present in a basidiocarp. Logistic regression is not an appropriate method of analysis if a categorical predictor variable has one or more categories with 100% presence or absence. Therefore, contingency table analyses were used when a categorical predictor variable had one or more categories with 100% presence or absence. Spearman-rank correlations were used to reveal correlation between predictor variables on a continuous scale. To investigate the relationships between number of bee-

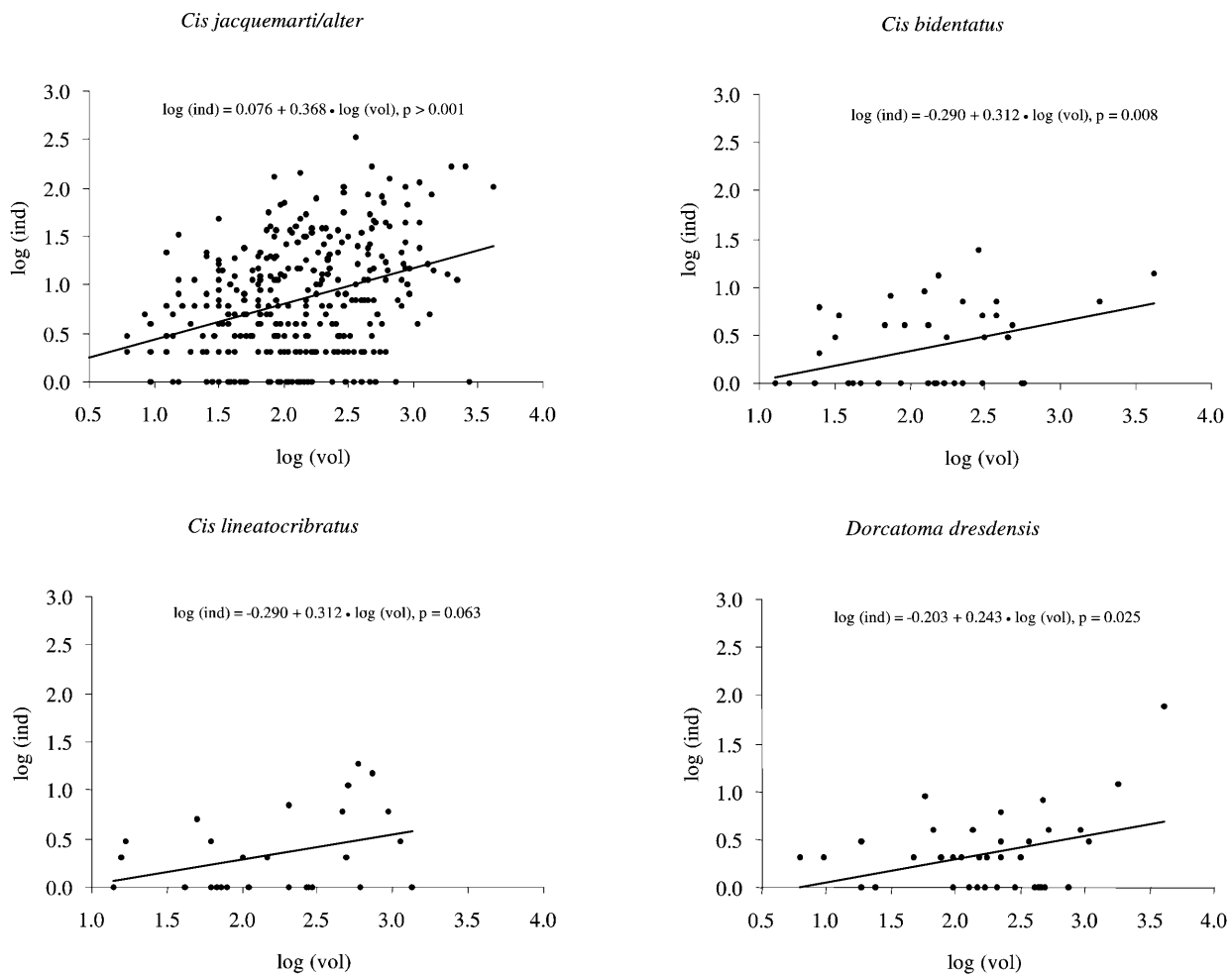


Fig. 1. Linear regressions relating number of individuals of each species to basidiocarp volume of inhabited basidiocarps. Included are the equations of the linear regressions and their p-values.

tles of each species and basidiocarp volume, linear regressions were calculated.

All the variables are described in Table 2. Non-linear relations between some of the variables were found. Therefore, the continuous predictor variables were categorised in the logistic regression analyses (see Hosmer & Lemeshow, 1989). All analyses were performed using the computer program JMP (SAS Institute Inc., 1997).

RESULTS

C. jacquemarti/alter was by far the most numerous and frequently found species in the 587 dead *F. fomentarius* basidiocarps sampled. Density of each species was measured as number of individuals per unit volume and weight of basidiocarp in the basidiocarps inhabited by that particular species. The density of *C. jacquemarti/alter* was far higher than that of the other species (Table 3).

Large basidiocarps had more individuals of *C. jacquemarti/alter*, *C. bidentatus*, *C. lineatocribratus* and *D. dresdensis* than small basidiocarps (Fig. 1). There was no such trend for *E. cornutum* ($p > 0.50$)

Basidiocarp size also affected the incidence of *C. jacquemarti/alter* and *D. dresdensis*. Multiple logistic regression models indicate that large basidiocarps were

more likely to be inhabited by these beetles than small basidiocarps (Table 4 and Fig. 2).

The presence of some of the beetles was associated with "height above ground". Basidiocarps at the ground level were more likely to be inhabited by *C. jacquemarti/alter* than those above ground level, while the opposite applied to *E. cornutum* and *D. dresdensis* (Table 4 and Fig. 2).

The presence of *C. bidentatus* and *C. lineatocribratus* was significantly associated with the moisture content of the basidiocarps (Table 4 and Fig. 2). *C. bidentatus* occurred more frequently in the driest basidiocarps than in the moister ones. For *C. lineatocribratus* the overall trend was the reverse, i.e. increased presence in the more moist basidiocarps.

The patterns of incidence shown by some of the species were not independent (Table 4). The presence of *C. jacquemarti/alter* and *D. dresdensis* was positively correlated with that of *C. bidentatus* and *E. cornutum* respectively, whilst presence of *D. dresdensis* was negatively associated with that of *B. reticulatus*. In the analysis of the interaction between *C. lineatocribratus* and *C. bidentatus*, logistic regressions could not be applied because the category C. lin[1] had no basidiocarps containing *C.*

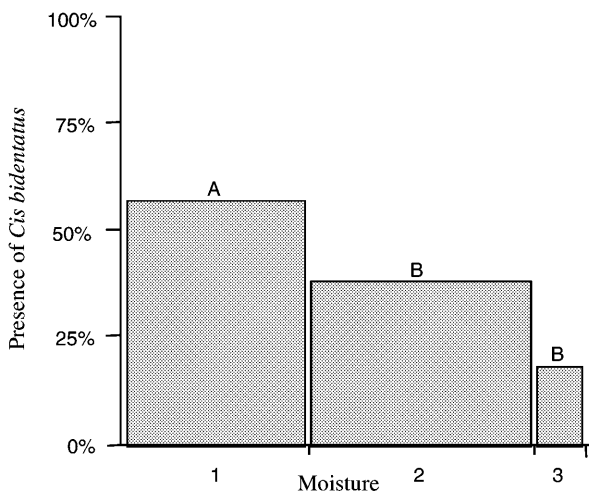
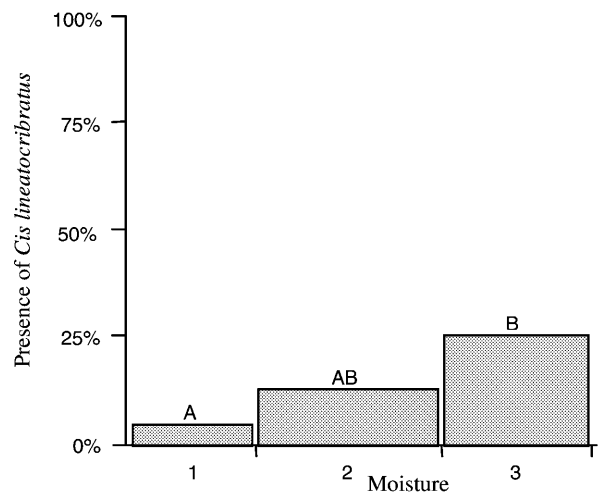
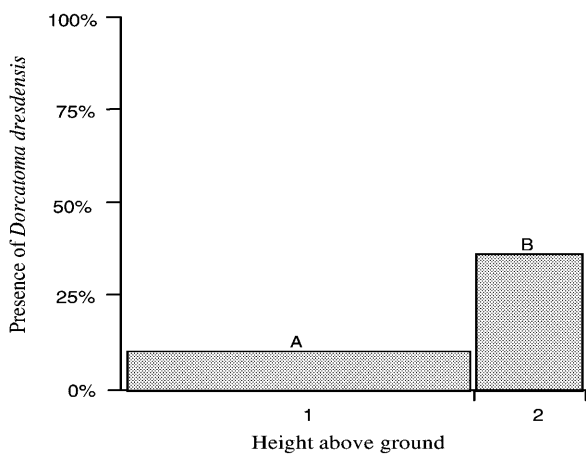
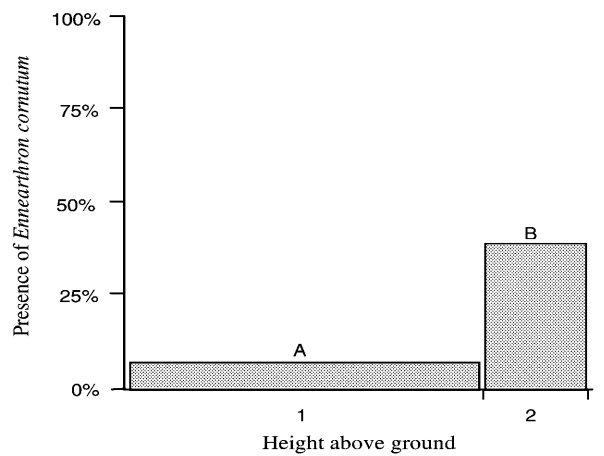
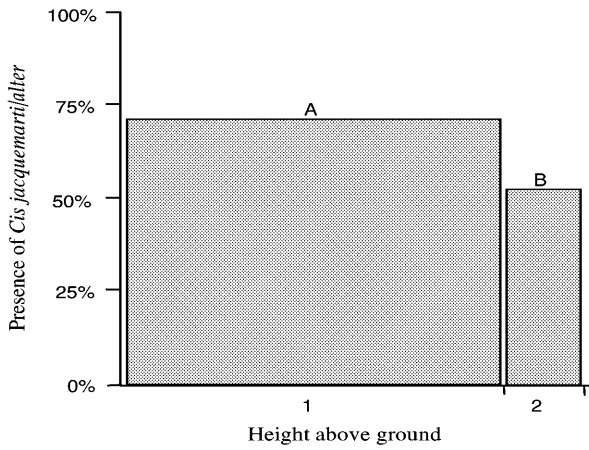
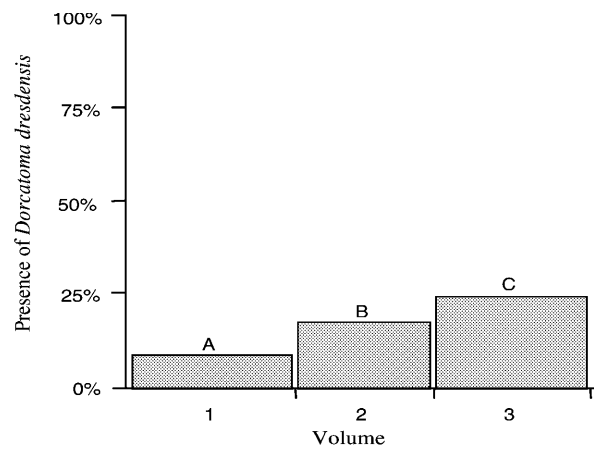
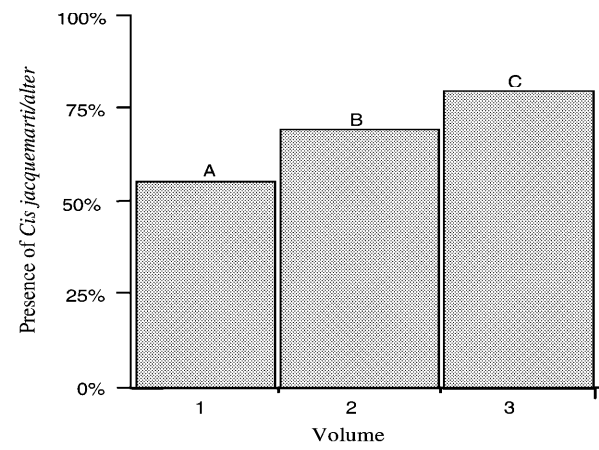


Fig. 2. Percentage presence of each species of beetle in different categories of the variables entering the multiple logistic regression models. The width of the columns reflects the relative number of observations (basidiocarps) in each category. Columns with different letters were significantly different in the multiple logistic regression analyses.

TABLE 2. Description of predictor variables (Var.) and their values (Value).

Var.	Description	Values
B. ret	Presence vs. absence of <i>Bolitophagus reticulatus</i> . Presence was defined as at least one beetle being present in a basidiocarp.	[0]: absence, [1]: presence
C. bid	Presence vs. absence of <i>Cis bidentatus</i> . Presence was defined as at least one adult beetle being present in a basidiocarp.	[0]: absence, [1]: presence
C. lin	Presence vs. absence of <i>Cis lineatocribratus</i> . Presence was defined as at least one adult beetle being present in a basidiocarp.	[0]: absence, [1]: presence
C. jac	Presence vs. absence of <i>Cis jacquemarti/alter</i> . Presence was defined as at least one adult beetle being present in a basidiocarp.	[0]: absence, [1]: presence
D. dre	Presence vs. absence of <i>Dorcatoma dresdensis</i> . Presence was defined as at least one adult beetle being present in a basidiocarp.	[0]: absence, [1]: presence
Degr	Percentage degradation of a basidiocarp.	[1]: <1, [2]: 1–24, [3]: 25–50, [4]: >50
E. cor	Presence vs. absence of <i>Ennearthron cornutum</i> . Presence was defined as at least one adult beetle being present in a basidiocarp.	[0]: absence, [1]: presence
Hag	The height above ground describes whether a basidiocarp was situated at or above the ground level.	[1]: at the ground level, [2]: above the ground level
Mois	The moisture of a basidiocarp measured by dividing the weight on collection day by the weight after drying for 4 months at 20°C.	[1]: <1.50 (Dry), [2]: 1.50–2.50 (Medium dry), [3]: >2.50 (Moist)
Vol	The volume of a basidiocarp in cm ³ estimated by 1/4 volume of an ellipsoid $((4/3) \times \pi \times r_1 \times r_2 \times r_3)$.	[1]: <75, [2]: 75–200, [3]: >200

bidentatus. A contingency table analysis showed that *C. lineatocribratus* was present in 19% (28/150) of the basidiocarps that lacked *C. bidentatus* and in none (0/17) where *C. bidentatus* was present (Contingency table analysis: Pearson- $\chi^2 = 3.81$, $p = 0.05$).

The percentage degradation of the basidiocarp (Degr) was not included in the multiple logistic regression models because this characteristic is probably too much modified by the presence of the beetles themselves. In the univariate analyses (Table 5 and Fig. 3) Degr was related to the presence of *C. jacquemarti/alter*, *E. cornutum* and *D. dresdensis*. *E. cornutum* was more likely to be present in basidiocarps of intermediate (25–50%) degradation than in more or less degraded ones (Degr[3] vs. Degr[4] was almost significantly different, $p = 0.09$). Incidence of *C. jacquemarti/alter* was lower in the least degraded basidiocarps compared to other grades. Additionally, no *D. dresdensis* (0/22) was present in the least degraded basidiocarps, while the rest of the basidiocarps roughly had the same presence (Contingency table analysis: Pearson- $\chi^2 = 6.19$, $p = 0.10$).

Some predictor variables had univariate significant affect on the presence of some study species (Table 5) without entering the multiple regression model of the respective species (Table 4). This was probably because these variables were confounded with others, which entered the models. Notably, for all species moisture content of the basidiocarps decreased with height above ground (Table 6).

DISCUSSION

This study revealed that microhabitat variables differently affected the presence of beetle species in basidiocarps of *F. fomentarius*. An earlier study, in the same area (Rukke, 2000), showed that habitat variables at higher

spatial scales also differently influenced the incidence of the beetle species, while the responses to the landscape variables “increased habitat isolation” and “decreased habitat size” were more uniform and reduced beetle presence on basidiocarp trees. Together the results from these studies at different scales better explain the beetles’ spatial distribution than would a single-scale perspective, and argues for a multi-scale approach when studying ecological systems.

Volume of basidiocarps

This study revealed that basidiocarp size is an important habitat variable for several dead wood fungivores. Incidence of *C. jacquemarti/alter* and *D. dresdensis* was higher in large than in small basidiocarps. In another study Jonsell et al. (1999) found similar results for several beetles, including *C. jacquemarti*, *C. alter* and *D. dresdensis*, and the same trend was also reported for *B. reticulatus* (Midtgaard et al., 1998). There may be several reasons why the number of fungivorous beetles is higher in large compared to small basidiocarps. If large basidiocarps have stronger visual and/or olfactory cues, they may be more easily located by beetles searching for a habitat. Regarding olfactory cues, Jonsell and Nordlander (1995) observed that beetles of the family Ciidae breeding in basidiocarps of *Fomitopsis pinicola* were strongly attracted to the odour of this fungus. However, in the same study species of the similar ciid guild associated with *F. fomentarius* were not attracted to the fungal odours of *F. fomentarius*. Another explanation relates the increased presence of beetles in large basidiocarps to the prolonged period of possible colonisation and inhabitancy. Compared to small basidiocarps larger ones probably last longer before they are totally degraded, and once colonised there is also more food available for consumption. Finally, size can be important because micro-

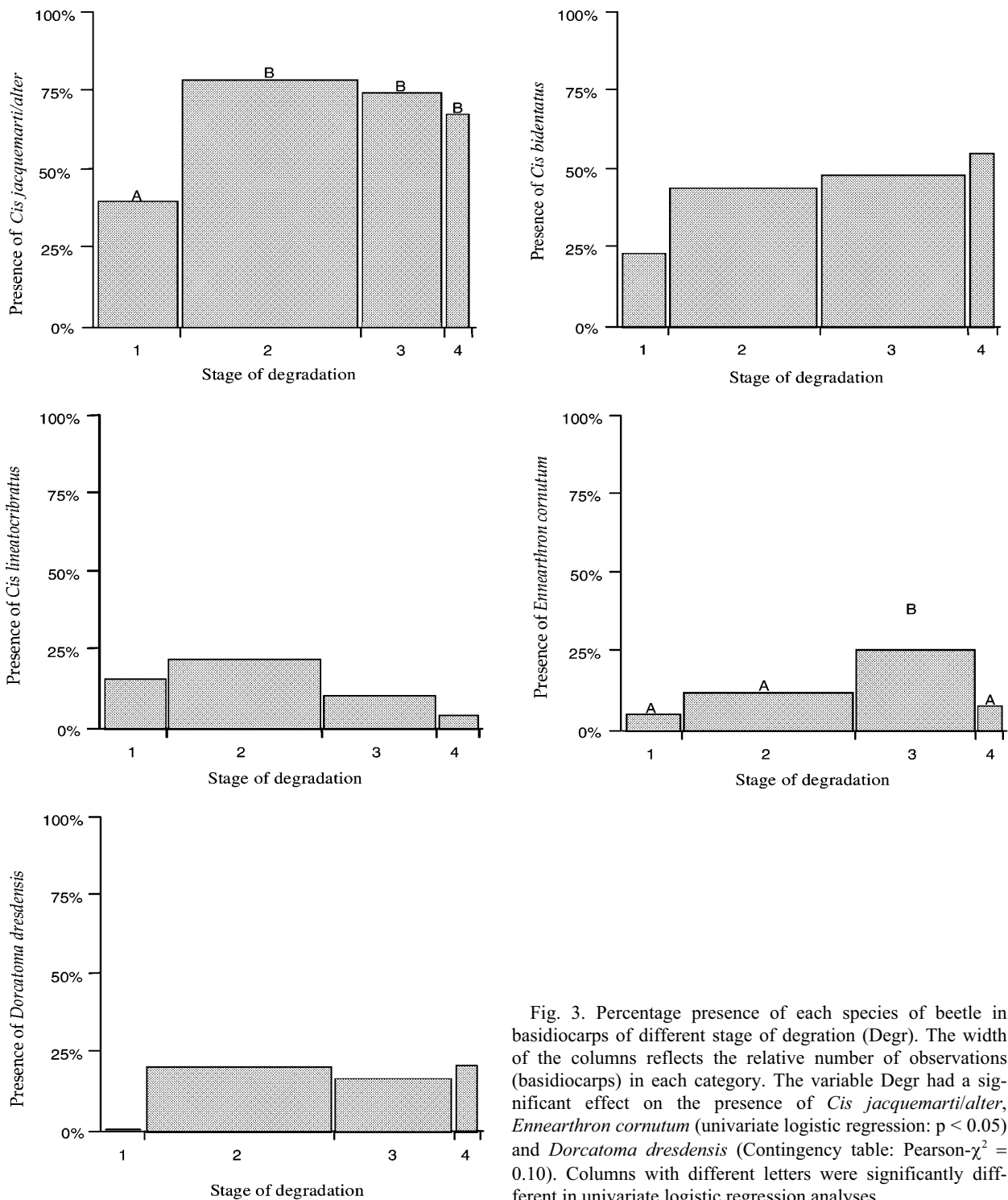


Fig. 3. Percentage presence of each species of beetle in basidiocarps of different stage of degradation (Degr). The width of the columns reflects the relative number of observations (basidiocarps) in each category. The variable Degr had a significant effect on the presence of *Cis jacquemarti/alter*, *Ennearthron cornutum* (univariate logistic regression: $p < 0.05$) and *Dorcatoma dresdensis* (Contingency table: Pearson- $\chi^2 = 0.10$). Columns with different letters were significantly different in univariate logistic regression analyses.

climatic conditions may be more stable in larger basidiocarps. In them changes in moisture and temperature are most likely dampened compared to small basidiocarps.

C. jacquemarti/alter, *C. bidentatus*, *C. lineatocribratus* and *D. dresdensis*, were more numerous in large basidiocarps. The number of *B. reticulatus* also increases with basidiocarp size (Midtgaard et al., 1998). If individuals from all basidiocarps on a tree constitute a local population of a beetle species (Rukke, 2000), large basidiocarps with their higher number of individuals more substan-

tially contribute to reduce the risk of local population extinction than small basidiocarps. This is because increasing population size generally decreases the risk of stochastic extinction (Williamson, 1981; Diamond, 1984; Soulé, 1986).

There was a variation between species in abundance and density in the basidiocarps. *C. jacquemarti/alter* had both a higher incidence and density than the other beetles. A dominant position of *C. jacquemarti* and *C. alter* regarding incidence and density among fungivorous bee-

TABLE 3. Abundance and density of beetles in the basidiocarps. Included is the total number of specimens sampled (No. spec.), number of basidiocarps with presence (No. bas.), percentage of basidiocarps with presence (Perc.) and density measured as average number of specimens per unit volume (cm³) in inhabited basidiocarps (No./vol.) and average number of specimens per unit weight (g) in inhabited basidiocarps (No./wei.) for each species.

Species	No. spec.	No. bas.	Perc.	No./vol.	No./wei.
<i>Cis jacquemarti/alter</i>	6783	386	66 %	0.065	0.252
<i>Cis bidentatus</i>	168	46	8 %	0.013	0.045
<i>Cis lineatocribratus</i>	110	32	5 %	0.011	0.041
<i>Ennearthron cornutum</i>	122	55	9 %	0.011	0.022
<i>Dorcatoma dresdensis</i>	181	40	7 %	0.012	0.041

bles in basidiocarps of *F. fomentarius*, has also been reported earlier (Fossli & Andersen, 1998; Jonsell, 1999).

Height above ground

Position of basidiocarps, at or above ground level, differently affected the presence of *C. jacquemarti/alter* and *E. cornutum* and *D. dresdensis*. This probably reflects that basidiocarps at the ground level are a different kind of habitat from those higher above ground. The former have a higher moisture content (Table 6), and they are probably less exposed to temperature extremes, than basidiocarps above ground level as they are less exposed to sun and may be covered by snow during winter. The incidence of *C. jacquemarti/alter* was highest in basidiocarps at ground level. Other studies confirm both *C. jacquemarti*'s and *C. alter*'s preference for ground level basidiocarps (Fossli & Andersen, 1998; Jonsell et al., 1999). In the present study this preference cannot be attributed to moisture component of this variable since *C. jacquemarti/alter* did not show preference for basidiocarps of any moisture level (Table 5).

In contrast to *C. jacquemarti/alter*, *E. cornutum* and *D. dresdensis* were more frequently found in basidiocarps above ground level. Here the moisture content probably influenced the beetles' presence because the moister basidiocarps had reduced presence of both species (Table 5). Additionally, due to less vegetation and absence of snow cover the basidiocarps above ground level probably were more exposed to sun which increased larval development speed. This would promote survival as the period of exposure to predators and parasites/parasitoids is reduced. Accordingly, Fossli & Andersen (1998) only found *E. cornutum* in basidiocarps in warm microclimates (exposed and southwest facing slopes with dry ground).

Contrary to other studies (Fossli & Andersen, 1998; Jonsell & et al., 1999), *C. lineatocribratus* apparently did not show a significant preference for basidiocarps at ground level. However, this apparent lack of preference probably can be attributed to a low number of above

TABLE 4. Multiple logistic regression models explaining presence/absence of each species of beetle in the basidiocarps. Included is the order (Step) in which the variables (Var) entered into the model. Likelihood ratio test-value (G) and level of significance of a chi square-table (p-value) for each step and the odds ratio (O.R.) and 95 % – confidence interval (95 %-CI) of each variable's categories are also presented. For a given category (x) the odds ratio is given as: odds (x) / odds (x-1).

Species	Step	Var	G	p-value	O.R.	95%-CI
<i>Cis jacquemarti/alter</i> (n = 463)	1	Vol[2]	21.99	< 0.001	1.79	1.11–2.89
		Vol[3]			1.89	1.10–3.22
<i>Cis bidentatus</i> (n = 92)	2	Hag[2]	10.12	0.001	0.43	0.25–0.72
	1	C. jac[1]	4.18	0.041	3.11	1.16–8.37
<i>Cis lineatocribratus</i> (n = 167)	2	Mois[2]	7.56	0.023	0.35	0.13–0.92
		Mois[3]			0.47	0.09–2.59
<i>Ennearthron cornutum</i> (n = 312)	1	Mois[2]	8.56	0.013	2.51	0.65–9.70
		Mois[3]			2.19	0.89–5.35
<i>Dorcatoma dresdensis</i> (n = 199)	1	Hag[2]	35.49	< 0.001	6.45	3.34–12.45
	2	D. dre[1]	5.50	0.019	3.11	1.24–7.83
<i>Dorcatoma dresdensis</i> (n = 199)	1	Hag[2]	15.09	< 0.001	6.69	2.38–15.79
	2	Vol[2]	8.50	0.014	3.58	1.19–10.75
		Vol[3]			1.64	0.66–4.05
	3	B. ret[1]	6.88	0.009	0.28	0.10–0.78

ground basidiocarps (only twelve of the 167 basidiocarps) giving low statistical power to reveal this particular trend.

Moisture of basidiocarps

The incidence of *B. reticulatus* is reduced in moist compared to dry basidiocarps (Midtgaard et al., 1998). In the present study, *C. bidentatus* had a similar response, whereas *C. lineatocribratus* preferred moister basidiocarps. As mentioned above, *E. cornutum* and *D. dresdensis* preferred drier basidiocarps, but this tendency disappeared in the multiple model due to this variable's correlation with height above ground. Some beetle species may prefer dry basidiocarps due to better winter survival in them than in moister basidiocarps. *B. reticulatus* is freeze-tolerant and freeze-avoidant in dry and moist basidiocarps respectively, and survival is poorer in inoculated frozen than extensively super-cooled specimens (Gehrken et al., 1991). Additionally, when the moisture content in their environment increases, many insects have a reduced tolerance of high temperatures (Harmon et al., 1986). This may promote preference for dry basidiocarps. Another factor possibly contributing to this preference could be an oxygen deficit in soaked basidiocarps, which delimits the biological activity to only the outer parts. The advantages of occupying dry basidiocarps must be outweighed by other factors facilitating *C. lineatocribratus* presence in moister basidiocarps. Since most dead wood fungivores favour dry and somewhat sun-exposed conditions (Jonsell, 1999), one advantage may be reduced

TABLE 5. Univariate logistic regression models explaining presence / absence of each species of beetle in basidiocarps. Included are the predictor variables' total significance-level (p-value) and each category's percentage of trees with presence (Perc.), odds ratio (O.R.) and 95%-confidence interval (95% -CI). For a given category (x) the odds ratio is given as: odds (x) / odds (x-1).

<i>Cis jacquemarti/alter</i> (n = 463)					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
B. ret	0.292	[0]	69		
		[1]	74	1.30	0.80–2.12
C. bid	0.171	[0]	69		
		[1]	79	1.71	0.77–3.82
C. lin	0.168	[0]	69		
		[1]	81	1.93	0.72–5.21
D. dre	0.109	[0]	69		
		[1]	82	2.12	0.79–5.68
Degr	<0.001	[1]	42		
		[2]	81	5.74	3.44–9.57
		[3]	77	0.80	0.45–1.40
		[4]	70	0.70	0.30–1.67
E. cor	0.505	[0]	70		
		[1]	75	1.30	0.59–2.84
Hag	0.001	[1]	73		
		[2]	54	0.43	0.26–0.71
Mois	0.573	[1]	64		
		[2]	70	1.20	0.71–2.00
		[3]	72	1.30	0.71–1.79
Vol	<0.001	[1]	57		
		[2]	71	1.86	1.16–2.98
		[3]	82	1.82	1.07–3.08
<i>Cis bidentatus</i> (n = 92)					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
B. ret	0.467	[0]	47		
		[1]	39	0.70	0.27–1.83
C. jac	0.041	[0]	31		
		[1]	53	2.51	1.13–5.60
D. dre	0.350	[0]	43		
		[1]	56	1.68	0.56–4.97
Degr	0.419	[1]	25		
		[2]	46	2.55	0.60–10.96
		[3]	50	1.18	0.47–2.95
		[4]	57	1.33	0.26–6.83
E. cor	0.931	[0]	45		
		[1]	46	1.05	0.35–3.18
Hag	0.613	[1]	43		
		[2]	49	1.24	0.54–2.84
Mois	0.043	[1]	59		
		[2]	40	0.45	0.19–1.10
		[3]	20	0.38	0.07–1.97
Vol	0.338	[1]	40		
		[2]	58	2.02	0.79–5.17
		[3]	44	0.59	0.13–2.70
<i>Cis lineatocribratus</i> (n = 167)					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
B. ret	0.128	[0]	19		
		[1]	11	0.47	0.17–1.32
C. jac	0.614	[0]	14		
		[1]	18	1.28	0.48–3.41
D. dre	0.544	[0]	16		
		[1]	25	1.71	0.33–8.92

TABLE 5 (continued).

<i>Cis lineatocribratus</i> (n = 167)					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
Degr	0.175	[1]	17		
		[2]	23	1.44	0.48–4.41
		[3]	12	0.44	0.16–1.22
		[4]	6	0.44	0.05–3.94
E. cor	0.783	[0]	17		
		[1]	20	1.26	0.25–6.27
Hag	0.380	[1]	17		
		[2]	8	0.43	0.05–3.48
Mois	0.014	[1]	7		
		[2]	15	2.51	0.65–9.70
		[3]	28	2.19	0.89–5.38
Vol	0.506	[1]	14		
		[2]	18	1.33	0.51–3.46
		[3]	24	1.42	0.43–4.70
<i>Ennearthron cornutum</i> (n = 312)					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
B. ret	0.627	[0]	16		
		[1]	18	1.17	0.62–2.22
		[2]	16	1.18	0.49–2.85
C. bid	0.517	[0]	16		
		[1]	18	1.18	0.49–2.85
C. lin	0.716	[0]	17		
		[1]	11	0.63	0.14–2.81
C. jac	0.445	[0]	19		
		[1]	15	0.78	0.41–1.48
D. dre	0.001	[0]	14		
		[1]	41	4.21	1.82–9.73
Degr	0.004	[1]	6		
		[2]	13	2.25	0.63–7.97
		[3]	27	2.41	1.25–4.64
		[4]	9	0.27	0.06–1.24
Hag	<0.001	[1]	9		
		[2]	41	6.86	3.59–13.11
Mois	<0.001	[1]	35		
		[2]	11	0.24	0.12–0.48
		[3]	10	0.81	0.34–1.90
Vol	0.491	[1]	15		
		[2]	20	1.41	0.72–2.75
		[3]	14	0.62	0.25–1.53
<i>Dorcatoma dresdensis</i> (n = 199)					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
B. ret	0.093	[0]	22		
		[1]	12	0.49	0.20–1.18
C. bid	0.085	[0]	17		
		[1]	31	2.23	0.92–21.56
C. lin	0.842	[0]	19		
		[1]	17	0.85	0.18–4.06
C. jac	0.888	[0]	18		
		[1]	19	1.06	0.48–2.35
E. cor	<0.001	[0]	15		
		[1]	58	7.94	2.93–21.56
Hag	<0.001	[1]	12		
		[2]	39	4.47	2.11–9.45
Mois	0.012	[1]	32		
		[2]	18	0.47	0.21–1.05
		[3]	9	0.44	0.15–1.26
Vol	0.056	[1]	11		
		[2]	20	1.99	0.76–5.24
		[3]	26	1.47	0.64–3.37

TABLE 6. Spearman rank correlation between pairs of variables for each species of beetle. Only correlations with Spearman Rho < -0.30 and > 0.30 are included in the table (n = 463, 92, 167, 312 and 199)

Species	Variable against	Variable	Spearman Rho	p-value
<i>Cis jacquemarti/alter</i>	Mois	Hag	-0.395	< 0.001
<i>Cis bidentatus</i>	Mois	Hag	-0.300	0.005
<i>Cis bidentatus</i>	Vol	C. jac	0.360	< 0.001
<i>Cis bidentatus</i>	Vol	B. ret	0.407	< 0.001
<i>Cis lineatocribratus</i>	Mois	Hag	-0.367	< 0.001
<i>Ennearthron cornutum</i>	Mois	Hag	-0.416	< 0.001
<i>Ennearthron cornutum</i>	Hag	C. jac	-0.320	< 0.001
<i>Dorcatoma dresdensis</i>	Mois	Hag	-0.485	< 0.001
<i>Dorcatoma dresdensis</i>	Hag	C. jac	-0.318	< 0.001
<i>Dorcatoma dresdensis</i>	Hag	E. cor	0.355	< 0.001

interspecific competition in moist basidiocarps. It is also possible that *C. lineatocribratus* may be less resistant to desiccation forcing them to live in more moist basidiocarps.

Interspecific interactions

Presence of *C. bidentatus* in basidiocarps was positively associated with the presence of *C. jacquemarti/alter*, and that of *E. cornutum* with *D. dresdensis*. In contrast, *D. dresdensis* was negatively associated with the presence of *B. reticulatus*, and *C. lineatocribratus* with *C. bidentatus*. Through their tunnelling, major fungivorous beetles can provide easier access to the interior of *F. fomentarius* basidiocarps for other species (Matthewman & Pielou, 1971). Thus, presence of the numerous *C. jacquemarti/alter* and *D. dresdensis* may improve habitat conditions for *C. bidentatus* and *E. cornutum*. In addition, resource competition is common between fungivorous insects (Hanski, 1989), and important competitors in dead wood fungi in North America are Tenebrionidae (like *B. reticulatus*) and Anobiidae (like *D. dresdensis*) (Lawrence, 1973). Therefore, *B. reticulatus* may be a superior competitor to the smaller *D. dresdensis*.

Degradation of basidiocarps

The successional stage of a basidiocarp is an important factor determining the presence of beetles inhabiting basidiocarps of dead wood fungi (Midtgaard et al., 1998; Jonsell et al., 1999). In this study percentage degradation, which indicates the amount of resources removed from the basidiocarps, was used as a measure of successional stage. One problem in assessing the importance of this variable was that some of the degradation categories had low numbers of observation (Fig. 3). This reduces the likelihood of discovering real effects of successional degradation. Trends were, however, noticeable for *C. jacquemarti/alter*, *E. cornutum* and *D. dresdensis*. Since *C. jacquemarti/alter* and *D. dresdensis* probably substantially contribute to the degradation process, it is not surprising that they are less frequently present in minimally degraded (< 1%) than in highly degraded basidiocarps.

The peak of presence of *E. cornutum* occurs somewhat later in the succession than the other two species, and it may need other species to modify the microhabitat conditions inside the basidiocarps before it can utilise this resource. Jonsell et al. (1999) using another measurement of basidiocarp succession, showed that *E. cornutum* entered dead basidiocarps rather late in the succession. Observing that only *E. cornutum* had a distinct drop in incidence among the most degraded basidiocarps may be a result of this last category being too wide ranging (50–100% degradation) and coarse to indicate lack of resources for most species.

CONCLUSION

The present study shows how beetle species inhabiting *F. fomentarius* basidiocarps differ in their microhabitat requirements. This indicates that basidiocarps of just one species, *F. fomentarius*, are a heterogeneous resource varying at a local scale. Earlier, the importance of large-scale variables for the presence of the same species on basidiocarp trees has been documented (Rukke, 2000). Together these results have important implications for the conservation of these beetles. There is a need to consider both the landscape ecological and microhabitat aspects in order to better assess and counteract the consequences of human activities. A conservation strategy of leaving behind sufficient amount of this heterogeneous resource within a certain degree of isolation is needed to preserve these and possibly other species of beetles inhabiting basidiocarps of dead wood fungi. In other words, providing plentiful dead wood and their associated basidiocarps in forests is essential because only this will ensure a proper supply of basidiocarps of different quality within the dispersal range of these beetles.

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