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Distribution and abundance of diurnal Lepidoptera on a raised bog in southern Finland

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Species diversity and composition of the assemblages of butterflies and day-active moths were studied using a belt transect method on a concentric raised bog in southeastern Finland. The species richness of the mire was lower than that of the adjacent mineral land. On a vegetational gradient across the mire, the highest number of species and individuals were found on the lagg and marginal slope. The fauna appeared very similar along separate mire transects, while the mineral land samples differed more distinctly from each other. Multivariate analyses grouped the study sites into open minerotrophic mires, open raised bogs, pine bogs, coniferous forests and mineral lands with clear-fellings. Similar analysis of vegetation divided the transect section more distinctly into mires and mineral lands. The composition of the species assemblages of Lepidoptera was mostly related to the structural characteristics of the mire, especially to the tree height, and to a lesser degree to the floristic characteristics of undergrowth. The floristically poor pine bogs near the forest-mire edge maintain a peculiar and diverse fauna of butterflies and moths.

1. Introduction

The fauna of the boreal zone is characterized by species of mature forests, of different successional stages of forests and of different mires. Such habitats and sites form the backbone of conservation programmes in northern Europe. There is a distinctive fauna of butterflies and moths associated with mires and their natural succession, many of which have locally disappeared (Krogerus 1945, Hublin & Savolainen 1985, Järventausta et al. 1988, Marttila et al. 1990) and several species are now considered to be endangered in Europe (e.g. Heath 1981, Meineke 1981, Blab & Kudrna 1982, Kudrna 1986). If this fauna is to be preserved, it is necessary to have basic information e.g. on larval and adult host plants, habitat structure and microclimate, distribution and minimum size of suitable habitat patches, and the significance of landscape boundaries such as forest-mire edges.

Little attention has been paid to the community ecology of Lepidoptera on mires or peatlands in northern Europe since the classic work by

Krogerus (1960) on arthropods in general. Although dealing mostly with Coleoptera, this provided information on habitat preferences of many Lepidoptera, too. Recent papers by Mikkola (1976), Meineke (1981, 1982) and Mikkola & Spitzer (1983) added qualitative knowledge on various species, biogeographic differences in the fauna and possible reasons for the existence of particular mire species.

The relevance of ideas such as 'spreading the risk' or 'source-sink population structure' to the management of mire species depends on how the movement of individuals or the distribution of populations are affected by patch boundaries and landscape configuration (Wiens 1992). The aim of the present study was to obtain quantitative information on the significance of landscape boundaries and other habitat characteristics on the adult Lepidoptera for the purposes of nature conservation and habitat management. This was done by investigating the diversity and species assemblages of diurnal Lepidoptera on a vegetational gradient across a raised bog and an adjacent forest using a belt transect method.

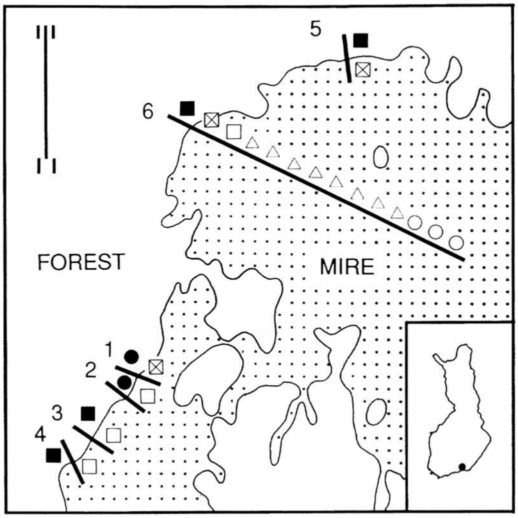

Fig. 1. A map of the study area on the Kananiemensuo mire, southeastern Finland, showing transects 1–6. The location of the study area is shown in the map of Finland inserted. For the scale, transects 1–5 are 200 m long. Symbols refer to the major habitat types of the sections as follows: Black square = forest; black dot = forest with clear-fellings; square with cross = pine bog (with *Ledum palustre*, *Vaccinium uliginosum*, *Betula nana*); open square = pine bog (with *Calluna vulgaris*, *Empetrum nigrum*, etc.); open triangle = open *Sphagnum* bog; open circle = aapa mire.

2. Material and methods

2.1. Study area

The study was carried out on the mire Kananiemensuo (60°34′N, 26°45′E, 18–22 m above sea level) at Pyhtää, southeastern Finland. The Kananiemensuo mire lies in the middle of the wider Munasuo–Kananiemensuo–Mustanjärvensuo mire area between the forks of the River Kymi. The vegetation and flora of Kananiemensuo were described by Tolonen (1968). The species of Lepidoptera recorded on the area were listed by Väisänen & Suoknuuti (1989). The butterfly and moth fauna of the mire is a rich combination of southern and northern elements.

The mire consists of two ombrotrophic raised bogs where dry hummocks and wet hollows lie concentrically around the higher bog centre. In addition, there are two minerotrophic areas which can be classified as aapa mires, where *Sphagnum papillosum* tall sedge fens with flarks spread widely and smoothly. The edges of the mire have several gulfs characterized by various types of pine and spruce mires.

2.2. Belt transect method

Methods based on transect counts have proved effective in assessing annual changes in the abundance of butterflies. The most widely known method was developed by Pollard (1977, 1982). The method can be successfully applied to studies on habitat preferences of different species and on the species diversity of various habitats.

Six belt transects were delimited in the western part of Kananiemensuo (Fig. 1) consisting of a concentric raised bog and its widened lagg, which on the basis of its vegetation and hydrology is an aapa mire (Tolonen 1968). Transects 1–5 were short, consisting of 100 m of mire and 100 m of mineral land. The mineral land was forested except in transects 1–2, which also included about 30 m sections of a clear-felling area bordering the mire. Transect 6 ran through a 100 m section of forest and across a raised bog (100 hectares) to an aapa mire (120 hectares), the mire section being in total 1300 m long. Thus, there were six comparable forest-mire transition belts and a longer gradient representing different seral stages of mire succession and two mire complex types (ombrotrophic raised bog and minerotrophic aapa mire; Ruuhijärvi 1982). The main tree species in the study area is the Scots pine (*Pinus sylvestris* L.), but in the forest sections the Norway spruce (*Picea abies* (L.)), birches (*Betula* spp.) and alders (*Alnus* spp.) are also common. A narrow forest road ran through all the mineral land transects.

The following criteria were used in order to provide a degree of standardization: Counts were started after 1045 hours summer time and completed before 1545 hours. They were not made when the temperature was below 13°C; when it was 13 to 17°C counts were made only in sunny conditions (60 % sunshine minimum); above 17°C conditions might be sunny or cloudy. In the present study, these original time limits were not strictly followed when conditions were otherwise good. The transects were divided into 5 × 5 m squares, which were marked by yellow tape in the field. The recorder (the author) walked at a uniform pace and recorded all butterflies and day-active moths seen within prescribed limits. The width of the belt was 5 m. Lepidoptera were recorded up to 5 m in front of the recorder. Stops were made to resolve identification problems, recording being resumed from the point where the walk was interrupted.

Diurnal species were used in the counts based on 5 × 5 m squares. The data was not analysed according to the time of day (see Dreisig 1986), although the time was recorded. All species belonging to the superfamilies Zygaenoidea, Hesperioidea, Papilionoidea, Drepanoidea, Geometroidea, Bombycoidea, Sphingoidea and Noctuoidea seen in flight on the belt transects were included in the study. All individuals were identified to the species level. The nomenclature follows Varis et al. (1987). Since the flight periods of diurnal mire species are concentrated in June and July in this area (Väisänen & Suoknuuti 1989), the counts were also carried out mostly during that period. The transects were walked twice or four times (*) a day on the following dates: June 12*, 13, 14, 19, 20 and 27*, July 1, 10 and 20, and August 1*, 1986; May 10 and 23, July 6*, 7*, 21 and 22*, and August 22, 1987. Thus, the transects were counted 46 times, totalling 110.4 km of belt, yielding a total of 8060 individual observations on Lepidoptera.

2.3. Vegetation

The vegetation of the transects was investigated in August 1987. The habitats were subjectively classified into six major habitat classes:

1) forest,
2) forest with small clear-cut areas,
3) pine bogs with *Vaccinium uliginosum* L., *Ledum palustre* L., *Betula nana* L. etc.,
4) pine bogs with *Calluna vulgaris* (L.) Hull, *Empetrum nigrum* L. etc.,
5) open ombrotrophic *Sphagnum* bogs, and
6) open minerotrophic mire predominated by *Sphagnum papillosum* tall sedge fens.

Additional vegetational data from each 5 × 5 m square were recorded to provide a basis for statistical analyses:

Maximum height of trees, species composition and number of trees in height classes 0.5–2 m, 2–5 m and more than 5 m.
Coverages of different undergrowth species using four randomly selected (in very uniform aapa squares 3) subsquares of 0.25 × 0.25 m.
Distance from mineral land.

Vascular plants were identified to species level, except grasses (Poaceae) and sedges (*Carex* spp.). In the analyses, a group of forest herbs (i.e. *Linnaea*, *Epilobium*, *Lathyrus*, *Vicia* and *Melampyrum* spp.) with a very small coverage was pooled. Mosses were classified into three groups, viz. *Sphagnum* spp., other mire mosses (*Aulacomnium palustre* (Hedw.) Schwaegr., *Drepanocladus* spp., *Polytrichnum commune* Hedw., etc.) and forest mosses (*Dicranum polysetum* Sw., *D. scoparium* Hedw., *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) B.S.G., etc.).

The mean values of the variables in the major habitat classes are given in Table 1. The DCA ordination of 20 square sections based on the data on the lower vegetation is shown in Fig. 2 (for statistical analysis, see below). The ordination divided the major habitat classes distinctly into mires and mineral lands, while forests and clear-cuts did not differ from each other. The sections of pine bogs (lagg and marginal slope) and open bog (bog centre), as well as the aapa mire were grouped into separate clusters.

Table 1. The mean values (per 5 × 5 m squares) of the environmental variables in the major habitat classes. For the variables used in the final analysis acronyms are given. Habitat classes: 1 = forest, 2 = forest with clear-cut areas, 3 = pine bogs with *Vaccinium uliginosum*, *Ledum palustre*, *Betula nana* etc., 4 = pine bogs with *Calluna vulgaris*, *Empetrum nigrum* etc., 5 = open ombrotrophic *Sphagnum* bogs, 6 = open minerotrophic mires predominated by *Sphagnum papillosum* tall sedge fens.

Variable Habitat class:	1	2	3	4	5	6
Coverage (%) of						
Betula nana (BETN)	–	–	1.0	1.5	1.0	0.7
Salix spp.	0.3	–	–	–	–	–
Calluna vulgaris (CALV)	1.5	10.0	2.7	22.0	9.0	0.3
Ledum palustre	0.0	0.5	8.3	4.8	0.3	0.0
Arctostaphylos uva-ursi	0.5	13.0	–	–	–	–
Andromeda polifolia	–	–	0.7	2.3	4.4	1.3
Vaccinium oxycoccos	–	–	0.7	0.8	0.8	0.0
V. vitis-idaea	7.3	4.5	0.0	0.0	–	–
V. uliginosum (VACU)	0.5	1.0	13.7	8.0	0.1	0.0
V. myrtillus	16.5	16.0	0.7	0.0	–	–
Empetrum nigrum	0.0	0.5	1.7	4.3	0.6	–
Drosera spp.	–	–	0.6	0.0	0.0	0.0
Rubus chamaemorus (RUBC)	–	–	13.7	14.8	4.4	–
Potentilla palustris (POTP)	–	–	1.3	–	–	–
Menyanthes trifoliata	–	–	5.7	–	–	0.0
forest herbs	8.0	6.0	0.0	–	–	–
Scheuchzeria palustris	–	–	–	–	0.0	1.0
Eriophorum spp.	0.0	–	4.0	5.0	8.6	0.0
Carex spp.	0.3	–	4.7	0.5	1.0	6.7
Poaceae	5.3	2.0	–	–	0.0	–
Sphagnum mosses	2.0	0.5	35.3	31.8	64.5	78.3
other mire mosses	–	–	0.0	1.5	0.6	0.0
forest mosses	40.3	32.0	4.7	1.3	–	–
lichens	0.5	1.0	0.3	1.8	0.8	–
no plant cover	17.3	13.0	0.3	–	3.8	11.7
Maximum tree height, m (HGHT)	12.8	7.3	5.6	3.4	0.6	–
Number of trees, >2 m (TREE)						
Pinus sylvestris	1.4	1.4	3.9	2.3	0.1	–
Picea abies	1.6	0.4	0.0	–	–	–
Deciduous trees	1.0	0.8	0.4	0.1	0.0	–
All species	4.0	2.5	1.4	2.3	0.1	–
Number of bushes, 0.5–2 m (BUSH)						
Pinus sylvestris	0.3	1.3	2.1	4.1	0.9	–
Picea abies	1.0	0.9	0.1	–	–	–
Deciduous bushes	1.7	2.1	0.3	–	–	–
All species	3.1	4.3	2.6	4.2	0.9	–
Distance from mineral land, m (DIST)	0	0	50	75	600	1150

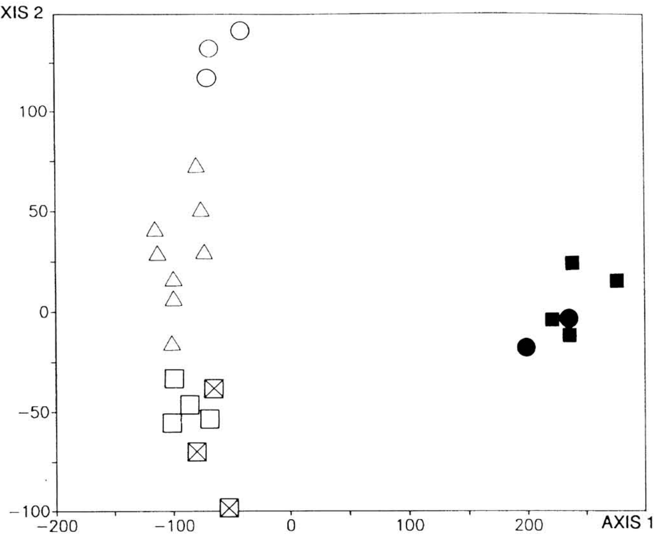

Fig. 2. The 20 square (100 m) sections of the transects plotted on the 1st and 2nd axes of a detrended correspondence analysis (DCA) according to their vegetation (undergrowth) on the Kananiemensuo mire. The eigenvalue of axis 1 is 0.66 and that of axis 2 is 0.24. Symbols as in Fig. 1.

2.4. Statistical analyses

The species richness along the transects was analysed using rarefaction corrected values of species number (Simberloff 1978, James & Rathbun 1981) in addition to the actual number of species observed.

The major statistical program used in the analyses was CANOCO (Ter Braak 1987). Detrended correspondence analysis (DCA) was used for the ordination of both the data on vegetation and that on butterflies and moths using the same sections of 20 squares (100 m). The species data were square-root transformed. Detrending was made by second order polynomials. In DCAS, attention was first focused on the major pattern of variation in community composition so that no prior hypothesis was needed regarding what environmental variables are relevant. The similarity of Lepidopteran samples from forest and mire sections was also compared by the Czekanowski-Sørensen index of proportional similarity (e.g. Krebs 1989).

Further, the relation between Lepidoptera and environmental variables was analysed using canonical correspondence analysis (CCA). In CCA, the ordination axes are chosen in the light of known environmental variables by imposing the extra restriction that the axes be linear combinations of environmental variables (Ter Braak 1985, 1986, Ter Braak & Prentice 1988). A detrended canonical correspondence analysis (DCCA; detrending by second order polynomials) was used to remove the arch effect (i.e. to prevent the CCA from selecting weighted sums of environmental variables that are approximately polynomials of previous axes), which remained in the CCA although less interesting environmental variables were discarded. The preliminary analyses showed that the variables omitted were superfluous and correlated with the other variables (Table 2). The means ($n = 20$) of the following environmental variables were used in the DCCA analysing the Lepidopteran data:

Coverage of *Betula nana* L. (BETN),
Coverage of *Calluna vulgaris* (L.) Hull (CALV),
Coverage of *Vaccinium uliginosus* L. (VACU),
Coverage of *Rubus chamaemorus* L.(RUBC) and
Coverage of *Potentilla palustris* (L.) Scop. (POTP),
Maximum tree height per square (HGHT),
Number of trees higher than 2 m (TREE),
Number of bushes between 0.5 and 2 m (BUSH),
Distance from mineral land (DIST).

In another DCCA, only BETN, CALV, VACU, RUBC and POTP were used as environmental variables and HGHT as covariable. CANOCO gives an ordination of the residual variation in the species data that remains after fitting the effects of the covariables. The ordination axes are made uncorrelated to the covariables. The constrained ordination axes represent the effect that is uniquely attributable to the environmental variables and not to the covariables.

The eigenvalue is a measure of separation of the species' distributions along the ordination axis. The canonical coefficients in the DCCA are the coefficients of a weighted multiple regression of the sample scores on the standardized environmental variables. The Student's *t*-test is not appropriate for tests of significance of canonical coefficients. However, when the *t*-value of a variable is less than 2.1 in absolute value, the variable does not contribute much to the fit of the species data. The variable then does not have an effect that is uniquely attributable to that particular variable and can be deleted without much affecting the canonical eigenvalues. The interset correlations of environmental variables with the DCCA axes are the correlation coefficients between the environmental variables and the species axes consisting of sample scores. They do not become unstable when the environmental variables are correlated with each other. If the variance inflation factor (VIF) of a variable is large (>20), the variable is highly correlated with the other variables.

In order to make the between-species comparisons of habitat preferences of diurnal Lepidoptera more concrete, some characteristics of the squares occupied by certain species were calculated using the original unpooled square data (length of each section 5 m).

3. Results

3.1. Species richness and abundance

The total sample comprised 8060 individual observations on Lepidoptera belonging to 125 species. The mean number of each species on the 100 m sections of major habitat classes are presented in Table 3. When the forest-mire edges (transects 1–6) were examined, the number of individuals per transect section (a 100 m, $n = 12$) recorded with the same counting effort on the mineral land (mean 271.3, *SD* 163.8) was about

Table 2. Correlations of the coverages of different plant species with the variables used in the lepidopterological analyses.

Plant species	BETN	CALV	VACU	RUBC	POTP	HGHT	TREE	BUSH	DIST
Salix spp.	−0.21	−0.25	−0.24	−0.27	−0.07	0.52	0.01	0.08	−0.15
Ledum palustre	0.34	0.10	0.98	0.78	0.38	−0.22	0.45	0.17	−0.31
Arctostaph. uva-ursi	−0.31	−0.01	−0.30	−0.39	−0.11	0.20	0.06	0.26	−0.21
Andromeda polifolia	0.46	0.48	−0.23	0.16	−0.09	−0.73	0.69	−0.19	0.53
Vaccinium oxycoccos	0.70	0.07	0.13	0.26	−0.20	−0.43	0.15	0.02	0.16
V. vitis-idaea	−0.41	−0.31	−0.39	−0.52	−0.14	0.69	0.38	0.29	−0.29
V. myrtillus	−0.49	−0.39	−0.48	−0.64	−0.18	0.82	0.32	0.31	−0.36
Empetrum nigrum	0.59	0.53	0.51	0.79	−0.24	−0.35	0.06	0.35	−0.20
Drosera spp.	0.05	−0.15	0.40	−0.03	1.00	0.01	0.32	0.03	−0.11
Menyanthes trifoliata	0.18	−0.26	0.50	−0.00	0.93	−0.01	0.46	0.01	−0.14
Forest herbs	−0.41	−0.33	−0.44	−0.51	−0.14	0.73	0.08	0.16	−0.28
Scheuchzeria palustris	0.01	−0.22	−0.23	−0.19	−0.07	−0.32	0.41	−0.42	0.77
Eriophorum spp.	0.38	0.31	0.13	0.33	0.02	−0.69	0.48	−0.27	0.39
Carex spp.	0.29	−0.32	0.28	−0.01	0.04	−0.19	0.11	−0.20	0.16
Poaceae	−0.48	−0.43	−0.49	−0.60	−0.16	0.88	0.33	0.09	−0.33
Sphagnum	0.34	0.09	0.08	0.28	−0.02	−0.85	0.60	−0.56	−0.79
Other mire mosses	0.45	0.73	0.10	0.44	−0.20	−0.46	0.36	0.20	−0.03
Forest mosses	−0.55	−0.42	−0.45	−0.66	−0.04	0.85	0.46	0.14	−0.42
Lichens	0.35	0.60	0.01	0.14	0.03	−0.28	0.10	0.24	−0.18
No plant cover	−0.49	−0.47	−0.60	−0.70	−0.17	0.66	0.10	−0.15	−0.04

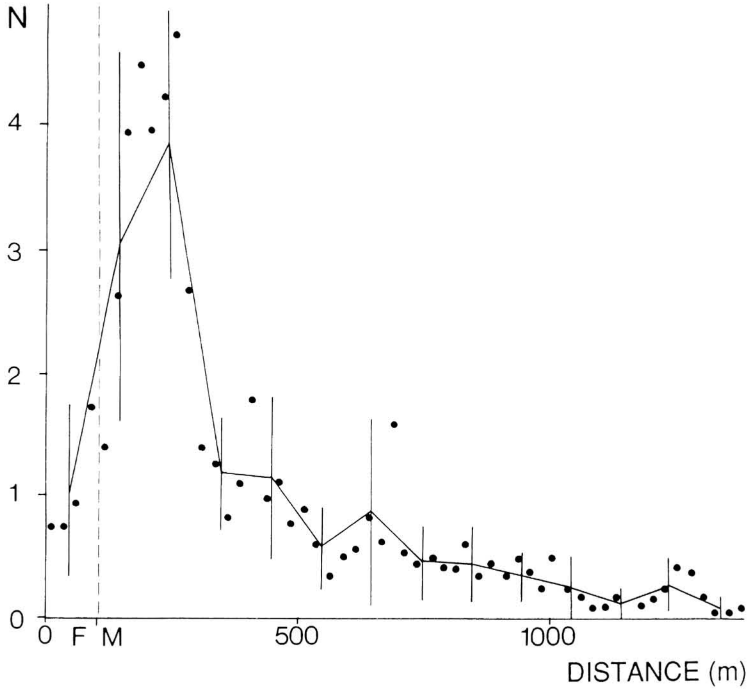

Fig. 3. Number of individuals of Lepidoptera observed per square along transect 6 on the Kananiemensuo mire, from forest-mire edge (F/M) towards the centre of the mire using both the 5 and 20 square data. The 20 square (100 m) values are indicated by a solid line with standard deviation shown by vertical lines, and the 5 square (25 m) values by black dots.

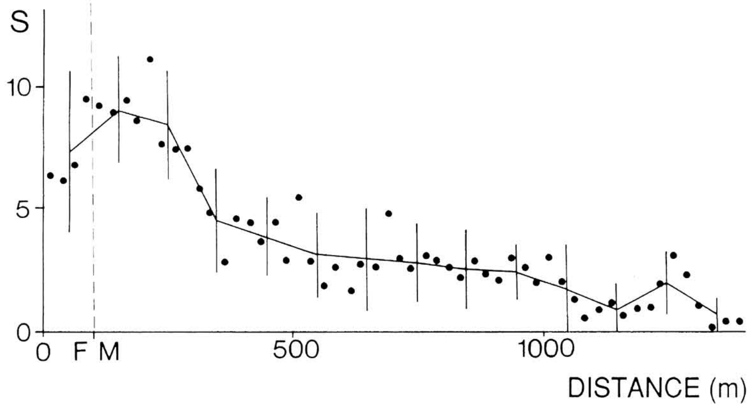

Fig. 4. Number of Lepidoptera species observed per square along transect 6 on the Kananiemensuo mire, from forest-mire edge (F/M) towards the centre of the mire using both the 5 and 20 square data. Symbols as in Fig. 3.

one third of that on the mire (mean 751.7, *SD* 212.1). The difference was statistically significant (Mann-Whitney *U*-test, $U = 1$, $P = 0.002$). However, the species number in the forest samples was on average about as high (mean 40.8, *SD* 5.5) as in the mire samples (mean 40.3, *SD* 4.5). The number of individuals and species along the long mire gradient (transect 6) was highest near the forest-mire edge, i.e. on the lagg and the marginal slope, decreasing towards the ombrotrophic bog centre and the subsequent minerotrophic aapa mire (Figs. 3–4).

The mean number of individuals in the forest with clear-cuts was about three times as high as in the four other forest transects (the means 477.5, *SD* 55.9, vs. 154.3, 25.5), but the mean number of species was about the same (the means 40.0, *SD* 4.2, vs. 41.5, 7.1; $U = 0$, $P = 0.13$). This was largely due to the large amounts of butterflies, especially *Plebejus argus*, on the clear-cuts.

Table 3. The mean number of butterfly and moth individuals observed in the 100 m sections of six major habitat classes, and total number of observed individuals. Nomenclature follows Varis et al. (1987). Habitat classes: 1 = forest, 2 = forest with clear-cut areas, 3 = pine bogs with *Vaccinium uliginosum, Ledum palustre, Betula nana* etc., 4 = pine bogs with *Calluna vulgaris, Empetrum nigrum* etc., 5 = open ombrotrophic *Sphagnum* bogs, 6 = open minerotrophic mires predominated by *Sphagnum papillosum* tall sedge fens. Tyrphobiont species are indicated by T and tyrphophilous species by t (according to Mikkola & Spitzer 1983, and Väisänen & Suoknuuti 1989).

Species Habitat class:	1	2	3	4	5	6	Ind.
Zygaenidae							
Rhagades pruni (Denis & Schiffermüller)^{T}	–	–	0.7	2.3	0.4	0.3	15
Adscita statices (Linnaeus)	–	0.5	–	–	–	–	1
Zygaena viciae (Denis & Schiffermüller)	0.3	–	–	–	–	–	1
Hesperiidae							
Carterocephalus silvicola (Meigen)	0.5	–	–	–	–	–	2
Thymelicus lineola (Ochsenheimer)	0.8	1.0	–	–	–	–	5
Ochlodes venatus (Bremer & Gray)	1.3	–	1.3	–	–	–	9
Papilionidae							
Papilio machaon Linnaeus^{t}	–	1.0	–	0.3	–	–	3
Pieridae							
Leptidea sinapis (Linnaeus)	0.3	–	–	0.3	–	–	2
Pieris napi (Linnaeus)	0.3	–	–	0.8	–	–	3
Colias palaeno (Linnaeus)^{T}	0.5	0.4	6.3	4.0	–	–	45
Gonopteryx rhamni (Linnaeus)	0.3	–	0.3	0.3	0.1	–	4
Lycaenidae							
Callophrys rubi (Linnaeus)^{t}	3.8	3.0	4.7	1.3	–	–	40
Lycaena phlaeas (Linnaeus)	–	0.1	–	–	–	–	2
Heodes virgaureae (Linnaeus)	1.8	2.0	0.7	0.3	–	–	14
Celastrina argiolus (Linnaeus)	–	–	0.3	–	–	–	1
Plebejus argus (Linnaeus)^{t}	20.8	332.5	88.3	340.8	66.4	2.0	2913
Vacciniina optilete (Knoch)^{t}	2.0	3.0	27.7	11.3	0.3	–	144
Agrodiaetus amandus (Schneider)	0.5	–	0.3	–	–	–	3
Nymphalidae							
Aglais urticae (Linnaeus)	–	–	–	–	0.1	–	1
Vanessa cardui (Linnaeus)	–	0.5	–	–	–	–	1
Fabriciana adippe (Denis & Schiffermüller)	0.3	1.5	–	–	–	–	4
Brenthis ino (Rottemburg)^{t}	1.0	3.0	16.3	25.3	2.8	–	182
Boloria aquilonaris (Stichel)^{T}	–	–	10.6	3.5	1.9	1.7	66
Proclossiana eunomia (Esper)^{T}	–	0.5	3.3	11.5	7.5	–	117
Clossiana selene (Denis & Schiffermüller)^{t}	1.3	0.5	1.7	–	–	–	11
C. euphrosyne (Linnaeus)^{t}	3.5	6.0	7.0	12.8	–	–	98
Mellicta athalia (Rottemburg)	–	1.0	0.3	–	–	–	3
Hypodryas maturna (Linnaeus)	0.8	1.5	–	0.6	–	–	9
Satyridae							
Erebia ligea (Linnaeus)	0.5	–	–	–	–	–	2
Aphantopus hyperantus (Linnaeus)	3.0	0.5	1.0	–	–	–	16
Coenonympha tullia (Müller)^{T}	–	2.0	6.3	5.0	5.0	2.3	90
C. glycerion (Borkhausen)	0.5	–	–	–	–	–	2
Lasiommata maera (Linnaeus)	1.8	1.5	0.7	0.8	–	–	15
Drepanidae							
Falcaria lacertinaria (Linnaeus)	0.3	–	–	–	–	–	1
Ochropacha duplaris (Linnaeus)	0.3	–	–	–	–	–	1
Geometridae							
Chlorissa viridata (Linnaeus)^{T}	–	–	3.3	2.8	0.6	–	26
Thalera fimbrialis (Scopoli)^{T}	–	–	–	1.5	0.4	–	9
Jodis putata (Linnaeus)	5.5	2.5	0.7	0.8	–	–	32
Cyclophora albipunctata (Hufnagel)	0.3	1.0	–	–	–	–	3
Scopula ternata Schrankt	9.0	5.0	11.0	7.0	0.1	–	108
S. immorata (Linnaeus)	–	1.0	0.3	–	–	–	3
S. floslactata (Haworth)	8.0	8.5	1.7	1.5	–	–	60
S. immutata (Linnaeus)^{t}	–	–	1.0	–	–	–	3
S. virgulata (Denis & Schiffermüller)^{T}	–	–	–	2.8	0.3	–	13
Idaea serpentata (Hufnagel)	–	0.5	0.3	–	–	–	2
I. muricata (Hufnagel)^{T}	–	–	–	–	–	0.3	1
I. pallidata (Denis & Schiffermüller)	–	0.5	–	–	–	–	1
I. aversata (Linnaeus)	0.3	0.5	–	–	–	–	2
Scotopteryx chenopodiata (Linnaeus)	2.0	0.5	0.3	–	–	–	10
Xanthorhoe spadicearia (Denis & Schiffermüller)	2.8	1.5	–	–	–	–	14
X. quadrifasciata (Clerck)	0.3	0.5	0.3	–	–	–	3
X. montanata (Denis & Schiffermüller)	6.5	–	1.3	–	–	–	30
Epirrhoe alternata (Müller)	0.5	–	0.3	–	–	–	3
Mesoleuca albicillata (Linnaeus)	0.5	0.5	–	–	–	–	3
Eulithis testata (Linnaeus)^{t}	5.8	3.0	26.0	26.8	6.3	3.0	273
E. populata (Linnaeus)^{t}	2.3	1.0	5.3	2.0	0.1	–	36
Ecliptopera silaceata (Denis & Schiffermüller)	0.5	–	–	–	–	–	2
Chloroclysta citrata (Linnaeus)	0.3	0.5	–	–	–	–	2

Species Habitat class:	1	2	3	4	5	6	Ind.
C. infuscata (Tengström)^{T}	0.8	–	6.0	–	–	–	21
C. latefasciata (Staudinger)	0.8	–	–	–	–	–	3
C. truncata (Hufnagel)	2.5	0.5	–	–	–	–	11
Thera obeliscata (Hübner)	–	0.5	0.3	–	–	–	2
T. variata (Denis & Schiffermüller)	0.8	–	–	–	–	–	3
Electrophaes corylata (Thunberg)	2.8	–	–	0.3	–	–	12
Hydriomena ruberata (Freyer)	–	–	0.3	–	–	–	1
Spargania luctuata (Denis & Schiffermüller)	0.3	1.5	–	–	–	–	4
Rheumaptera hastata (Linnaeus)	0.8	0.5	–	0.3	–	–	5
R. subhastata (Nolcken)^{t}	–	–	0.3	–	–	–	1
R. undulata (Linnaeus)^{t}	1.3	1.0	0.3	0.3	–	–	9
Euphyia unangulata (Haworth)	0.3	–	–	–	–	–	1
Eupithecia plumbeolata (Haworth)	–	0.5	–	–	–	–	1
E. intricata (Zetterstedt)	0.5	–	0.7	–	–	–	4
E. vulgata (Haworth)	0.3	–	0.7	–	–	–	3
E. nanata (Hübner)	0.3	–	–	–	–	–	1
E. tantillaria Boisduval	1.8	–	–	–	–	–	7
Chloroclystis rectangulata (Linnaeus)	0.3	–	–	–	–	–	1
C. debiliata (Hübner)^{t}	0.5	–	–	–	–	–	2
Carsia sororiata (Hübner)^{T}	–	–	3.7	15.3	21.5	16.7	294
Hydrelia flammeolaria (Hufnagel)	0.8	0.5	0.3	–	–	–	5
Lomaspilis marginata (Linnaeus)	1.5	0.5	–	–	–	–	7
Semiothisa notata (Linnaeus)	0.5	0.5	0.7	0.3	–	–	6
S. alternaria (Hübner)	0.5	1.0	0.3	–	–	–	5
S. signaria (Hübner)	0.5	–	0.7	–	–	–	4
S. liturata (Clerck)	1.0	1.0	1.3	0.5	–	–	12
S. clathrata (Linnaeus)	2.7	–	0.7	0.4	–	–	12
S. carbonaria (Clerck)^{T}	–	–	2.3	3.5	1.4	–	32
Itame brunneata (Thunberg)^{t}	1.0	3.0	7.0	3.0	1.4	2.0	60
Plagodis pulveraria (Linnaeus)	2.5	–	–	–	–	–	10
Opisthograptis luteolata (Linnaeus)	0.5	–	–	–	–	–	2
Angerona prunaria (Linnaeus)^{t}	0.3	1.5	0.3	0.8	–	–	8
Alcis repandatus (Thunberg)^{t}	3.0	2.0	3.7	1.0	–	–	31
Arichanna melanaria (Linnaeus)^{T}	6.8	1.0	59.0	10.5	–	–	248
Aethulura punctulata (Denis & Schiffermüller)^{t}	–	–	0.3	–	–	–	1
Ematurga atomaria (Linnaeus)^{t}	21.5	45.0	269.7	323.0	10.8	1.0	2366
Bupalus piniarius (Linnaeus)	0.5	–	0.7	0.3	–	–	5
Cabera pusaria (Linnaeus)	12.3	13.0	1.7	0.3	–	–	81
C. exanthemata (Scopoli)	1.3	–	–	–	–	–	5
Hylaea fasciaria (Linnaeus)^{t}	0.3	–	2.0	0.3	–	–	8
Parietaria sordaria (Thunberg)	0.3	–	–	–	–	–	1
Aspitates gilvaria (Denis & Schiffermüller)^{T}	–	–	–	–	0.1	1.7	6
Perconia strigillaria (Hübner)^{t}	–	1.0	–	8.5	0.3	–	38
Lasiocampidae							
Lasiocampa quercus (Linnaeus)^{t}	0.3	–	0.7	1.5	0.4	–	12
Sphingidae							
Hyles gallii (Rottemburg)	–	–	–	0.3	–	–	1
Arctiidae							
Cybosia mesomella (Linnaeus)^{T}	–	–	–	0.5	0.1	–	3
Eilema lutarellum (Linnaeus)^{t}	–	–	1.7	1.5	1.4	–	22
Coscinia cribraria (Linnaeus)^{t}	–	0.5	–	0.3	0.5	–	6
Parasemia plantaginis (Linnaeus)^{t}	–	1.0	0.3	0.3	–	–	4
Diacrisia sannio (Linnaeus)^{t}	–	7.5	3.7	10.0	0.8	–	72
Noctuidae							
Pechipogo strigilata (Linnaeus)	0.3	–	–	–	–	–	1
Polypogon tentacularius (Linnaeus)	1.8	–	0.3	–	–	–	8
Hypenodes humidalis Doubleday^{T}	–	–	0.3	1.8	0.3	–	10
Hypena crassalis (Fabricius)	5.3	–	0.3	–	–	–	22
Callistege mi (Clerck)^{t}	–	–	–	0.8	0.3	0.3	6
Euclidia glyphica (Linnaeus)	0.5	–	–	–	–	–	2
Deltote uncula (Clerck)^{t}	–	–	7.3	0.3	0.3	0.7	27
Nola aerugula (Hübner)^{T}	–	–	2.3	3.5	–	–	21
Syngrapha microgamma (Hübner)^{T}	–	–	2.0	0.2	–	–	7
S. interrogationis (Linnaeus)^{t}	–	–	–	0.8	0.1	–	4
Anarta myrtilli (Linnaeus)^{t}	–	0.5	–	0.8	–	–	4
A. cordigera (Thunberg)^{T}	–	–	1.3	3.3	0.1	–	19
Polia bombycina (Hufnagel)^{t}	–	–	0.3	–	–	–	1
Noctua chardinyi (Boisduval)	–	–	–	0.3	–	–	1
Lycophotia porphyrea (Denis & Schiffermüller)^{t}	–	–	–	0.3	–	–	1
Eugraphe subrosea (Stephens)^{t}	–	–	–	–	0.1	–	1
Diarsia mendica (Fabricius)	0.3	–	–	–	–	–	1
Number of 100 m sections	4	2	3	4	8	3	

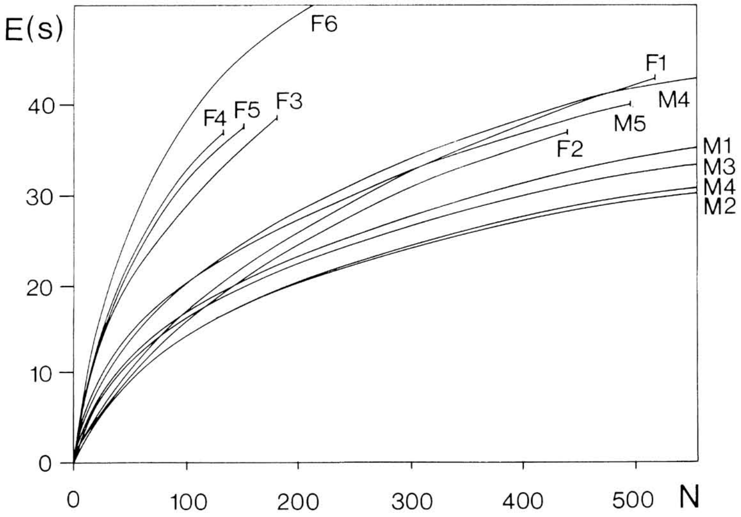

Fig. 5. Rarefaction curves for Lepidoptera samples from the forest-mire edges of transects 1–6. Each curve is calculated for a 100 m section of the transect. E(S) = Expected number of species, N = number of individuals observed. F = mineral land samples (F1 and F2 include clear-cut areas, others are mature forests), M = mire samples.

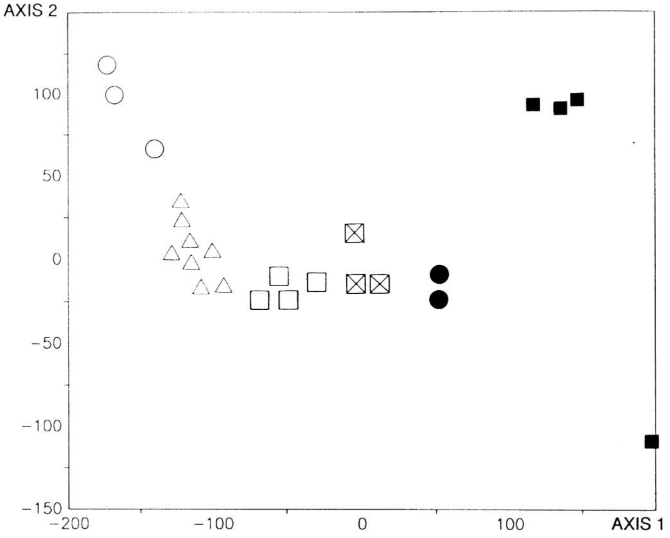

Fig. 6. The 20 square (100 m) sections of the transects plotted on the 1st and 2nd axes of a detrended correspondence analysis (DCA) according to their species assemblages of diurnal Lepidoptera. The eigenvalue of axis 1 is 0.46 and that of axis 2 is 0.19. Symbols as in Fig. 1.

Rarefaction curves (Fig. 5) show that the expected species numbers were higher among the forest samples than in the mire samples (when using the rarefaction corrected values for 100 individuals, *U* = 5, *P* = 0.04). The expected species number was lower in the forest transects with than in those without clear-cuts (the means 16.8, *SD* 0.78, vs. 33.1, 4.1) but the difference was not significant (*U* = 0, *P* = 0.13). No difference could be found between the mire transects (rarefaction corrected species richness corresponding to sample size 100: the means 15.6, *SD* 1.6, vs. 17.8, 3.0; sample size 400: the means 29.8, *SD* 2.8, vs. 33.4, 5.5).

3.2. Similarity of samples

The index of proportional similarity gathered the forest and mire samples into distinct clusters. The means of between-sample similarity in all the mire samples differed less from each other than those in all the forest samples (mire samples: mean 0.53, *SD* 0.08, $n = 15$; forest samples: index mean 0.65, *SD* 0.05, $n = 15$; $U = 24.5$, $P < 0.01$). The successive mire samples of transect 6 were more similar as to their species composition (index mean 0.66, *SD* 0.07, $n = 12$) than the adjacent forest and mire sample pairs at forest-mire edges (mean 0.42, *SD* 0.04, $n = 6$; $U = 1.5$, $P < 0.01$). The successive mire samples were about as similar as the mire samples at forest-mire edges of separate transects (mean 0.65, *SD* 0.05, $n = 6$).

To study the structure of the species assemblages in different sampling sites, the data on Lepidoptera was ordinated with the DCA using 20 square (100 m) sections of the transects (Fig. 6). The sampling sites were plotted by the DCA into clusters corresponding to the six major habitat classes. However, the forest section of transect 6 was relatively isolated.

3.3. Species assemblages of Lepidoptera in relation to environmental variation

The most abundant species in both the forest and mire sections were *Ematurga atomaria* and *Plebejus argus*, but there were distinct differences in the other dominant species (Table 3). For instance, *Carsia sororiata*, *Boloria aquilonaris*, *Nola aerugula* and *Anarta cordigera* were recorded from the mire sections only.

For more detailed analysis, the faunistic data was related to variation in the environment. The DCCA ordination diagrams (Fig. 7, Table 4) illustrate the fauna in relation to a few environmental variables. By comparing the arrow lengths in the DCCA ordination diagrams, one may obtain an idea of the significance of the environmental variables presented. The arrow points roughly in the direction of maximum variation in the value of the corresponding variable. The Monte Carlo permutation tests showed that the species are related to these environmental variables (99 random permutations, $P < 0.01$).

In the first DCCA, the maximum tree height (HGHT) obtained the highest absolute value on the first axis, but also the number of bushes (BUSH) contributed to the fit of the species data (Table 4). The VIF's were relatively low, indicating that the variables were not highly correlated with each other. The second axis was mainly related to the number of trees (TREE) and to the

Table 4. Canonical coefficients, variance inflation factors (VIFS) and the inter-set correlations of nine environmental variables with the first three axes of detrended canonical correspondence analysis (DCCA) of Lepidoptera in the Kananiemensuo area. Canonical coefficients with a *t*-value higher than 2.0 in absolute value are indicated by *. The environmental variables are the means ($n = 20$) of proportional coverages of *Betula nana* (BETN), *Calluna vulgaris* (CALV), *Vaccinium uliginosum* (VACU), *Potentilla palustris* (POTP) and *Rubus chamaemorus* (RUBC), of maximum tree heights (HGHT), the number of trees (TREE) and bushes (BUSH), and of the distance from the mineral land (DIST).

	Canonical coefficients			Correlation coefficients			VIFS
Axis:	1	2	3	1	2	3	
Eigenvalue	0.45	0.15	0.12				
Cumulative % variance explained	36.5	48.7	58.3				
BETN	0.06	0.06	−0.30*	−0.44	0.08	−0.24	2.1
CALV	0.09	0.06	−0.09	−0.45	−0.50	0.04	5.8
VACU	0.08	0.12	−0.02	−0.14	0.41	−0.32	6.9
POTP	−0.06	−0.16*	−0.25*	0.01	0.15	−0.12	2.1
RUBC	−0.13	−0.01	−0.42*	−0.39	0.22	−0.38	5.4
HGHT	0.86*	0.03	−0.75*	0.98	−0.03	0.01	11.0
TREE	0.08	0.60*	0.51*	0.67	0.47	−0.00	5.8
BUSH	−0.13*	−0.12*	0.42*	0.29	−0.38	0.16	3.3
DIST	−0.10	0.50*	0.10	−0.65	0.18	0.10	6.3

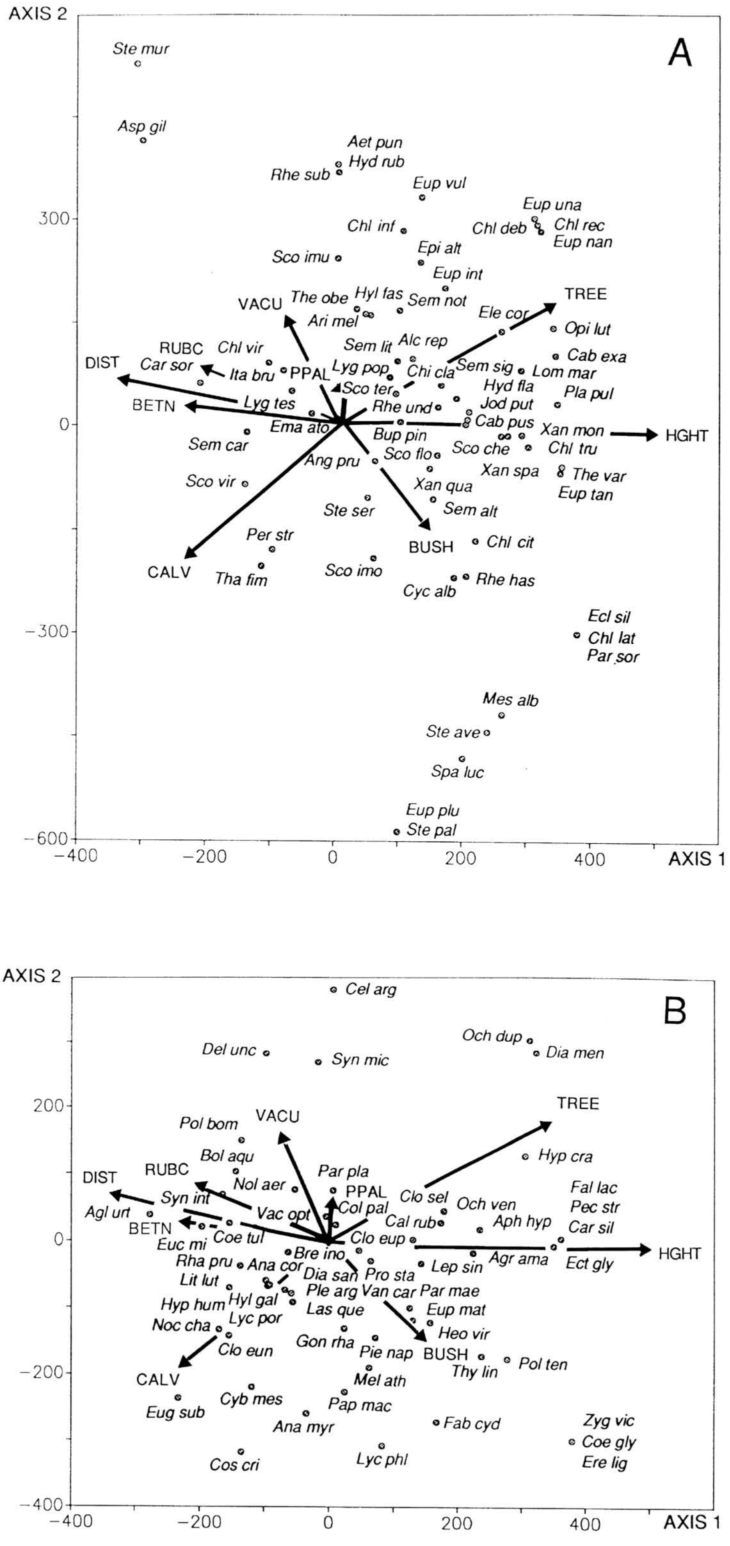

Fig. 7. Ordination diagram based on the detrended canonical correspondence analysis (DCCA) of the Lepidoptera on the Kananiemensuo mire, with respect to nine environmental variables (arrows). The species are abbreviated according to the first letter of their generic and the first three letters of their specific names (see Table 3 for full names). The environmental variables are the means (n = 20) of proportional coverages of *Betula nana* (BETN), *Calluna vulgaris* (CALV), *Vaccinium uliginosum* (VACU), *Potentilla palustris* (POTP) and *Rubus chamaemorus* (RUBC), of maximum tree heights (HGHT), the number of trees (TREE) and bushes (BUSH), and of the distance from the mineral land (DIST). — A. Geometridae. B. Other groups.

distance from the mineral land (DIST). The fraction of total variance in the environmental data extracted by the species axis 1 was 36.5 % and 12.2. % by the axis 2.

Tyrphobiont and tyrphophilous species (classification of Mikkola & Spitzer 1983, modified by Väisänen & Suoknuuti 1989 for local conditions) are concentrated on the left-hand side of the diagram (Fig. 7, cf. Table 3). *Idaea muricata*, *Aspitates gilvaria* and *Deltote uncula* which are species of open fens are situated at the upper left corner. Species occurring in both coniferous forests and pine bogs, e.g. *Chloroclysta infuscata*, *Hylaea fasciaria*, *Arichanna melanaria* and *Alcis repandatus*, were grouped mostly in the upper middle part. Only a couple of "wrong" classifications are obvious, all concerning very small samples like *Aglais urticae* and *Noctua chardinyi*, which normally do not live on the mire.

In the second DCCA (Table 5), the maximum tree height was used as covariable and the coverages of five plants as environmental variables. The proportional coverages of *Vaccinium uliginosum* (VACU) and *Calluna vulgaris* (CALV) were most determinate for the species composition along the first axis, and those of *C. vulgaris* (CALV) and *Betula nana* (BETN) along the second axis.

The characteristics of squares occupied by ten chosen species along the mire part of the transect 6 are given in Table 6. Since the original 5 × 5 m data was used in these calculations, the minor differences in habitat preferences within the major zones of the bog can also be seen in some species. Thus, the four abundant fritillaries *Brenthis ino*, *Boloria aquilonaris*, *Proclossiana eunomia* and *Clossiana euphrosyne* appeared to occur in largely different parts of the mire. *Carsia sororiata*, *Coenonympha tullia* and *B. aquilonaris* did not avoid the middle parts of the mire with open *Sphagnum* surfaces. Among the species of pine bogs, *Arichanna melanaria*, *Colias palaeno* and *Vacciniina optilete* seemed to prefer sites with *Vaccinium uliginosum* (and *Ledum palustre*), while *Perconia strigillaria*, *B. ino*, *C. euphrosyne* and *P. eunomia* were mostly encountered in semi-open pine bogs with *Calluna vulgaris*. The mire squares with *C. euphrosyne* and *B. ino* had on an average taller trees than those occupied by *P. eunomia*.

4. Discussion

4.1. Belt transect method

Although the forest cover of the transect belts varied a lot, no real visibility problems were encountered. Certainly counts are more easily carried out on open ground, but this effect was counterbalanced by the more difficult terrain for walking on the wet open mire. The forests were

Table 5. Canonical coefficients and the inter-set correlations of five environmental variables, associated with undergrowth, with the first three axes of detrended canonical correspondence analysis (DCCA) of Lepidoptera, when the mean of the maximum tree height per square (HGHT) has been used as covariable. Canonical coefficients with a *t*-value higher than 2.0 in absolute value are indicated by *. The environmental variables are the means (n = 20) of proportional coverages of *Betula nana* (BETN), *Calluna vulgaris* (CALV), *Vaccinium uliginosum* (VACU), *Potentilla palustris* (POTP) and *Rubus chamaemorus* (RUBC).

	Canonical coefficients			Correlation coefficients			VIFS
Axis:	1	2	3	1	2	3	
Eigenvalue	0.17	0.09	0.04				
Cumulative % variance explained	37.0	57.7	66.8				
BETN	–0.02	–0.19*	–0.02	–0.27	–0.66	–0.22	1.4
CALV	–0.15*	0.33*	0.07*	–0.36	0.57	–0.11	1.7
VACU	–0.29*	0.01	–0.01	–0.85	–0.22	0.13	4.6
POTP	–0.03	–0.03	–0.20*	–0.25	–0.25	–0.84	1.7
RUBC	–0.15	–0.07	–0.08	–0.84	0.03	–0.31	4.9

relatively open, but, of course, individuals possibly present in the forest canopies could not be seen at all. However, the transect belts did not include dense bush sections, which might have caused real problems. In general, recording is considered difficult if the width is greater than 5 m (Pollard 1977, 1982).

Almost all the species included ('macros' and burnet moths) are easily recognizable by an experienced observer in the field. However, the number of several moths may be underestimated due to their inactivity in the daytime, and in the case of the noctuid *Hypenodes humidalis*, due to its small size. It is also possible that single individuals of *Lycaeides idas* would have been misidentified as *Plebejus argus*, a very abundant blue species.

Although some migratory species of diurnal Lepidoptera may easily fly several kilometres, most species do not, and commonly their flights are surprisingly short (Scott 1975, Ehrlich 1984, Thomas 1984). Because long flights entail energy loss and the risk of encountering an environment unfavourable for reproduction, flights should be as short as possible without sacrificing the necessary resources and dispersal. The transect method has a considerable potential for assessing the value of different habitats for Lepidoptera and for detecting the order of magnitude of population changes (Moore 1975, Pollard et al. 1975, Pollard 1984, 1991). One of the main objectives of the method is to assess the effects of habitat management on populations. However, there are a number of factors which make such an assessment difficult. Some species are mobile; the counts may reflect the attraction of the adult butterflies to nectar sources (Pollard 1977). The abundance of flowering plants, especially *Epilobium angustifolium* L., was obviously one reason for the high number of individuals observed in the clear-cut areas, and this number was not necessarily a good estimate of the abundance of the immature stage of the same species at the same site.

Although adult Lepidoptera are considered to be more opportunistic and less specific in diet than larvae (Gilbert & Singer 1975), the belt transect method gave similar results on habitat preferences of mire Lepidoptera to those given by Krogerus (1960) largely on the basis of larval data, as far as the abundance of different species in the major habitat classes is considered. The scale used in the study, of course, affects the results (see Wiens 1992). The 100 m section data of the present investigation was associated with the major zonation of the mire and was not seriously affected by misleading interpatch flights. Although adult Lepidoptera are mobile insects, they seem to spend most of their time within the same zone where they live as larvae. Within this zone they can be encountered in other microhabitats, especially when there are nectar plants

Table 6. Mean values of environmental variables of the squares occupied by ten chosen species of Lepidoptera in the Kananiemensuo mire area. Results are given for each species calculated on the basis of the characteristics of the original unpooled 5 × 5 m squares in which the observations were made. The environmental variables are the distance from the mineral land (DIST), the maximum tree height (HGHT), and the proportional coverage of *Vaccinium uliginosum* (VACU), *Calluna vulgaris* (CALV) and open *Sphagnum* moss (SPHA). N = total number of individuals observed.

Species	*n*	DIST (m)	HGHT (m)	VACU (%)	CALV (%)	SPHA (%)
Colias palaeno	45	98	4.5	15	13	23
Vacciniina optilete	144	74	5.0	13	10	30
Brenthis ino	182	195	3.5	5	23	34
Boloria aquilonaris	66	602	1.0	1	15	55
Proclossiana eunomia	117	320	1.7	3	17	48
Clossiana euphrosyne	98	113	4.3	11	21	26
Coenonympha tullia	90	585	0.8	1	9	63
Carsia sororiata	294	719	0.7	0	9	65
Arichanna melanaria	248	56	6.2	17	4	26
Perconia strigillaria	38	48	4.0	5	28	29

such as *Potentilla palustris* available. The habit of drinking water may also affect the microdistribution of adult Lepidoptera (Adler 1982), increasing the number of visiting individuals at hollows.

4.2. Mire Lepidoptera in relation to environmental variation

The tree cover of the habitat (HGHT and TREE) accounted for most of the variation between sites in the present data on boreal Lepidoptera. Similar results emphasizing the importance of habitat structure are available from Central European mires (Meineke 1981, 1982). The tree cover is obviously inversely related to the amount of sunshine, but small open spots existed even within dense forests. Similar observations on butterflies are also available from other habitats and regions. For instance, the effects of increased light explained almost all the major tendencies seen in the reconstruction of butterfly communities in Amazonian forest fragments (Brown in Lovejoy et al. 1986). Thermal conditions influence activity patterns and growth of insects in all life stages. In Lepidoptera, thermoregulatory behaviour or positioning has been reported for eggs, larvae, pupae and adults (Weiss et al. 1988). Mikkola & Spitzer (1983) considered bog physiognomy and meso- and microclimate the most important factors affecting the species composition of mires. Emphasizing the role of the structure of vegetation, the present results seem to agree with this hypothesis.

The species richness was higher on the mineral lands, especially in forests, than on the adjacent mire. This reflects the fact that there is a much larger pool of species, e.g. geometrids, living in different kinds of forests and forest clearings than on mires in the region. According to Väisänen & Suoknuuti (1989), less than one fifth of the species known from the Kananiemensuo reserve, which includes forest only as narrow margins, can be classified as tyrphobiont or tyrphophilous species. There was also plenty of variation in the mineral land habitats from clear-fellings to pine and mixed forests. In particular the small clear-cut areas were also relatively rich habitats with many species of adult Lepidoptera typical of pine bogs. Somewhat similar results are available on northern Finnish bird communities (Helle 1985). The pioneer stages of forest succession were occupied by open habitat birds breeding originally on open bogs or shores.

Butterfly and moth diversity on the mire was highest in the pine bogs of the lagg and the marginal slope, declining towards the open bog centre and the aapa mire. It is a general observation that butterflies avoid shade and are often encountered in calm sunny places (e.g. Douwes 1975, Dennis & Bramley 1985, Warren 1985, Pivnick & McNeil 1987). This condition is often fulfilled on semi-open pine bogs, especially on the lagg and the marginal slope. On the sunny, but windy, bog centre, the low density of adult Lepidoptera may be associated with the low density of larval food plants (e.g. *Vaccinium uliginosum*, *Ledum palustre*, *Empetrum nigrum*), many of which grow only on scattered drier hummocks. Even among the tyrphophilous and tyrphobiont species very few (*Aspitates gilvaria*, *Idaea muricata*) were found only in the middle parts of the mire.

In addition to the tree cover, at least the coverage of *Vaccinium uliginosum* (and/or *Ledum palustre*), *Calluna vulgaris* and *Betula nana* were associated with the composition of diurnal butterfly and moth assemblages. Many species of mire Lepidoptera are polyphagous and live on the same common food plants (Seppänen 1970). Habitat segregation on peatlands may thus be more important than segregation of food plant species. Closely related ecologically similar species are sometimes stratified along mountain slopes and vertically within a forest, or segregated among successional stages within an area (Gilbert & Singer 1975, Gilbert 1984). This kind of segregation was observed here at least in closely related fritillaries: *P. eunomia* (larva mostly on on *Vaccinium uliginosum*), *B. aquilonaris* (on *V. oxycoccos*), *B. ino* (on *Rubus chamaemorus*) and *C. euphrosyne* (on *Viola* species and *Vaccinium uliginosum*). The latter two butterfly species are also common on mineral lands (e.g. Marttila et al. 1990).

The tree cover or the 'architecture' of the habitat, probably associated with the microclimatic factors, were more important for the butterfly and moth species than the floristic composition of the undergrowth. The Lepidoptera fauna is richest on pine bogs (as noted already by Krogerus 1960 and Mikkola 1976), which otherwise have been considered biologically relatively monotonous and poor in Finland. Most birds seem to prefer wetter mires, and most endangered species of plants grow on rich fens. Obviously, it is most unwise to predict the invertebrate diversity simply from the flora or vegetation alone, not to mention birds. Similar conclusions have been drawn by Meineke (1981, 1982).

4.3. Effects of landscape boundaries

Although one could expect the mire fauna to be impoverished on the marginal parts of the mire, the numbers of both species and individuals were high on the lagg and on the marginal slope near the forest-mire edge. The spatial location of an edge adjacent to a different lanscape element may result in distinct environmental conditions and species that characterize the edge effect (Forman & Moore 1992). In the present material there seem to be no species strictly associated with the ecotone or the band of modified vegetation between the forest and the mire, unless the ecotone is understood to be the whole lagg plus the marginal slope.

The distance from mineral land (DIST) accounted for the variation in the fauna. The high number of species observed on the lagg of the mire may partly be explained by the edge-effect (see e.g. Wiens 1976, Harris 1988). Near the forest-mire edge, species living in one habitat may penetrate the other, often by 10–30 m but sometimes only by a few metres. Forest species were often encountered on the pine bogs, but most mire species avoided dense forest (see Table 3). However, mire species were more often seen in the clear-cut areas. Thus, for most mire species, forest constituted a distinct barrier while clear-cuts were more like filters.

Physical and vegetational barriers are one of the most obvious limitations to flight at the edge of the habitat (Scott 1975). This may quite apparently lead to flight along the edge and the gathering of relatively large numbers of individuals near these habitat margins (the sink function of the boundary; Forman & Moore 1992). Some evidence is available in a study of several insect groups between a forest and a clear-cut area in northern Finland (Helle & Muona 1985). The traps with a window perpendicular to the edge caught significantly more Diptera than the other traps. The results on Coleoptera were in general similar.

In the present study, observations of some mobile species, e.g. *Colias palaeno*, *Lasiocampa quercus* and *Clossiana* ssp., suggested that this kind of flight along the edge, rather than any preference for that particular habitat, could partly explain the high numbers of individuals on the lagg. It is more probable for conspecifics to be encountered on the narrow lagg at the outer edge of the concentric bog than on the wide open bog centre. This may have had a considerable effect on the behaviour of certain species. When there are high densities of adult Lepidoptera on the lagg, these outer margins of the raised bog may receive a high proportion of eggs laid by females, if there is no specialized behaviour to avoid this. However, there are no systematic studies available on this phenomenon.

The traditional approach to the study of distribution and abundance of insects has often concentrated on comparisons of obviously different habitats. The present results suggest that environmental gradients and particularly discontinuities along them should receive more attention. Abrupt landscape boundaries may have unexpected consequences for biotic diversity.

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