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THE CARABID COMMUNITIES OF NATURAL AND DRAINED PEATLANDS IN THE BIEBRZA VALLEY, NE POLAND

ABSTRACT: Comparisons between the carabid communities of natural and drained fens in the Biebrza Valley (NE Poland) were made on the basis of trapped material. Fen drainage appears to result in a restructuring of species composition as there is only a limited (20–40%) similarity between the communities in natural and drained areas. The lowest species diversity was noted for a drained meadow on alder peat. *Agonum moestum* was dominant on natural fens, and in the one not cultivated and periodically flooded site on drained fens and *Carabus granulatus* or *Pterostichus nigrita* on drained ones. Trophic structure also differed, with hemizoophages of the genera *Amara* and *Harpalus* associated with agrocoenoses being present on drained fens but absent from natural ones. *Chlaenius costulatus*, a species now rare in Poland, is typical of peatlands, but was not present on drained sites. The number of sites accesible for it have declined as a result of wetland drainage.
KEY WORDS: Carabidae, peatlands, drainage, community structure, seasonal dynamics.

1. INTRODUCTION

The basin of the Biebrza river, in north-east Poland, has extensive peatland areas of unique value to Europe's natural heritage and partly included within the Biebrzański National Park established in 1993. There are also many rare species of plants and animals (Dyrcz 1972; Pałczyński *et al.* 1975; Rąkowski 1983), but besides its undoubted natural value, the area is also of great economic significance. The land has been utilized since the 16th century, when trees and hay were taken and islets originally covered with forest (now with sand only) were brought under cultivation (Czerwiński 1983). Only about a century ago did reclamation of an extensive area of peatland fen become possible. The drainage carried out led to degradation of much of the area, with the vegetation cover being changed irreversibly (Pałczyński 1972), the range of river

floodplains confined and moorshing of peat occurring as a result of the lowering of the water table. The latter process is characterized by a decline in organic matter content which effectively causes peat to "disappear" as intensive mineralization progresses. The action is especially rapid in the first years after drainage (Marek 1965; Walczyna 1973); but the overall process can be slower or faster, depending on humidity conditions, the type of peat and the way in which it is utilized, as well as on the activity of soil organisms (Andrzejewska *et al.* 1983; Andrzejewska 1985; Kajak 1985; Kajak *et al.* 1985; Makulec and Chmielewski 1994; Pętal 1994; Wasilewska 1994).

Being mostly predatory, carabid beetles play an indirect role in the processes by which organic matter is mineralized and humified by way of their impact on saprophagous organisms and hence on the breakdown of organic matter and its transfer down the soil profile (Grüm 1973, 1976; Richards 1979; Benet and Fonseca 1980). It is thus of value to characterize the communities of carabids in peatlands from the point of view of their dominance and trophic structure and species diversity, as well as to define the changes they undergo as a result of the drainage of different types of peat and the passage of time.

2. STUDY AREA, METHODS AND MATERIALS

The Biebrza Wetlands, were formed in the course of the Central Poland Glaciation. At the time of the Baltic Glaciation, this was a proglacial river valley in which the processes of peat forming began to develop as soon as the ice retreated. Today, the Basin is an extensive depression divided into the Upper (Northern), Middle and Lower (Southern) Biebrza Basins, as well as the Wizna Fen. The area is relatively well-known from the environmental point of view (peat types and vegetation), especially in the Lower Biebrza and Wizna Fen (Marek 1965; Oświt 1965; Okruszko 1977; Liwski *et al.* 1984; Pałczyński 1972; Pałczyński and Stepa 1992).

The research described was done on natural fens in the Lower Biebrza Basin and in drained fens in the Wizna Fen (Fig. 1). The choice of the exact sites made reference to the type of peat, prevailing water relations and vegetation (Table 1).

2.1. NATURAL FENS

The characteristic feature here is the zonal distribution of plant communities that results from the extent of floods (Marek 1965; Oświt 1965). The several vegetation zones developed across the river valley:

zone I, closest to the river and characterized by immersed swamp vegetation with species like reed (*Phragmites communis*); sweet flag (*Acorus calamus*), swamp horsetail (*Equisetum limosum*), great reedmace (*Typha latifolia*) and lesser reedmace (*T. angustifolia*);

zone II, also of immersed vegetation consisting of wet tall-sedge swamp (Magnocaricetea). More than 90% of the area are covered by stiff sedge (*Caricetum strictae*). Also present are *Carex gracilis*

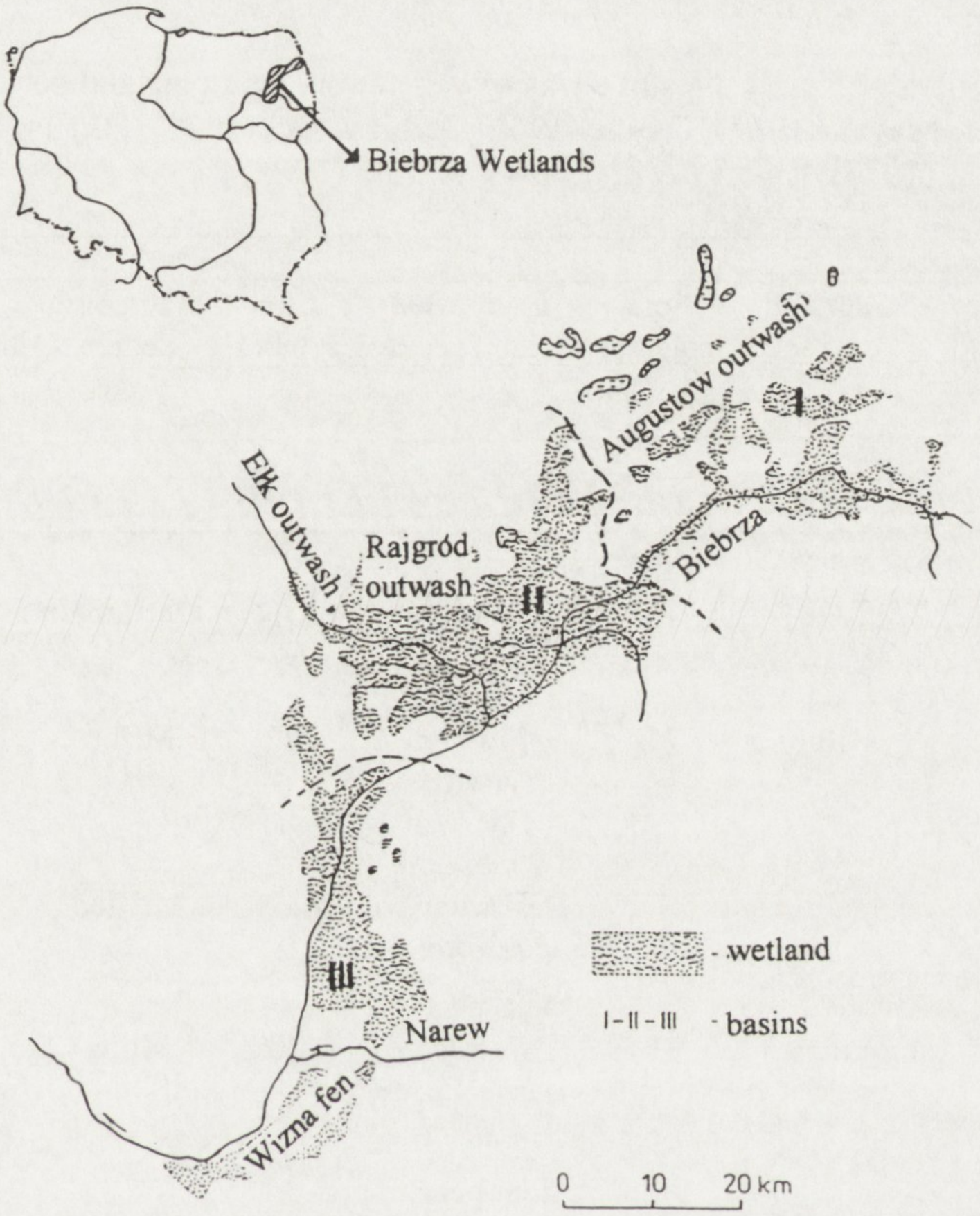

Fig. 1. Location of fens in the Biebrza Valley I – Upper (Northern) Basin, II – Middle Basin, III – Lower (Southern) Basin and Wizna Fen, after Okruszko (1990)

and lesser pond sedge *C. acutiformis*. The zone has a characteristic tussock structure. Bordering onto it directly are sedge moss communities of the class Scheuchzerio Caricetea, which form vegetation zones III and IV and are characterized by the presence of emersed species (Table 1);

zone III, also of tussock vegetation, has the sedge-moss association (*Caricetum paradoxae*), with other dominant species being slender sedge *C. lasiocarpa*, *C. fusca* and common cotton-grass (*Eriophorum angustifolium*);

zone IV, an association of lesser tussock sedge (*Caricetum diandre*) with a developed and species-rich mossy layer of mosses associated with permanent high water level;

zone V, furthest from the river, which is the alder swamp association (*Carici elongatae Alnetum boreale*) characterized by thickets of black alder *Alnus glutinosa*.

The research embraced zones II to V, namely the associations of stiff sedge (Cs), *Caricetum paradoxae* (Cp), lesser tussock sedge (Cd) and alder (Ce) (Table 1). The first two associatons are on sedge peat, while the association with lesser tussock sedge is on moss peat and the alder carr on alder swamp peat. In relation to the degree of marshiness, Okruszko (1977) and Liwski *et al.* (1984) divided these soils into three groups: slightly-marshy (Pt I), medium-marshy (Pt II) and strongly-marshy (Pt III) (Table 1). These soils have a markedly acid reaction, with pH values between 4.7 and 5.2 (Pałczyński 1972).

Water covers the study areas in spring. It falls gradually, fastest in the alder carr. The association with lesser tus-

Table 1. Characteristics of study sites in terms of vegetation, peat type and period of utilization, after: Marek (1965), Oświt (1965), Pałczyński (1972), Okruszko (1977), Liwski *et al.* (1984), Kajak (1985)

Natural fens					Drained fens			
Plant community (zonal arrangement in relation to river)	Site symbol	Swamping degree	Soil moisture	Dominated plant species	Site symbol	Moorshing degree	Soil moisture	Years after drainage
				Sedge peat				
Caricetum strictae (zone II)	Cs	PtIIbb*	75	*Caricetum gracilis*	MF	MtIIcb*	74	No data
Caricetum paradoxae (zone III)	Cp	PtIIbb	75	*Festuca rubra, Dactylis glomerata*	M2	MtIbb	65	1–2
				Deschampsia caesoitosa	M100	MtIIIcc	59	>100
				Moss peat				
Caricetum diandrae (zone IV)	Cd	PtIcc	81	*Festuca rubra, Carex rostrata*	M20A	MtIaa	80	15–20
				Alder peat				
Alder – *Carici elongatae Alnetum boreale* (zone V)	Ce	PtIIIab	No data	*Festuca rubra*	M20C	MtIIcc	55	15–20
				alder	A20C	MtIIcc	55	15–20

*Pt – natural peats, Mt – moorshed peats; Roman numerals denote degree of marshiness on a 3–point scale; letters a, b and c denote degree of decomposition of peat from the lowest to the highest, at a depth of 30–80 cm – first letter, at a depth of 80–130 cm – second letter (Liwski *et al.* 1984).

sock sedge is basically marshy throughout the year. At the time the research was carried out the extent of floodwaters was as follows: the association of stiff sedge (Cs) had water between tussocks until the end of June, while water retreated from the association with *Carex paradoxa* (Cp) about two weeks earlier. A high level of water was maintained in the alder carr site until May.

The fragments of the study areas with sedge associations nearest to the embankment were utilized, being mown in late June and early July.

The research on the natural fens was carried out in 1982. Carabids were trapped continuously between May and November, with traps being emptied every week. There were 10 traps (Ø – 7 cm, 10 cm deep) per site (plant association). In tussock associations (*Caricetum strictae* and *Caricetum paradoxae* the traps were placed alternately on tussocks and between them. A total of 850 samples were collected.

The natural fens acted as a control in relation to the drained fens described below.

2.2. DRAINED FENS

The study included two groups of drained fens used as mown meadows and dominated by sedges and grasses (Table 1). The first group comprised meadows on peaty soils of sedge origin, differing in the length of time after drainage 2–100 years (Table 1). The meadows sites were chosen in such a way as to permit the tracing of likely changes over time in the structure of the carabid communities of drained fens.

Mean seasonal moisture on the meadows ranged between 58 and 75% by weight (Table 1). The meadow with *Caricetum gracile* – that nearest the river – was flooded from time to time. Only this site was not cultivated, but mown. The soils were moderately acidic, with pH values of between 5.1 and 6.7 (Kajak *et al.* 1985).

The second study site consisted of drained fens used as meadows and located on peats of different origin (i.e. sedge, moss and alder- swamp peats), but all drained at the same time (Kajak *et al.* 1985), as well as swampy alder woodland. The meadows and woodland were selected with a view to deducing likely changes in the carabid communities of drained fens in relation to the type of peat.

The mean soil moisture ranged between 61 and 81% by weight. Values were lowest in the soil developed from alder peat and highest in those developed from moss peat (Table 1).The pH values were of 5.9 – 6.0 (Kajak *et al.* 1985). Okruszko (1977) and Liwski *et al.* (1984) divided peaty soils in relation to the degree of moorshing as weakly-moorshed (Mt I), moderately-moorshed (Mt II) and strongly-moorshed (Mt III). They also distinguished degrees of decomposition of peat from weak (a) to strong (c), with an intermediate level (b) (Table 1). The most moorshed soils were those of alder-swamp origin (Table 1).

Samples on the drained fens were taken in the years 1978–1979. In the former year, 20 traps (Ø – 7cm, 10cm deep) were set at each site and in the latter 10. The traps were placed once or twice a month for two days, in the period between the end of April and November. Totals of 270 and 780 samples were collected in 1978 and 1979 respectively.

2.3 METHODS OF ANALYSIS OF THE MATERIAL

The species similarity index of Marczewski and Steinhaus (1959), the Shannon and Weaver (1963) diversity index H' and Pielou's J index of evenness (1966) were analysed.

The similarrity index was calculated using the following formula:

$$s = \frac{w}{a + b - w}$$

where a – the number of individuals of given species in the community A, b – the number of individuals of given species in the community B, w – the number of individuals of common species for the communities A and B. Used in the calculation of the index of similarity were the numbers of individuals of different species over the whole research period. The following scale was adopted in describing the similarity of communities:

over 70% – very great similarity
50.01–70.00% – great similarity
40.01–50.00% – moderate similarity
20.00–40.00% – slight similarity

The diversity index was calculated using the following formula:

$$H' = \sum_{i=1}^{S} p_i \ln p_i$$

where S – is the number of species, p_i = ni/n, ni – is the numerical abundance of different species in the year of study and n – is the total number of individuals caught in that year.

The index of evenness was calculated by reference to the abundance of the different species in each year of study, in accordance with the formula

$$J = H'/\ln S$$

where S – is the number of species in a given community and H' the value of the diversity index for the given community.

The following scale was applied in describing dominance structure:

over 30.00 %	dominant
30.00–10.01 %	sub-dominant
10.00–5.01 %	recedent
below 5.00 %	accessory

The relative abundance of carabids was estimated by reference to the incidence of captures, i.e. the number of individuals trapped per trap per day (24 hours). The significance of differences between mean capture rates at the different study sites and in successive years were assessed using Wilcoxon's non-parametric test (Siegel 1956). In turn, the test from Hutchenson (1970) was applied to determine the significance of differences between coefficients of diversity.

To describe the environmental requirements of carabids, groups of species were distinguished by reference to: humidity preferences (hygrophilic, mesophilic and xerophilic); development type (applying the classic division of Larsson (1939) – as spring or autumnal; feeding strategy – zoophagous or hemizoophagous; flying ability – macropterous (able to fly), dimorphic (periodically capable of flight) or brachypterous (flightless). Species were also classed as large or small (longer or shorter than 13 mm).

3. RESULTS

3.1. COMMUNITIES OF CARABIDS ON NATURAL FENS

The highest capture rate was recorded from natural alder carr (Table 2). This rate differed statistically from those noted in the other plant associations, with the exception of the association of lesser tussock sedge adjacent to the carr community ($p > 0.05$). The lowest, significantly different, rates of capture of beetles were noted in *Caricetum strictae* (Cs) and *Caricetum paradoxae* (Cp), i.e. in the flooded zone ($p < 0.05$).

The population dynamics of Carabidae were characterized by spring and summer peaks in abundance (Fig. 2). The spring peak came earliest (in early June) in alder carr, with the shifts in the sedge associations where a high water level remained longest were to the end of June, or even into July in the case of the association with stiff sedge (Fig. 2).

In associations of tussock vegetation, the capture rates on and between tussocks did not differ significantly ($p > 0.05$), in spite of an observed intensification of activity between tussocks in summer (July) (Fig. 3).

Table 2. Mean capture rates of carabids (number of individuals captured per trap-day in period May-October) on natural fens (for whole community as well as in traps on or between tusssocks) and drained fens (site description in Table 1)

Site	1978	1979	1982		
			total community	tussocks	between tussocks
natural fens					
Cs	–	–	0.12±0.12	0.11±0.19	0.15±0.15
Cp	–	–	0.07±0.08	0.05±0.06	0.10±0.10
Cd	–	–	0.29±0.39	–	–
Ce	–	–	0.57±0.39	–	–
drained fens					
MF	–	0.36±0.70	–	–	–
M2	0.04±0.07	0.36±0.48	–	–	–
M20B	0.10±0.14	0.24±0.31	–	–	–
M100	0.12±0.15	0.04±0.06	–	–	–
M20A	0.03±0.03	0.09±0.10	–	–	–
M20C	0.19±0.23	0.94±0.93	–	–	–
A20C	0.15±0.21	0.39±0.61	–	–	–

The greatest number of carabid species (21) was recorded from alder carr. Numbers of species were lower (in the range 15 to 17) in the sedge associations (Appendix 1). The numbers of species increased successively with distance of an association from the river. 11 species were common to all the natural plant associations (Appendix 1), with *A. moestum* among them being the absolute dominant in all. Individuals of this species accounted for 44% of all beetles caught, while the remaining species were in the main accessory or recedent in most of the associations, achieving dominance in only a few cases (Appendix 1).

As a species now rare in Poland, *Chlaenius costulatus* was an important find in the lesser tussock sedge association. This species is typical of natural fens, and the number of sites has declined as ever more drainage work has been carried out (Karpiński and Makólski 1954; Burakowski *et al.* 1974).

The natural fens studied showed great similarity in their communities of carabid species (Fig. 4). Most similar (with indices over 70%) were the faunas of *Caricetum paradoxae* (Cp) and *Caricetum strictae* (Cs) and *Caricetum paradoxae* and *Caricetum diandrae* (Cp). The carabid communities in the emersed zone (*Caricetum diandrae* association) were more similar to those of alder carr than that from the flooded zone (*Caricetum strictae*) (Fig. 4). Groupings from adjacent fens are thus more similar to one another than those that are separated in space.

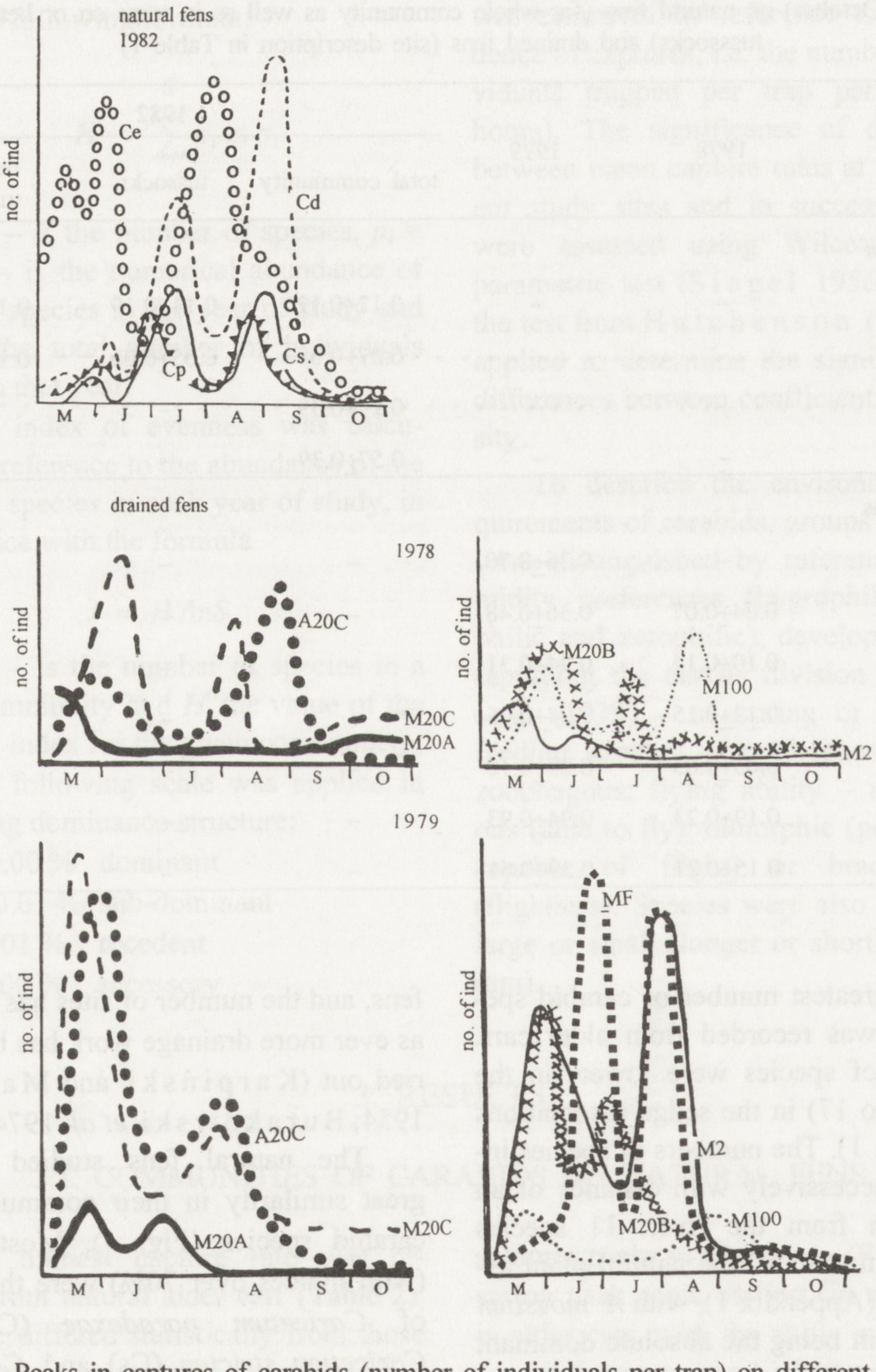

Fig. 2. Peaks in captures of carabids (number of individuals per trap) on different sites of natural fens (Cs, Cp, Cd., Ce) and on different sites of drained fens (MF, M2, M20B, M100, M20A, M20C, A20C (period May-October, site description see Table 1)

The species diversities of the sedgeland associations (Cs, Cp and Cd) were significantly lower than that in alder carr (Ce) (Table 3), but did not differ significantly from one another (Table 3). Values for the coefficient of evenness showed similar trends to those for species diversity, i.e. showed highest species evenness for the carabid community of alder carr (Table 3).

The dominance structures of the carabid communities on the natural fens studied were characterized by the large proportion of accessory and recedent spe-

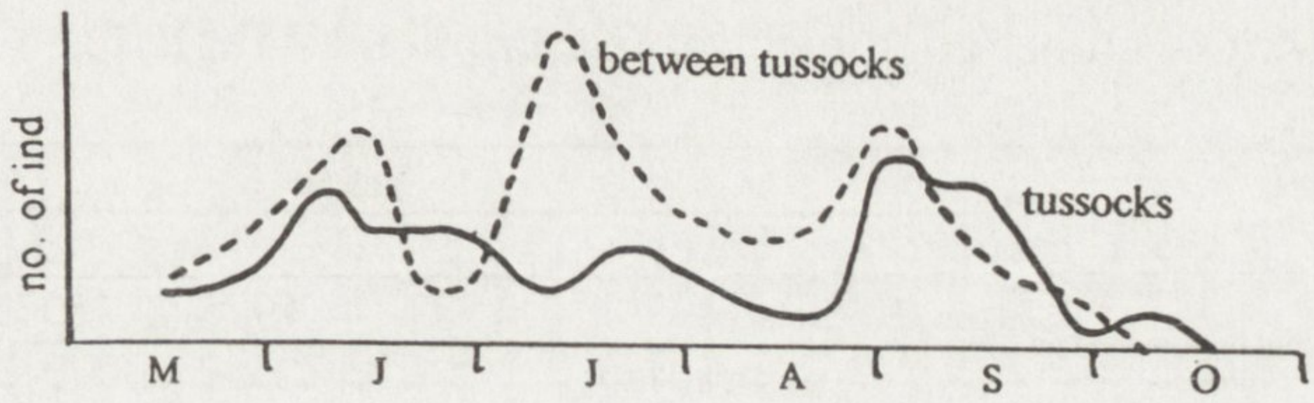

Fig. 3. Peaks in captures of carabids (number of individuals per trap) on and between hummocks of the *Caricetum strictae* (Cs) and *Caricetum paradoxae* (Cp) associations of natural fens (period May-October)

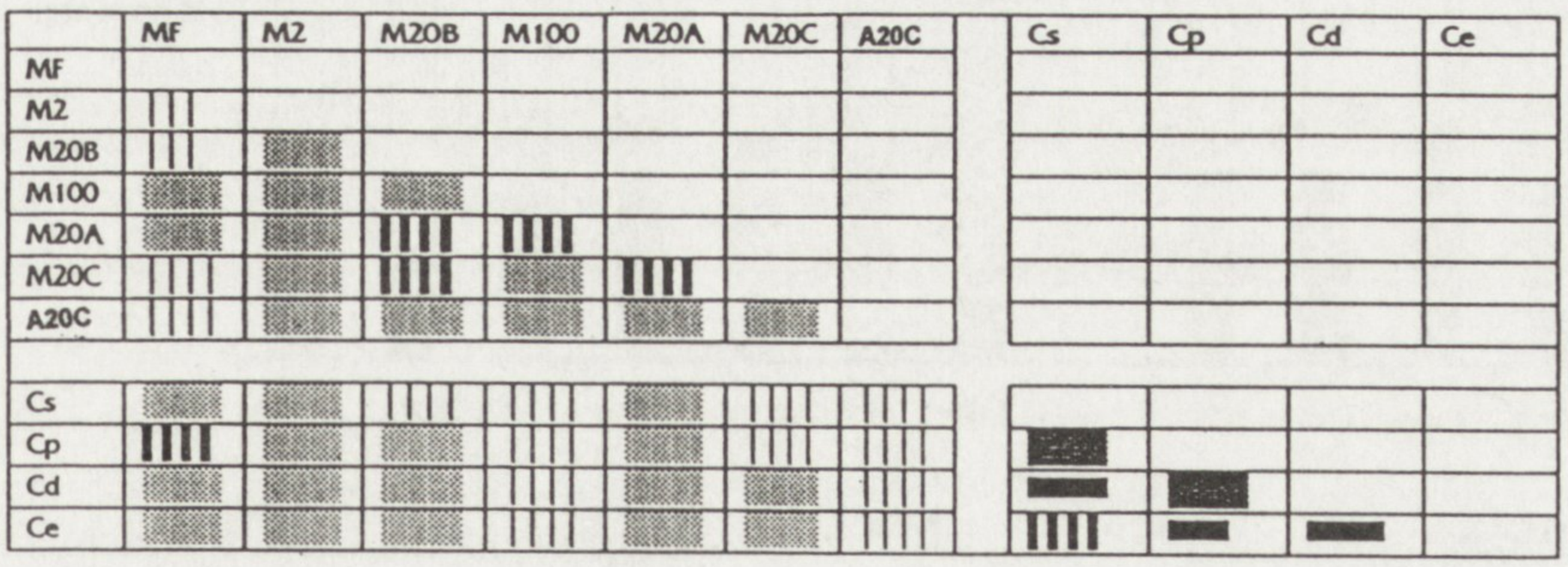

Fig. 4. Species similarity of the carabid communities different sites of natural (Cs, Cp, Cd, Ce) and drained (MF, M2, M20B, M100, M20A, M20C, A20C) fens (values of Marczewski and Steinhaus index (1959) for data May-October, for site description see Table 1)

cies (Fig. 5). The most marshy site (*Caricetum diandre*, Cd) had no dominant species (Fig. 5).

From the point of view of environmental preferences, most of the carabids studied were hygrophilic. Mesophilic species also played a significant role, and one which was greater in communities further and further from the river. They attained greatest significance in alder

Table 3. Diversity of carabid communities estimated by reference to values for the Shannon–Weaver H' index and the index of evennes (J) of different sites (Cs, Cp, Cd, Ce) of natural and different sites (MF, M2, M20B, M100, M20A, M20C, A20C) of drained fens (May–October combined, site description as Table 1)

Site	Index					
	H'			J		
	1978	1979	1982	1978	1979	1982
natural fens						
Cs	–	–	1.79	–	–	0.66
Cp	–	–	1.74	–	–	0.63
Cd	–	–	1.64	–	–	0.58
Ce	–	–	2.15	–	–	0.70
drained fens						
MF	–	1.45	–	–	0.70	–
M2	2.24	1.71	–	0.93	0.69	–
M20B	1.38	2.21	–	0.71	0.86	–
M100	0.97	1.73	–	0.70	0.65	–
M20A	1.89	1.34	–	0.97	0.83	–
M20C	0.89	0.77	–	0.43	0.29	–
A20C	2.06	2.03	–	0.78	0.75	–

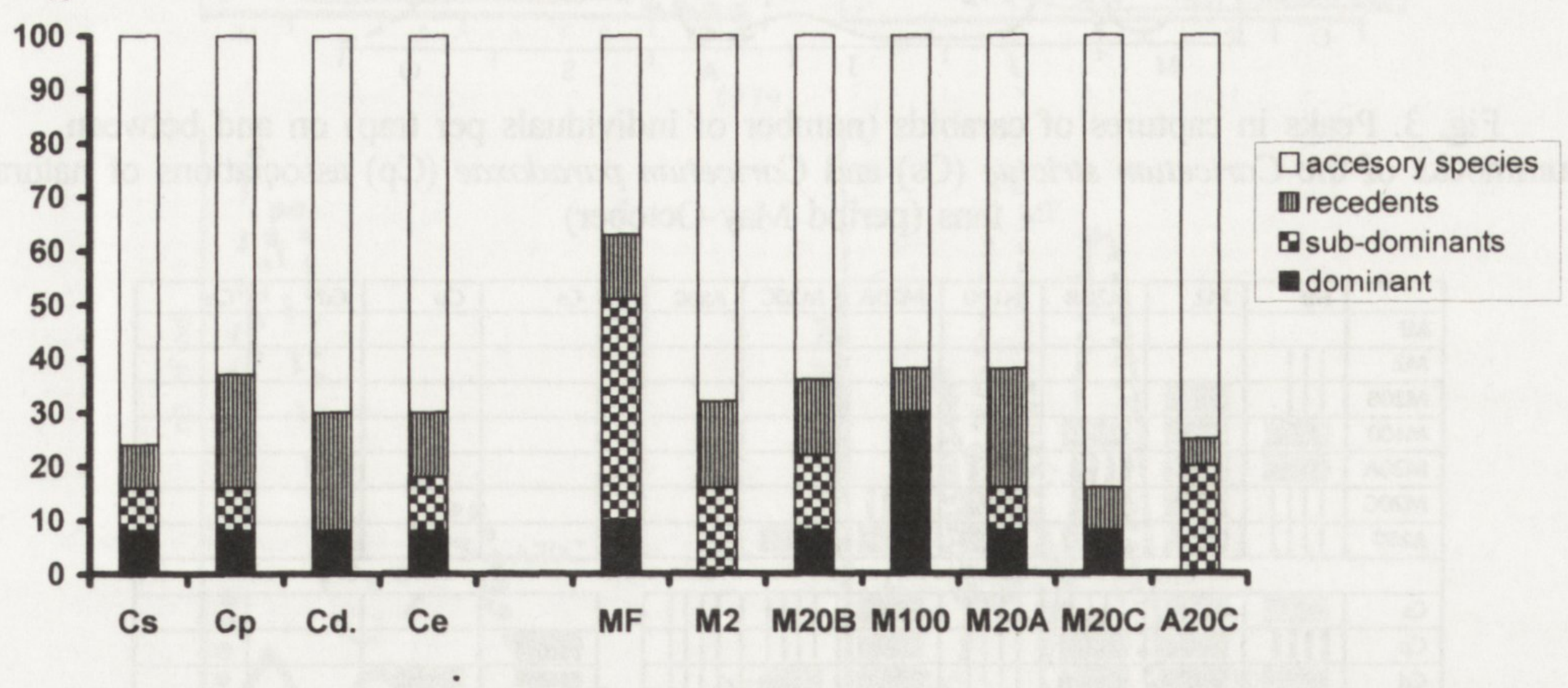

Fig. 5. Percentage shares of all material taken by species of different levels of dominance on different sites of natural (Cs, Cp, Cd., Ce) and drained (MF, M2, M20B, M100, M20A, M20C, A20C) fens (period May-October, for site description see Table 1)

carr. The relationship noted corresponded to the hydrological conditions prevailing in the environments studied (extent and duration of river flooding, see Table 1). Where developmental type was concerned, spring species of carabid accounted for the greatest proportion (Table 5). The share of autumn species was greater in associations further from the river and was greatest in alder carr (Table 5). Small zoophages (of body length mm) were prevalent in the communities, as were macropterous species, i.e. those capable of flight, and dimorphic species occasionally capable of flight. The share of flightless (brachypterous) species is greater in associations further from the river and greatest in alder carr (Table 5).

3.2. THE CARABID COMMUNITIES OF DRAINED FENS

The highest capture rates were noted on alder-swamp peats on a meadow (M20C) and in alder carr (A20C), while the lowest characterized the meadow on moss peat (M20A) and a sedge peat drained a century ago (M100) (Table 2). Capture rates were lower on all the sites in the first year than in the second (Table 2). However, the communities showed similar population dynamics in both years of study, on all the meadows examined. To be seen in all cases were two peaks in abundance, one in spring and one in summer (Fig. 2). The one exception was the meadow on moss peat drained 10–20 years previously (M20A), on which the 1978 research revealed one peak in the capture rate at the beginning of May (Fig. 1). On most of the studied meadows, the first (spring) peak was usually noted in late May or early June, and the second in mid July or August (summer) (Fig. 2).

Two species – *Carabus granulatus* and *Pterostichus nigrita* – were common to all the meadows on drained fen (Appendix 2). On most of the meadows, *C. granulatus* was dominant or sub-dominant (Appendix 2). Only on the meadow where drainage had taken place just 2 years before (M2), and on the most-moorshed, alder-peat meadow and the meadow inundated periodically (MF) was this an accessory or recedent species (Appendix 2). In contrast, *P. nigrita* was only dominant on the periodically-flooded meadow, as well as on moss peats. At the remaining sites it was an accessory species (Appendix 2).

The meadows on fens drained at the same time were characterized by carabid communities with moderate values of the species similarity index (40.1–50.0%), irrespective of the type of peat. In contrast, the group of meadows on sedge peats drained at different times – located in different parts of the valley – had carabid communities of limited similarity (indices in the range 20.0–40.0%) or no similarity. Only on meadows which had been drained a relatively long time ago did carabid groupings show moderate values of the similarity index (40.1–50.0%), in spite of the considerable distances between sites.

The two years of study featured similar trends for the carabid diversity of meadows on the different peats. Diversity was lowest on the meadow on alder-peats (M20C), higher on the one on moss peats (M20A) and highest of all on that on sedge peats (M20B) (Tables 3 and 4). The indices of evenness took on very different values on the meadows studied (from 0.29 to 0.97, Table 3). The lowest species evenness characterized the carabid communities of meadows on alder-

Table 4. Significance of differences between H' diversity indices for the different sites on drained peats in the different years of study (for site description see Table 1)

Significance of differences between years		M.2	M20B	M100	M20A	M20C	A20C	MF	M2	M20B	M100	M20A	M20C	A20C
–	MF	–	–	–	–	–	–		+++	+++	ns	ns	+++	++
+	M2		+++	+++	+	+++	ns			+	ns	ns	+++	+
+++	M20B			++	+	++	++				+++	+	+	+++
+	M100				+++	ns	+++					+++	+++	+
ns	M20A					+++	+						+	++
ns	M20C						+++							+
ns	A20C													

ns – not significant, $p>0.05$; + $p<0.05$; ++ $p<0.01$; +++ $p<0.001$

swamp peat (Table 3). Values for this index did not always coincide with those for the diversity index. This was the case for meadows on moss and sedge peats, on which carabids were often characterized by high evenness despite low species diversity (Table 3).

Four of the meadows had a dominant species (i.e. one accounting for more than 30% of all individuals, Appendix 2). Such a species was only lacking on meadows on sedge peat which had been drained 2 or 10–20 years previously (M2 and M20B). The alder carr (A20C) also had no dominant carabid within the grouping (Appendix 2). The meadows on the different peats all drained at the same time (M20A, M20B and M20C) had 2 dominant species: *Carabus granulatus*, dominant on meadows on moss peat, where it accounted for c. 33% of all individuals, and *Pterostichus caerulescens*, accounting for 82% of the carabids on the meadow with alder-swamp peat. There were also 2 dominant species on the series of meadows on sedge peats which had been drained at different times. The meadow drained 100 years before (M100) had a community dominated by *C. granulatus* and *P. vulgaris*, which accounted for 45 and 47% of individuals respectively, while the periodically-flooded meadow (MF) had *Agonum moestum* as a dominant accounting for over 55% of the total carabid population.

Trends in the dominance structure of communities were the same in both years, with accessory species being in the majority (Fig. 5). Their role was greatest on meadows on alder peat and drained most recently (Fig. 5). There was also a lack of sub-dominants in the communities of the most-moorshed peats – the alder peat (M20C) and the peat drained 100 years ago (M100) (Fig. 5). The largest share in the carabid community of the peri-

Table 5. Ecological characteristics of carabid groupings on different sites (Cs, Cp, Cd, Ce) of natural fens (N – no. of species, % share of species among all those recorded, excluding indeterminates; site description as in Table 1)

Groups	Site							
	Cs		Cp		Cd		Ce	
	N	%	N	%	N	%	N	%
Feeding group								
zoophages:								
small	12	80	13	81	13	77	18	86
large	3	20	3	19	4	23	3	14
hemizoophages	–	–	–	–	–	–	–	–
Development type:								
spring	15	100	15	94	15	88	18	86
autumn	–	–	1	6	2	12	3	14
Humidity group:								
hygrophilic	14	93	15	94	14	82	17	81
mesophilic	1	7	1	6	3	18	4	19
xerophilic	–	–	–	–	–	–	–	–
Flying ability:								
macropterous (flying)	9	60	9	56	8	47	11	52
dimorphic (transitorily capable of flight)	5	33	6	38	6	35	6	29
brachypterous (not flying)	1	7	1	6	2	12	4	19

Table 6. Ecological characteristics of carabid groupings on different sites (MF, M2, M20B, M20A, M20C, A20C, M100) of drained fens (N – no. of species, % – share of species among all those recorded, excluding intdeterminates; site description as in Table 1), for whole study period

Groups	Site													
	MF		M2		M20B		M20A		M20C		A20C		M100	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Feeding group														
zoophages:														
small	7	87	10	62	11	79	6	60	9	60	15	79	5	62
large	1	13	4	25	2	14	3	30	2	13	2	10	3	38
hemizoophages	–	–	2	12	1	7	1	10	4	27	2	10	–	–
Development type:														
spring	8	100	13	81	13	93	8	80	13	81	14	70	6	75
autumn	–	–	5	19	1	7	2	20	3	19	6	30	2	25
Humidity group:														
hygrophillic	8	100	11	65	10	71	6	60	7	44	12	60	5	62
mesophilic	–	–	6	35	4	29	4	40	8	50	7	35	3	38
xerophilic	–	–	–	–	–	–	–	–	1	6	1	5	–	–
Flying ability:														
macropterous (flying)	5	62	8	50	8	57	5	50	10	62	10	52	4	50
dimorphic (transitorily caable of flight)	3	38	8	50	6	42	5	50	6	37	7	37	4	50
brachypterous (not flying)	–	–	–	–	–	–	–	–	–	–	2	10	–	–

odically-flooded meadow was taken by accessory and sub-dominant species (Fig. 5).

Hemizoophages occurred on almost all the meadows (species of the genera *Amara* and *Harpalus* associated with agrocoenoses). The greatest proportion of such species was noted on the meadow on alder-swamp peat (Tables 6). The predominant species were those of the spring type of development, with the greatest share of autumnal species being noted on the sedge-peat meadow drained 100 years ago (Table 6). There was also a prevalence of hygrophilic species, with xerophilic species appearing on sites located on alder-swamp peat (A20C and meadow M20C), where humidity was lower than at sites on the other types of peat. Species capable of flight were dominant in the communities studied, while flightless (brachypterous) species were only present in alder carr (site A20C, Tables 6).

4. DISCUSSION

The environmental conditions of the fens (i.e. cyclical flooding of rivers and permanent marshiness in the case of natural sites, or periodic desiccation and agrotechnical measures in the case of drained fens) ensure that the carabid communities present are adapted to variable conditions and show certain characteristic features (Table 7).

Two peaks for beetle capture rates were noted on both natural and drained peats. The latter had earlier peaks than the former, though this does not imply an extended period of carabid activity. Such dynamics for captures may however attest to the influence of river flooding in the case of natural peats, and to periodic summer desiccation in the case of drained ones.

The communities of carabids on natural and drained peats are dominated by species capable of flight, with spring-type development (wintering of the

Table 7. Comparison of carabid communities of natural and drained fens

Characteristic	Natural fens	Drained fens
Seasonal dynamics	two peaks of activity later in season	two peaks of activity earlier in season
Species similarity	limited	
Species diversity	highest in alder carr lowest at most moorshed site	highest in alder carr lowest at most moorshed site
Index of evenness	lowest at most moorshedsite	lowest at most moorshed site
Dominance structure	one dominant	one dominant
Share of species in different dominance groups	accessory species dominant	accessory species dominant
Trophic structure	zoophages	zoophages, hemizoophages
Flying ability	mainly able to fly	mainly able to fly
Development type	mainly spring	mainly spring
Humidity	predominantly hygrophilic	hygrophilic and mesophilic
Environment	species associated with marshy areas and wet meadows	species associated with meadows and arable fields

imago). A capacity to move about rapidly allows the beetles to avoid either flooded or dried-out areas. Seasonal migrations of carabids linked with the search for optimal breeding and wintering sites have been described in relation to marsh and field communities (Desender 1982; Wallin 1987; Fråmbs 1994). The places on natural fens where beetles might survive the winter or periods of flooding may thus be considered to be alder carr and mineral islands.

A prevalence of species of spring-type development has been linked by Larsson (1939), Lindroth (1949) and Paarman (1979) with a continental climate and a short growing season. In contrast, Thiele (1977) made the link with humidity conditions, considering species of spring-type development characteristic of wetland environments. The fens studied are characterized by a short growing season lasting 180–200 days and by the occurrence of only 80 frost-free days (Czerwiński 1983; Rąkowski 1983). For this reason, the area also has species reproducing earlier in the season, and hence of spring-type development, whose larvae develop in early summer (Larsson 1939), i.e. in the most favourable period (when floods have ended and soils have not dried out).

The carabid communities characteristic of marshland environments undergo a complete change in species composition following fen drainage. The species appearing (e.g. those of the genera *Amara* and *Harpalus*) are of different environmental preferences, being characteristic of agricultural areas. Mesophilic species also take on a greater role in these communities, and a further distinguishing feature is the presence of hemizoophages (Table 7). Similar changes in the carabid communities of drained peatland environments were noted by Fråmbs (1994), and spiders (*Araneae*) have also been shown to react in the same way (Kajak and Kaczmarek 1994). In contrast, in the cases of other soil organisms like nematodes, earthworms, springtails and ants, there is apparently no total reconstruction of the species composition of groupings (Wasilewska 1991; Makulec 1991; Pętal 1991; Kaczmarek unpublished data; Kajak unpublished data). The communities of natural and drained fens show only limited similarity in terms of species, suggesting that they are distinct (Table 7). Species not present previously would seem to appear in carabid communities relatively quickly – a fact attested to by the limited similarity of communities of these beetles between meadows on peatlands drained in different years (Fig. 4). Perhaps indicative of the significant influence that fen drainage and agrotechnical measures exert on carabid species composition is the great similarity between the communities noted on natural peatlands, and on the unmanaged meadow periodically subject to flooding (MF) (Fig. 4).

Carabid species diversity was linked with the marshiness and degree of moorshing of peats (Table 7). The influence of the latter factor was seen most clearly on the meadow on the most-moorshed alder-peat, which had the community of the lowest diversity. A significant difference between this meadow and the others on sedge and moss peats has also been noted in the case of other invertebrates, with the abundance and species richness of saprophagous and predatory species being lower, and numbers of phytophages periodically high (Kajak *et al.* 1985, 1991). Kaczmarek (1991) and Wasilewska (1991) both considered this an indication of the ecological instability of the meadow on the most moorshed peat, which is prone to periodic

desiccation. It is therefore possible to advance a general conclusion that natural fens are characterised by specific carabid communities which are as permanent as the environmental conditions permit, since those subject to the action of powerful environmental factors (drainage and agricultural utilization) experience a complete rearrangement of their species composition.

5. SUMMARY

The carabid communities of natural and drained fens in the Biebrza Valley (NE Poland) (Table 1, Fig. 1) were analysed in relation to material trapped in the 1978–1982 seasons. Species composition, similarity and diversity were determined.

The dynamics of capture featured two peaks in the course of the season, which came earlier on the drained fens than on the natural ones (Fig. 2). Where the latter were tussocky (i.e. with the associations of stiff sedge or *Carex paradoxa*), the capture rates did not differ greatly between trapping sites on and between the tussocks (Table 2). The only exception came in July, when more beetles were captured between tussocks (Fig. 3).

Study of the different habitats revealed the occurrence of two species common to all the natural and drained fen sites, i.e. *Carabus granulatus* L. and *Pterostichus nigrita* (Fabr.) (Appendix 1 and 2). The species similarity of the beetles of natural and drained fens was weak (Fig. 4), with the only communities displaying greater similarity being the periodically-flooded meadow (MF) and the *Caricetum paradoxae* association (Fig. 4).

The lowest species diversity was noted for the meadows on the most moorshed and marshy peats (Tables 3 and 4).

On natural fens, the absolute dominant species was *Agonum moestum* (Duft.), which accounted for over 44% of the carabid beetles caught. However, proportional representation of this species was successively lower in environments less and less marshy in character. On the drained fens, different species of carabid were predominant on different meadows. The different meadows that had been drained at the same time had *Carabus granulatus* L. as the dominant where peat was mossy (accounting for over 33% of all beetles captured), and *Pterostichus cerulescens* (L.) as the dominant where the peat was of alder-swamp origin (80% of individuals). The absolute dominants on the meadows drained 100 years ago were again *C. granulatus* and *P. vulgaris*, whose shares were 45 and 47% respectively. *A, moestum* was dominant on the periodically-flooded, unmanaged meadow. Accessory species were in a decided majority in all the communities studied (Fig. 5), while a further characteristic feature was the prevalence of species of spring-type development and the ability to fly (Tables 5 and 6). Under the influence of the drying-out of fens there is a change in living conditions and a rebuilding of the species composition of carabid communities. Hygrophilic species associated with wetland habitats are replaced by the mesophiles characteristic of managed meadows and arable fields. Changes in trophic structure also occur, with hemizoophages of the genera *Amara* and *Harpalus* appearing on the drained peatlands (Appendix 2 and Table 6).

The need for natural fens to be protected is indicated by the presence of rare species of plant and animal on them (Dyrcz 1972; Pałczyński 1975). The carabid communities studied did include a species that is now rare in Poland, i.e. *Chlaenius costulatus* Motsch.

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