

Effects of habitat fragmentation: increased isolation and reduced habitat size reduces the incidence of dead wood fungi beetles in a fragmented forest landscape

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Negative effects of habitat fragmentation (increased isolation and reduced habitat size) affected presence of several beetle species inhabiting *Fomes fomentarius* (L.) Kickx basidiocarps in a fragmented forest landscape. At the scale of individual trees (tree level), incidence of *Cis jacquemarti* Mell./*C. nitidus* (F.) (not distinguished between individuals of these two species, abbreviated *C. jacquemarti/nitidus*), *C. bidentatus* (Ol.), *C. lineatocribratus* Mell., *Ennearthron cornutum* (Gyll.) (all Coleoptera, Cisidae) and *Dorcatoma dresdensis* Herbst (Coleoptera, Anobiidae) was reduced with increased habitat isolation and reduced habitat size. Additionally, increased habitat size at a larger scale (forest island level) also gave higher incidence of all species.

Some of the microhabitat variables measured influenced upon the presence of the study species. Fallen trees had a higher probability of *C. jacquemarti/nitidus* presence than standing trees, whilst the opposite was the case for *C. bidentatus*. There was also increased incidence of *C. bidentatus* on trees in denser forests and of *E. cornutum* in grey alder *Alnus incana* compared with birch trees (*Betula* spp.).

Increased volume of basidiocarps on a tree resulted in a higher number of individuals of *C. jacquemarti/nitidus* and *C. lineatocribratus*.

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Destruction of habitat around the world (Morris 1995) often leaves the remainder severely fragmented creating landscapes with smaller, more isolated habitats (Meffe and Carroll 1997). This process of habitat fragmentation is believed to create problems for the existence of the organisms living there in two ways: 1) by limiting their dispersal abilities due to higher degree of isolation, the colonization probability of habitats is reduced (Hanski and Gilpin 1997), and 2) by reducing the population size as the habitats get smaller, the extinction probability among populations is increased (Williamson 1981, Diamond 1984, Schoener and Spiller 1995, Lande 1998). Negative effects of increased isolation and reduced habitat size have been documented for a wide range of animal groups: insects (e.g. Kindvall

and Ahlén 1992, Thomas et al. 1992, Hanski et al. 1994, van Dongen et al. 1994), spiders (Schoener and Spiller 1995), birds (e.g. van Dorp and Opdam 1987, Opdam 1991, Dunning et al. 1995), small mammals (e.g. Verboom and van Apeldoorn 1990, Peltonen and Hanski 1991, Hanski 1993) and large mammals (Newmark 1995). As the human habitat destruction commences globally, such documentation is of increasing importance to implement countermeasures against species extinction.

Insects associated with dead wood fungi are an animal group vulnerable to habitat fragmentation. Forestry practices where only small dimensional remnants are left behind in large clear-cuts, have reduced the amount of dead wood (Haila et al. 1994, Esseen et

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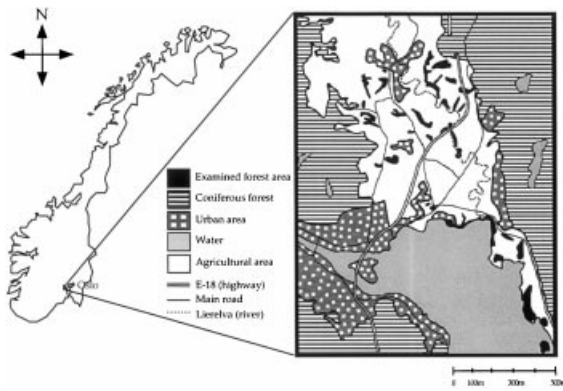


Fig. 1. Map over the study area.

al. 1997) and their associated basidiocarps (Bredesen et al. 1994, Bader et al. 1995) and increased the isolation between such habitats. Previous studies concerning *Bolitophagus reticulatus* (L.) (Coleoptera, Tenebrionidae), a monophagous beetle on tinder fungus (*Fomes fomentarius*), have indicated reduced incidence of the

species as a result of habitat fragmentation through incidence (Rukke and Midtgaard 1998, Sverdrup-Thygeson and Midtgaard 1998) and mark-recapture studies (Nilsson 1997). A genetic survey of *B. reticulatus* (Knutsen et al. in press) concluded that habitat fragmentation impedes dispersal of this species.

Studies including other species are required to further strengthen the empirical knowledge of consequences of habitat fragmentation for insects associated with dead wood fungi. The present study investigates effects of habitat fragmentation (increased isolation and reduced habitat size) on the incidence of several other beetle species inhabiting *F. fomentarius* basidiocarps in the same fragmented forest landscape as Rukke and Midtgaard (1998) and Knutsen et al. (in press) did their incidence and genetic study of *B. reticulatus*. The study is performed at two spatial scales, tree- and forest island level, to reduce the chance of making interpretational errors (e.g. Milne 1991) because different patterns may emerge at different scales (Wiens 1989, Roland and Taylor 1997). Additionally, effects of microhabitat variables on the presence of the study species are investigated.

Table 1. Description of the predictor variables (Var.) at the two scales and the values of their categories (Value).

Var.	Description	Value
Ang	Ground inclination where the tree was situated (degrees).	[1]: < 15, [2]: 15–25, [3]: > 25
Cc/cv	The terrain shape where the tree was situated.	[1]: Concave, [2]: Flat/convex
Dia	Diameter of the tree trunk 1.3 meters above the ground level (cm).	[1]: < 12, [2]: 12–20, [3]: > 20
Exp	Exposition of the slope where the tree was situated.	[1]: No slope, [2]: W and N-W, [3]: Other directions
Hei	Forest height in the tree's closest surroundings (m).	[1]: < 15, [2]: ≥ 15
IsoB	Distance to the nearest tree with presence of <i>Cis bidentatus</i> (m).	[1]: < 25, [2]: 25–500, [3]: > 500
IsoD	Distance to the nearest tree with presence of <i>Dorcatoma dresdensis</i> (m).	[1]: < 75, [2]: 75–600, [3]: > 600
IsoE	Distance to the nearest tree with presence of <i>Enneathron cornutum</i> (m).	[1]: < 50, [2]: 50–450, [3]: > 450
IsoJ	Distance to the nearest tree with presence of <i>Cis jacquemarti/nitidus</i> (m).	[1]: < 7, [2]: 7–40, [3]: > 40
IsoL	Distance to the nearest tree with presence of <i>Cis lineatocribratus</i> (m).	[1]: < 15, [2]: 15–200, [3]: > 200
Lig	Light condition as crown cover percentage around the tree.	[1]: < 40, [2]: 40–60, [3]: > 60
Num	Number of basidiocarps on the tree.	[1]: < 4, [2]: ≥ 4
Pos	Position of the tree.	[1]: Standing, [2]: Fallen
Rel	Basal area around the tree measured by relascope according to Fitje (1989) (m ² ha ⁻¹).	[1]: < 15, [2]: 15–25, [3]: > 25
Typ	The type of wood the basidiocarp(s) grew upon.	[1]: Birch (<i>Betula</i> spp.), [2]: Grey alder (<i>Alnus incana</i>)
Veg	Type of vegetation in the tree's closest surroundings according to Fremstad and Elven (1987): A2: pine forest with lichens and heather, C3: strongly man-influenced broad-leaved forest, E0: shrub communities, E2: grey alder- ash forest, E3: grey alder-bird cherry forest and E4: broad-leaved forest, strongly influenced by man.	[1]: A2, [2]: C3 and E4, [3]: E0, E2 and E3
VolT	Total volume of dead basidiocarps on the tree (cm ³).	[1]: < 200, [2]: 200–700, [3]: > 700
Area	Area of the forest island (m ²).	[1]: < 8000, [2]: 8000–20 000, [3]: > 20 000
DistC	Shortest distance to continuous forest around the study area (m).	[1]: < 1000, [2]: ≥ 1000
DistF	Distance to nearest forest island (m).	[1]: 120, [2]: ≥ 120
NumF	Number of trees with basidiocarps per forest island.	[1]: 1, [2]: 2–5, [3]: > 6
Sha	Shape index of the forest island: $\frac{\text{forest} - \text{island} - \text{perimeter}}{2\sqrt{\pi \cdot \text{Area}}}$	[1]: < 1.89, [2]: 1.89–2.40, [3]: > 2.40
VolF	Total volume of dead basidiocarps on the forest island (cm ³).	[1]: < 200, [2]: 200–2000, [3]: > 2000

Table 2. Description of the categorised predictor variables at a continuous scale (n = 185 trees and 42 forest islands).

Variable	Minimum	25%-quartile	Median	75%-quartile	Maximum
Ang	0°	10°	20°	30°	50°
Dia	4 cm	11 cm	16 cm	23 cm	51 cm
Hei	4 m	10 m	13 m	16 m	20m
IsoB	1 m	32 m	274 m	851 m	2686 m
IsoD	1 m	23 m	173 m	573 m	1080 m
IsoE	1 m	13 m	66 m	444 m	1710 m
IsoJ	1 m	4 m	15 m	51 m	1420 m
IsoL	1 m	37 m	165 m	574 m	1727 m
Lig	15%	40%	50%	56%	100%
Num	1	1	2	3	19
Rel	5 m ² ha ⁻¹	16 m ² ha ⁻¹	20 m ² ha ⁻¹	27 m ² ha ⁻¹	47 m ² ha ⁻¹
VolT	2 cm ³	90 cm ³	224 cm ³	729 cm ³	16 575 cm ³
Area	729 m ²	4467 m ²	8640 m ²	21 675 m ²	63 386 m ²
DistC	20 m	358 m	733 m	1345 m	2000 m
DistF	10 m	39 m	105 m	219 m	650 m
NumF	1	1	2	6	20
Sha	1.24	1.83	2.08	2.57	4.34
VolF	13 cm ³	92 cm ³	498 cm ³	2177 cm ³	38 292 cm ³

Material and methods

The study area consisted of 58 forest patches ("forest islands") in an agricultural area (1585 ha) in Lier municipality, 30 km southwest of Oslo, Norway (59°48'N, 10°16'E) (Fig. 1). The size of the forest islands varied from 729 to 63 386 m². Comparing small scale maps and aerial views with what was observed during sampling in spring 1993, it became clear that the area of the forest islands had not been essentially reduced in size over the last decade. All dead *F. fomentarius* basidiocarps (according to Matthewman and Pielou 1971) (n = 587) in the study area from 185 trees (125 birches (*Betula* spp.) and 60 grey alder *Alnus incana*) on 42 forest islands were collected and dissected to reveal their contents of beetles. Earlier the presence of *B. reticulatus* on these trees has been investigated in the multi-scale study of Rukke and Midtgaard (1998). Boreal deciduous trees dominated the tree species on the forest islands, and *F. fomentarius* was by far the most common dead wood fungus in the study area (unpubl.).

The study was performed at two spatial scales. At the smallest scale, the tree level, a tree having at least one basidiocarp of *F. fomentarius* (a basidiocarp tree) constituted a study unit, whilst at the larger scale, the forest island level, each forest patch with at least one basidiocarp tree represented a study unit.

All adults of the beetle species in the basidiocarps were recorded, but only some species had sufficient incidence for presence/absence analyses: *Cis jacquemarti* Mell./*C. nitidus* (F.), *C. bidentatus* (Ol.), *C. lineatocribratus* Mell., *Ennearthron cornutum* (Gyll.) (all Coleoptera, Cisiidae) and *Dorcatoma dresdensis* Herbst (Coleoptera, Anobiidae). During classification of the beetles it was difficult (because individuals were desiccated) to classify individuals as *C. glabratus* (F.), *C. jacquemarti* or *C. nitidus* (Ligaard pers. comm.). Since

C. glabratus is rarely found in *F. fomentarius* (e.g. Økland 1995, Fossli and Andersen 1998, Jonsell 1999), all these individuals were treated as an assemblage of the two species *C. jacquemarti* and *C. nitidus* which is abbreviated *C. jacquemarti/nitidus*.

All study species are found in central Europe (Lucht 1987) and Scandinavia (Lindroth 1960, Vik 1991). They inhabit one or several species of dead wood fungi (Paviour-Smith 1960, Thunes 1994, Kaila et al. 1994, Økland 1995, Fossli and Andersen 1998, Jonsell 1999), but *F. fomentarius* probably is the most important host fungus in the study area due to its dominance among dead wood fungi there. Little is known about the generation time of the beetles, but it probably does not take them more than two years to complete their life cycle. Therefore, a large dead *F. fomentarius* basidiocarp may support several generations of the beetles studied as it can persist many years before disintegrating totally. Additionally, the basidiocarps on a tree usually do not die simultaneously sometimes making a basidiocarp tree a suitable habitat patch for more than a decade.

Table 3. Abundance of the study species. Included are total number of specimens sampled (No. spec.), number of basidiocarp trees with presence (No. trees) and number of forest islands with presence (No. forest islands) (n = 185 trees and 42 forest islands).

Species	No. spec.	No. trees	No. forest islands
<i>Cis jacquemarti/nitidus</i>	6783	130	29
<i>Cis bidentatus</i>	168	16	10
<i>Cis lineatocribratus</i>	110	22	13
<i>Ennearthron cornutum</i>	122	41	14
<i>Dorcatoma dresdensis</i>	181	24	10

Table 4a-e. Results of univariate logistic regression where the response variable was presence/absence of each of the study species on each tree. 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) (n = 185). For a given category (x) the odds ratio is given as: odds (x)/odds (x-1).

a) <i>Cis jacquemarti nitidus</i>				b) <i>Cis bidentatus</i>				c) <i>Cis lineatocribratus</i>									
Var.	p-value	Cat.	Perc.	O.R.	95%-CI	Var.	p-value	Cat.	Perc.	O.R.	95%-CI	Var.	p-value	Cat.	Perc.	O.R.	95%-CI
Ang	0.555	[1]	67	1.50	0.69-3.27	Ang	0.375	[1]	5	2.42	0.67-8.70	Ang	0.851	[1]	14	0.74	0.25-2.18
		[2]	75	0.88	0.37-2.08			[2]	12	0.76	0.23-2.56			[2]	11	1.11	0.33-3.68
		[3]	73	1.03	0.74-1.44			[3]	10	0.75	0.44-1.25			[3]	12	1.00	0.65-1.63
Cc/cv	0.846	[1]	70	2.53	1.15-5.58	Cc/cv	0.281	[1]	7	1.65	0.35-7.70	Cc/cv	0.918	[1]	12	3.87	1.16-12.96
		[2]	72	1.58	0.63-3.96			[2]	5	2.21	0.64-7.62			[2]	12	0.52	0.19-1.45
		[3]	84	1.27	0.75-2.16			[3]	15	0.85	0.26-2.76			[3]	11	1.80	0.74-4.42
Dia	0.002	[1]	56	1.48	0.95-2.30	Dia	0.121	[1]	3	2.47	1.00-6.08	Dia	0.064	[1]	6	1.84	0.82-4.14
		[2]	76	1.81	0.92-3.59			[2]	11	1.52	0.54-4.24			[2]	20	2.34	0.95-5.81
		[3]	84	0.74	0.32-1.74			[3]	14	0.86	0.27-2.78			[3]	11	0.22	0.06-0.73
Exp	0.037	[1]	25	0.34	0.16-0.76	Exp	0.083	[1]	4	0.27	0.07-1.10	Exp	0.080	[1]	3	1.50	0.51-4.43
		[2]	73	0.86	0.40-1.84			[2]	6	1.86	0.47-7.36			[2]	14	1.54	0.50-4.71
		[3]	77	1.30	0.58-2.92			[3]	11	1.09	0.33-3.54			[3]	13	0.93	0.32-2.71
Hei	0.081	[1]	67	11.11	2.58-47.89	Hei	0.430	[1]	7	2.17	0.74-6.36	Hei	0.063	[1]	8	3.33	1.32-8.40
		[2]	78	2.47	1.74-3.51			[2]	14	0.67	0.40-1.12			[2]	24	2.35	1.12-4.95
		[3]	82	1.35	0.59-3.13			[3]	7	2.53	0.29-21.80			[3]	16	1.55	0.41-5.92
IsoJ	0.002	[1]	77	0.95	0.45-1.99	IsoB	0.067	[1]	14	2.59	0.87-7.73	IsoL	0.047	[1]	8	1.16	0.44-3.08
		[2]	77	0.80	0.57-1.11			[2]	12	0.81	0.45-1.45			[2]	22	0.86	0.52-1.41
		[3]	52	0.96	0.77-1.91			[3]	4	1.41	0.60-3.32			[3]	10	0.68	0.37-1.25
Lig	0.803	[1]	72	0.80	0.57-1.11	Lig	0.575	[1]	7	1.21	0.48-3.08	Lig	0.733	[1]	9	0.85	0.44-1.64
		[2]	69	0.96	0.77-1.91			[2]	6	0.84	0.20-3.52			[2]	14	2.60	0.78-8.70
		[3]	75	0.86	0.53-1.41			[3]	15	2.74	0.66-11.31			[3]	21	1.66	0.57-4.80
Num	<0.001	[1]	64	2.47	1.74-3.51	Num	0.173	[1]	7	0.84	0.20-3.52	Num	0.013	[1]	9	1.66	0.57-4.80
		[2]	95	1.35	0.59-3.13			[2]	14	0.67	0.40-1.12			[2]	24	2.35	1.12-4.95
		[3]	64	0.95	0.45-1.99			[3]	7	2.53	0.29-21.80			[3]	16	1.55	0.41-5.92
Pos	<0.001	[1]	46	0.80	0.57-1.11	Pos	0.127	[1]	14	0.81	0.45-1.45	Pos	0.006	[1]	3	1.16	0.44-3.08
		[2]	83	0.96	0.77-1.91			[2]	7	1.41	0.60-3.32			[2]	16	0.86	0.52-1.41
		[3]	67	0.86	0.53-1.41			[3]	3	1.21	0.48-3.08			[3]	8	0.68	0.37-1.25
Rel	0.775	[1]	67	0.80	0.57-1.11	Rel	0.063	[1]	3	0.81	0.45-1.45	Rel	0.694	[1]	8	0.85	0.44-1.64
		[2]	73	0.96	0.77-1.91			[2]	7	1.41	0.60-3.32			[2]	12	2.60	0.78-8.70
		[3]	72	0.86	0.53-1.41			[3]	16	2.74	0.66-11.31			[3]	14	1.66	0.57-4.80
Typ	0.182	[1]	75	2.47	1.74-3.51	Typ	0.468	[1]	10	0.84	0.20-3.52	Typ	0.539	[1]	13	1.66	0.57-4.80
		[2]	65	1.35	0.59-3.13			[2]	7	1.41	0.60-3.32			[2]	10	0.86	0.52-1.41
		[3]	70	0.95	0.45-1.99			[3]	4	1.21	0.48-3.08			[3]	22	0.68	0.37-1.25
Veg	0.629	[1]	70	0.80	0.57-1.11	Veg	0.658	[1]	4	1.21	0.48-3.08	Veg	0.339	[1]	10	0.85	0.44-1.64
		[2]	74	0.96	0.77-1.91			[2]	10	0.84	0.20-3.52			[2]	10	2.60	0.78-8.70
		[3]	67	0.86	0.53-1.41			[3]	9	2.74	0.66-11.31			[3]	12	1.66	0.57-4.80
VolT	<0.001	[1]	54	3.86	1.67-8.93	VolT	0.257	[1]	7	0.84	0.20-3.52	VolT	0.030	[1]	6	2.60	0.78-8.70
		[2]	82	2.36	0.67-8.26			[2]	6	1.41	0.60-3.32			[2]	14	1.66	0.57-4.80
		[3]	91	0.86	0.53-1.41			[3]	15	2.74	0.66-11.31			[3]	21	1.66	0.57-4.80

Table 4a-e. (Continued)

d) <i>Ennearthron cornutum</i>				e) <i>Dorcatoma dresdensis</i>							
Var.	p-value	Cat.	Perc.	O.R.	95%-CI	Var.	p-value	Cat.	Perc.	O.R.	95%-CI
Ang	0.840	[1]	21	1.14	0.49-2.65	Ang	0.261	[1]	10	2.25	0.81-6.25
		[2]	23	1.13	0.47-2.72			[2]	19	0.55	0.19-1.60
		[3]	25					[3]	12		
Cc/cv	0.218	[1]	18	1.26	0.87-1.83	Cc/cv	0.018	[1]	6	1.85	1.05-3.23
		[2]	25					[2]	18		
		[3]	31	2.48	0.95-6.44			[3]	15	0.44	0.13-1.49
Dia	0.025	[1]	14	1.32	0.59-2.99	Dia	0.261	[1]	7	2.50	0.74-8.49
		[2]	25					[2]	16		
		[3]	31	1.71	1.00-2.95	Exp	0.502	[1]	8	1.42	0.71-2.85
Exp	0.154	[1]	16	0.87	0.54-1.42			[2]	20	1.12	0.61-2.05
		[2]	33	0.92	0.45-1.87			[3]	17	0.44	0.17-1.17
Hei	0.808	[1]	23	0.75	0.35-1.61	Hei	0.085	[1]	8	0.18	0.06-0.57
		[2]	22	0.14	0.03-0.65			[2]	27	0.35	0.04-3.21
		[3]	31			IsoD	<0.001	[1]	6	0.43	0.16-1.15
IsoE	<0.001	[1]	25	0.45	0.20-1.01			[2]	11	1.09	0.33-3.54
		[2]	33	0.90	0.35-2.32			[3]	11	6.50	2.62-16.12
		[3]	17	2.83	1.33-6.04	Lig	0.196	[1]	7	0.88	0.56-1.37
Lig	0.085	[1]	33	0.72	0.51-1.04			[2]	15	0.86	0.30-2.46
		[2]	19					[3]	17	0.56	0.19-1.67
		[3]	33	1.17	0.48-2.84	Num	<0.001	[1]	5	0.50	0.27-0.94
Num	0.008	[1]	18	0.36	0.14-0.90			[2]	22	1.33	0.71-2.47
		[2]	38	0.53	0.33-0.84			[3]	16	0.38	0.16-0.91
		[3]	31			Pos	0.572	[1]	5	2.60	0.78-8.70
Pos	0.079	[1]	19	0.90	0.56-1.46			[2]	26	2.11	0.75-5.92
		[2]	28	0.56	0.32-1.00			[3]			
		[3]	14			Rel	0.451	[1]			
Rel	0.062	[1]	25	2.37	0.94-5.98			[2]			
		[2]	28	2.15	0.90-5.14			[3]			
		[3]	14			Typ	0.014	[1]			
Typ	0.003	[1]	29					[2]			
		[2]	10					[3]			
		[3]	39			Veg	0.051	[1]			
Veg	0.083	[1]	23					[2]			
		[2]	16					[3]			
		[3]	16			VolT	0.007	[1]			
VolT	<0.001	[1]	12					[2]			
		[2]	24					[3]			
		[3]	40								

Table 5a–e. Multiple logistic regression models at the tree level explaining presence/absence of each of the study species. Included are the order (Step) which the variables (Var.) entered the model, the likelihood ratio test-value (G) and the level of significance from a χ^2 -table for each step (p-value). The odds ratio (O.R.) and 95%-confidence interval (95%-CI) of the categories of each variable are also presented. Enter- and check-back-criteria was $p < 0.05$ and $p > 0.06$ respectively, except for *C. bidentatus* where the criteria was set to 0.10 and 0.11 respectively ($n = 185$). For a given category (x) the odds ratio is given as: odds (x)/odds (x–1).

a) <i>Cis jacquemarti/nitidus</i>					
Step	Var.	G	p	O.R.	95%-CI
1	Pos [2]	27.19	<0.001	2.64	1.73–4.00
2	Num [2]	13.79	<0.001	7.58	1.61–35.61
3	Dia [2]	11.42	0.003	1.90	0.73–4.91
	Dia [3]			2.36	0.80–7.19
4	IsoJ [2]	8.80	0.012	0.58	0.21–1.62
	IsoJ [3]			0.41	0.16–1.05
b) <i>Cis bidentatus</i>					
Step	Var.	G	p	O.R.	90%-CI
1	Rel [2]	5.55	0.062	2.83	0.44–18.26
	Rel [3]			2.60	0.96–7.06
2	IsoB [2]	5.04	0.080	0.77	0.25–2.31
	IsoB [3]			0.20	0.06–0.71
3	Dia [2]	5.60	0.061	2.41	0.62–9.36
	Dia [3]			1.97	0.51–6.07
4	Pos [2]	2.80	0.094	0.61	0.38–0.99
c) <i>Cis lineatocribratus</i>					
Step	Var.	G	p	O.R.	95%-CI
1	Num [2]	6.19	0.013	4.36	1.45–13.13
2	Hei [2] × IsoL [2]	17.50	0.004	6.12	0.35–107.93
	Hei [2] × IsoL [3]			9.78	0.78–108.50
	Hei [2]			0.22	0.02–2.01
	IsoL [2]			0.07	0.01–0.59
	IsoL [3]			0.55	0.09–3.25
d) <i>Ennearthron cornutum</i>					
Step	Var.	G	p	O.R.	95%-CI
1	IsoE [2]	14.73	<0.001	0.86	0.38–1.93
	IsoE [3]			0.15	0.03–0.71
2	Typ [2]	6.48	0.011	1.79	1.10–2.91
3	Dia [2]	6.54	0.038	2.96	1.18–8.19
	Dia [3]			1.01	0.42–2.43
e) <i>Dorcatoma dresdensis</i>					
Step	Var.	G	p	O.R.	95%-CI
1	Num [2]	16.41	<0.001	4.48	1.73–11.71
2	IsoD [2]	12.40	0.002	0.22	0.07–0.72
	IsoD [3]			0.42	0.02–7.65

Univariate and forward, stepwise, multiple logistic regressions (see Hosmer and Lemeshow 1989) were used to reveal effects of landscape and microhabitat variables on presence/absence pattern of the beetles at both scales. The criteria for entering the multiple logistic model was set to $p < 0.05$ (check-back level: $p < 0.06$) for all species except for *C. bidentatus* at the tree level where it was $p < 0.10$ (check-back level: $p < 0.11$). This was done to prevent exclusion of several nearly statistical significant variables of probable biological significance for *C. bidentatus*. All two-way interactions were considered in the multiple logistic regressions. Since logistic regression is not an appropriate analysis method in presence/absence analyses if a predictor variable has one or more categories with 100% presence or

absence, contingency table analyses and Spearman-rank correlations between continuous version of the predictor variables were used when needed. Spearman-rank correlations were also used to reveal correlation between continuous version of the predictor variables at the same scale. Linear regressions were used to investigate the relationship between number of beetle individuals and total volume of basidiocarps per tree. All analyses were performed in the computer program JMP (Anon. 1997). In the presence/absence analyses presence of a study species was defined as at least one adult being present in the study unit (tree or forest island).

Using the eyeball test described in Hosmer and Lemeshow (1989), unlinearities in the data material were detected. Therefore, the continuous predictor vari-

ables were categorised to achieve more robust results from the logistic regression analyses. The predictor variables are described in Table 1, whilst description of the continuous variables before categorisation are shown in Table 2.

Results

Cis jacquemarti/nitidus was by far the most numerous and frequently found of the beetles (Table 3). *Cis bidentatus*, *C. lineatocibratus*, *E. cornutum* and *D. dres-*

Table 6. Spearman-rank correlations between the predictor variables at the tree-level. Correlations < -0.30 and > 0.30 and their level of significance are included in the table (n = 185).

Variable against	Variable	Spearman Rho	p
Num	Pos	0.335	<0.001
Num	VolT	0.637	<0.001
Ang	Exp	0.597	<0.001
Dia	VolT	0.464	<0.001
Hei	Typ	-0.325	<0.001
Hei	Cc/cv	-0.347	<0.001
Hei	Rel	0.460	<0.001
Lig	Cc/cv	-0.335	<0.001
Lig	Rel	0.351	<0.001
IsoJ	Exp	-0.317	<0.001
IsoJ	Hei	0.307	<0.001
IsoD	Exp	-0.376	<0.001
IsoD	VolT	-0.376	<0.001
IsoL	Veg	0.332	<0.001

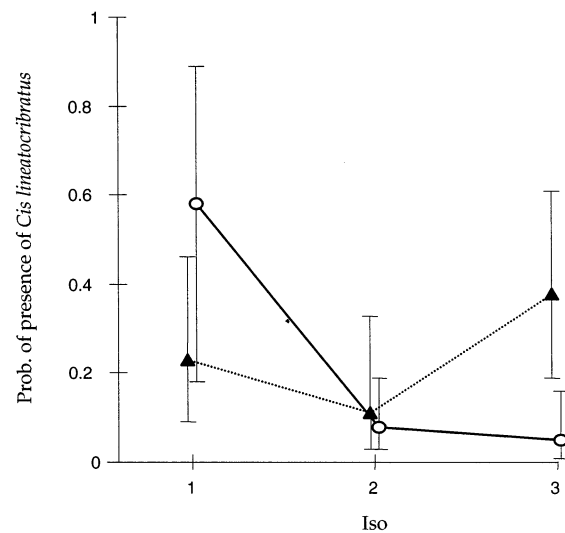


Fig. 2. The interactive effect of isolation and forest height on the probability of presence of *C. lineatocibratus* based on the multiple logistic regression model shown in Table 5c. Open circles represent the estimated probabilities of presence on trees in different categories of isolation (Iso) in the low forest type, whilst the filled triangles represent the same in the high forest type. The error bars show the 95% confident intervals of the probability estimates.

Table 7a–e. Results of univariate logistic regression where the response variable was presence/absence of each of the study species on each forest island. Included are the predictor variables' total significance-level (p-value) and each category's percentage of forest islands with presence (Perc.), odds ratio (O.R.) and 95%-confidence interval (95%-CI) (n = 42). For a given category (x) the odds ratio is given as: odds (x)/odds (x - 1).

a) <i>Cis jacquemarti/nitidus</i>					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
DistC	0.548	[1]	68	1.53	0.38–6.21
		[2]	76		
		[3]	74		
DistV	0.700	[1]	68	0.76	0.20–2.93
		[2]	79		
		[3]	71		
Sha	0.703	[1]	79	0.68	0.12–3.83
		[2]	71		
		[3]	64		
0.72	[1]	64	0.72	0.15–3.54	
	[2]	71			
	[3]	64			
b) <i>Cis bidentatus</i>					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
Area	0.245	[1]	11	3.56	0.54–23.38
		[2]	31		
		[3]	36		
DistC	0.443	[1]	28	1.28	0.23–7.05
		[2]	18		
		[3]	18		
DistV	0.702	[1]	26	0.55	0.12–2.52
		[2]	21		
		[3]	21		
NumF	<0.001	[1]	6	0.76	0.18–3.20
		[2]	15		
		[3]	70		
Sha	0.879	[1]	29	2.83	0.23–43.92
		[2]	15		
		[3]	70		
1	[1]	29	14.01	1.86–105.33	
	[2]	21			
	[3]	21			
0.16–6.08	[1]	29	0.68	0.12–3.83	
	[2]	21			
	[3]	21			
1	[1]	29	1	0.16–6.08	
	[2]	21			
	[3]	21			
c) <i>Cis lineatocibratus</i>					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
Area	0.043	[1]	11	6.86	1.10–42.76
		[2]	46		
		[3]	45		
DistC	0.858	[1]	32	0.97	0.21–4.87
		[2]	29		
		[3]	29		
DistV	0.553	[1]	35	0.89	0.23–3.38
		[2]	26		
		[3]	26		
Sha	0.896	[1]	36	0.67	0.18–2.54
		[2]	40		
		[3]	40		
0.72	[1]	36	0.72	0.15–3.54	
	[2]	40			
	[3]	40			
1	[1]	36	1	0.19–5.15	
	[2]	40			
	[3]	40			
d) <i>Ennearthron cornutum</i>					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
Area	0.020	[1]	11	6.86	1.10–8.73
		[2]	46		
		[3]	55		
DistC	0.260	[1]	40	1.40	0.28–7.01
		[2]	24		
		[3]	24		
DistV	0.120	[1]	43	0.46	0.12–1.83
		[2]	21		
		[3]	21		
Sha	0.461	[1]	36	0.35	0.09–1.38
		[2]	43		
		[3]	21		
0.36	[1]	36	1.35	0.29–6.18	
	[2]	43			
	[3]	21			
0.07–1.91	[1]	36	0.36	0.07–1.91	
	[2]	43			
	[3]	21			
e) <i>Dorcatoma dresdensis</i>					
Var.	p-value	Cat.	Perc.	O.R.	95%-CI
Area	0.342	[1]	11	3.35	0.54–23.37
		[2]	31		
		[3]	27		
DistC	0.195	[1]	28	0.84	0.14–4.97
		[2]	12		
		[3]	12		
DistV	0.414	[1]	26	0.34	0.06–1.90
		[2]	16		
		[3]	16		
Sha	0.230	[1]	29	0.53	0.11–2.49
		[2]	29		
		[3]	7		
1	[1]	29	1	0.19–5.15	
	[2]	29			
	[3]	7			
0.02–2.00	[1]	29	0.19	0.02–2.00	
	[2]	29			
	[3]	7			

densis had lower number of individuals and lower number of presence on trees and forest islands.

Univariate logistic regressions relating predictor variables to presence/absence of the study species on separate trees are shown in Table 4. Several predictor variables had significant univariate effect on presence/absence of the study species (*C. jacquemarti/nitidus*: Exp and VolT, *C. lineatocribratus*: Pos and VolT, *E. cornutum*: VolT and *D. dresdensis*: Typ, Cc/cv and VolT) without entering the multiple logistic regression model (Table 5) much due to correlation with variables entering the model (Table 6).

Multiple logistic regression models were created for each beetle species at the tree level. Four variables entered the model concerning *C. jacquemarti/nitidus* (Table 5a). Fallen trees had a significantly higher probability of presence than standing trees. Additionally, trees with a larger number of basidiocarps (> 4), greater diameter and lesser degree of isolation had increased incidence of *C. jacquemarti/nitidus*.

Basal area, degree of isolation, tree diameter and tree position had (on a 10%-significance level) significant effect on *C. bidentatus* presence (Table 5b). Trees with the highest degree of isolation and which were fallen over, had lower odds of presence than those less isolated and standing. There was no significant difference between the different categories of the other variables, but their overall trend suggests that denser forest (higher basal area) and increasing tree diameter were positive for *C. bidentatus* presence.

Number of basidiocarps per tree and the interaction term between forest height and isolation entered the multiple model concerning *C. lineatocribratus* (Table 5c). Trees with more than four basidiocarps had higher odds of presence than the other trees. The nature of the interaction term is illustrated in Fig. 2. In the low forest type, the probability of presence decreased with increasing isolation. However, in the high forest type there was no significant trend regarding isolation.

For *E. cornutum*, isolation, type of tree and tree diameter entered the multiple logistic model (Table 5d). There was a significantly reduced probability of *E. cornutum* presence on trees with the highest degree of isolation compared to the less isolated ones. Additionally, grey alder and trees with medium or large diameter had higher incidence than birch and trees with small diameter.

Finally, two variables, number of basidiocarps on the tree and degree of isolation, entered the model regarding the presence/absence of *D. dresdensis* (Table 5e). Trees having more than four basidiocarps and trees having the lowest degree of isolation had significantly higher odds of presence than the other categories of these variables.

Number of individuals of *C. jacquemarti/nitidus* and *C. lineatocribratus* per tree increased as the total volume of basidiocarps there increased (linear regression: *C. jacquemarti/nitidus*: $\log(\text{no. of individuals}) = -0.37 + 0.60 \times \log(\text{VolT})$, $F_{1,128} = 60.65$, $p < 0.001$, $R_{\text{Adj}}^2 = 0.32$, $n = 130$ and *C. lineatocribratus*: $\log(\text{no. of individuals}) = -0.48 + 0.31 \times \log(\text{VolT})$, $F_{1,20} = 7.06$, $p = 0.015$, $R_{\text{Adj}}^2 = 0.22$, $n = 22$). For the other species no such significant trend was found ($p > 0.5$).

By using a combination of logistic regression, contingency tables and Spearman rank-correlations, trends in presence/absence pattern of the study species at the forest island level could be revealed despite some predictor variables having categories with 100% presence or absence (Table 7 and 8). When the variables creating the “problems” above (category(s) with 100% presence/absence) had been removed and analysed by contingency tables (Table 8), only one variable for three of the beetle species entered the multiple logistic regression model: number of trees with basidiocarps for *C. bidentatus* and area for *C. lineatocribratus* and *E. cornutum* (Table 7b–d).

Summing up the analyses at the forest island level, increasing number of trees or volume of basidiocarps on a forest island increased the incidence of all study species (Table 7b and 8). Forest islands with larger area had

Table 8. Contingency tables presenting the association between the presence of different study species and the predictor variables VolF, NumF and Area which had at least one category with 100% presence or absence of the species on each forest island ($n = 42$).

	VolF [1]	VolF [2]	VolF [3]	Pearson- χ^2
<i>Cis jacquemarti/nitidus</i>	31% (4/13)	81% (13/16)	100% (13/13)	$p < 0.001$
<i>Cis bidentatus</i>	8% (1/13)	0% (0/16)	69% (9/13)	$p < 0.001$
<i>Cis lineatocribratus</i>	0% (0/13)	31% (5/16)	62% (8/13)	$p = 0.003$
<i>Ennearthron cornutum</i>	0% (0/18)	36% (5/14)	90% (9/10)	$p < 0.001$
<i>Dorcatoma dresdensis</i>	0% (0/13)	13% (2/16)	54% (7/13)	$p = 0.01$
	NumF [1]	NumF [2]	NumF [3]	Pearson- χ^2
<i>Cis jacquemarti/nitidus</i>	33% (6/18)	100% (14/14)	100% (10/10)	$p < 0.001$
<i>Cis lineatocribratus</i>	0% (0/18)	36% (5/14)	80% (8/10)	$p < 0.001$
<i>Ennearthron cornutum</i>	0% (0/18)	36% (5/14)	90% (9/10)	$p < 0.001$
<i>Dorcatoma dresdensis</i>	0% (0/18)	29% (4/14)	50% (5/10)	$p = 0.001$
	Area [1]	Area [2]	Area [3]	Pearson- χ^2
<i>Cis jacquemarti/nitidus</i>	50% (9/18)	77% (10/13)	100% (11/11)	$p = 0.04$

greater probability of presence of *C. lineatocribratus*, *E. cornutum* and *C. jacquemarti/nitidus* than the smallest islands (Table 7c, d and 8). These variables significantly affecting the probability of beetle presence on the forest islands were strongly correlated (Spearman rank correlation: VolF vs NumF = 0.77, VolF vs Area = 0.46 and Area vs NumF = 0.64, $p < 0.001$ for all correlations, $n = 42$).

Discussion

In this study, I report that presence of all study species on basidiocarp trees was reduced when isolation (distance to other inhabited trees) increased. Reduced habitat size at both investigated scales resulted in lower incidence of each of the study species. At the tree level other variables also had effect on the incidence of some of the beetles: position of the tree (standing or fallen) influenced *C. jacquemarti/nitidus* and *C. bidentatus* in opposite ways, increasing density of the forest was positive for *C. bidentatus* presence and grey alder trees had higher probabilities of *E. cornutum* presence than birch trees.

Effect of spatial variables

That all study species responded similarly to changes in the landscape variables isolation and habitat size (tree diameter, number of basidiocarps or total volume of basidiocarps per tree) at the tree level, indicates that important demographic processes take place at this scale. Individuals of each beetle species on a basidiocarp tree may constitute a local population of that particular species which sum up to a metapopulation when regarding all inhabited trees in the study area. As the habitat patches (basidiocarp trees) have a rather fast turn-over, the species must be able to track new habitats to avoid deterministic extinction. Therefore, the possible metapopulation dynamics of each of these species could resemble the concept of a "habitat-tracking metapopulation" (sensu Harrison and Taylor 1997). Studies of incidence (Rukke and Midtgaard 1998, Sverdrup-Thygeson and Midtgaard 1998), mark-recapture (Nilsson 1997) and genetics (Knutson et al. in press) of *B. reticulatus* imply that this species has a corresponding population dynamics.

All study species (except *C. lineatocribratus* in the higher forests type) responded negatively to increased isolation between the basidiocarp trees, and this indicates that the degree of isolation in the study area are sufficient to reduce the migration between the study units at the tree level. These results correspond well with the incidence and genetic studies of *B. reticulatus* in the same study area (Rukke and Midtgaard 1998, Knutson et al. in press). Generally, increased overall isolation in a regional system of discrete habitat patches is critical for the presence of species living there because it lowers incidence due to

reduced colonization probability of empty patches (Hanski and Gilpin 1997) and lowered rescue-effect in those already colonized (Brown and Kodrick-Brown 1977).

At the larger scale, the forest island level, the isolation indices "distance to surrounding forest" and "distance to the nearest forest island" did not have significant effect on the presence/absence pattern of the study species. Possibly these indices are not appropriate measures of isolation at this scale. In particular, the islands had an irregular shape making it difficult to obtain precise isolation measures. Another element possibly contributing to the apparent missing isolation effect at the forest island level is that the temporal scale of the resource dynamics is different from the one at the tree level. Forest islands persist longer than individual trees, and the habitat turn-over time for forest islands might be long enough to ensure a sufficient number of migratory individuals to prevent extinction on forest islands within the present isolation range. For isolation to influence the incidence of the study species on the forest islands, a higher degree of fragmentation giving more isolated forest islands may be needed to hinder sufficient spread of migrating individuals. The same two isolation indices did neither have any effect on the presence of *B. reticulatus* in the present study area (Rukke and Midtgaard 1998).

At both scales several predictor variables indicated that increased habitat size had positive effect on the presence of the study species. Due to the strong correlations between the three habitat size related variables at the tree level, tree diameter, number of basidiocarps per tree and basidiocarp volume per tree, it is sensible to take all three variables into account when discussing effects of habitat size at this scale. There may be several reasons why larger habitats should have increased incidence of the study species. Firstly, higher detection of larger habitat may enhance colonization of the habitat. It is at present not known how the study species detect suitable basidiocarp trees, but increased detection of large habitats due to visual clues and/or odour attraction may be a possible way. Secondly, the habitat size variables are likely to be positively correlated to the time basidiocarp resources are available to the beetles. This will improve colonization probabilities and reduce risk of deterministic extinction (resource depletion). Finally, trees with larger habitat size may be less subjected to stochastic extinction. Trees with higher volume of basidiocarps may have higher presence of *C. jacquemarti/nitidus* or *C. lineatocribratus* due to their larger population size. Larger demographic units generally have lower extinction risk due to stochastic processes (Shaffer 1981, 1987).

At the forest island level presence of all beetles studied were positively correlated with increasing volume of basidiocarps and number of basidiocarp trees, whilst increasing area of the forest islands had positive effect on *C. jacquemarti/nitidus*, *C. lineatocribratus* and *E. cornutum* presence. Corresponding trends have been observed for *B. reticulatus* on the same forest islands

(Rukke and Midtgaard 1998). Larger islands having higher number of basidiocarp trees (Rukke and Midtgaard 1998) and larger total basidiocarp volume are probably able to support larger amount of habitat for the study species over longer time spans. If then beetles on each basidiocarp tree are regarded as a local population, large islands can support a higher number of local populations for longer time than smaller islands. With more such demographic units and habitats present, chances are reduced that large islands will be without the beetles due to stochastic or deterministic processes.

Effects of microhabitat variables

At the tree level some microhabitat variables influenced the presence of the study species. *Cis jacquemarti/nitidus* was positively associated with laying trees, whilst *C. bidentatus* had higher probability of presence on standing trees. One factor differing between laying and standing logs are the moisture content where the former are more moist than the latter (Hunter 1990). This affects the faunal composition in the trunks (Palm 1951, 1959, Ehnström and Waldén 1986, Wikars 1990) and also possibly the presence of *C. bidentatus*, which prefers drier basidiocarps (Rukke unpubl.). Because *C. jacquemarti/nitidus* prefers basidiocarps on the ground level regardless of their moisture content (Rukke unpubl.), the higher incidence of *C. jacquemarti/nitidus* on laying trees is probably attributed to other things than the microclimatic moisture regime.

Trees in denser forests, indicated by basal area, had higher incidence of *C. bidentatus* than those in more open forests. As denser forests probably have moister microclimate, this apparently contradicts the species' preference for dry basidiocarps (Rukke unpubl.). Possibly some other factor has stronger influence on occurrence of the species than the moisture component of this variable.

Grey alder trees had higher probability of *E. cornutum* presence than birch trees. This result is opposite to what have been observed for *B. reticulatus* in the same study area (Rukke and Midtgaard 1998). Perhaps basidiocarps growing on different trees differ in chemical structure affecting the two species' habitat preference.

For *C. lineatocribratus* the interaction term "height above ground × isolation" entered the model indicating that the isolation effect in the higher forests diminished. There is no obvious explanation to this result, but perhaps microclimatic conditions in higher forests in some way are better reducing the negative effects of increased isolation there.

Implications for conservation

This study further pinpoints the severe effect gradual disappearance of dead wood and dead wood fungi from

the boreal forests have on the fauna associated with such habitats. All the study species, rather common, fungivorous species exploiting *F. fomentarius* were negatively influenced by reduced habitat size and increased isolation. Earlier incidence, mark-recapture and genetic studies of *B. reticulatus* exploiting the same resources, came to the same conclusion. Extrapolation of these results to other organisms must be done with caution, but when relatively common species experience such clear negative effects of habitat fragmentation, serious threats regarding existence of rarer species with limited dispersal abilities probably exist. Therefore, leaving more large dimensional dead wood in the forests is essential if the diversity of insects associated with dead wood and dead wood fungi shall be retained.

Further, the present study implies the value of large size forest patches in a fragmented region. Conservation of larger forest patches is desirable because they have a greater number of basidiocarp trees. This enables them to house more populations of vulnerable species exploiting such resources reducing the chance of regional extinction of these species.

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