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Spider assemblages (Arachnida: Araneae) as indicators for degraded oligotrophic moors in north-east Germany

Сообщества пауков (Arachnida: Araneae) как индикаторы деградирующих олиготрофных болот в северо-восточной Германии

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ABSTRACT. Oligotrophic moors (originally kettle-hole mires) and fens in north-east Germany are classified into six different stages of degradation based on physico-chemical soil parameters. Spiders were pitfall trapped at five sampling plots in moors from each stage of degradation. This paper aims to determine whether spider assemblages vary according to the stage of moor degradation. The data were analyzed using Kruskal-Wallis and Nemenyi-Nuy tests, and also Detrended Correspondence Analysis (DECORANA) and Discriminant Function Analysis (DFA). Only the lowest and the highest stages of degradation can be discriminated via spider assemblages by means of DECORANA. Medium stages cannot be distinguished properly because eurytopic species occur both at earlier and at later stages of the moor degradation. However, when comparing the ecological groups and preferred habitat types of species, discrimination between all stages of degradation is possible by performing a Kruskal-Wallis test. The abundance of forest species was shown to increase following the stages of degradation, i.e., the more degraded the moor, the greater the abundance of forest species. The abundance of species typical for oligotrophic moors, or those classified as even less hygrophilic, was highest at the medium stages of degradation (D2 and D3). DFA revealed that all stages of degradation can be discriminated based on the spider assemblages present. Therefore, spider assemblages may be used as indicators for degraded moors.

РЕЗЮМЕ. Исходя из физико-химических параметров почвы, олиготрофные болота (в первую очередь kettle-hole болота) и топи северо-восточной Германии классифицированы на шесть стадий деградации. Пауки собирались почвенными ловушками на пяти участках соответственно каждой из стадий деградации болота. Цель данной работы — определить, варьируют ли состав сообществ пауков в зависимости от стадии деградации болота. Данные проанализированы при помощи тестов Kruskal-Wallis и Nemenyi-Nuy, а также методоми главных компонент (DECORANA) и дискриминантного анализа функций (DFA). Только самую раннюю и самую позднюю стадии деградации можно различить при помощи DECORANA. Средние стадии деградации четко не разделяются из-за присутствия эвритопных видов. Однако, когда сравнивались экологические группы и предпочитаемые местообитания видов, различение всех стадий было возможно при помощи теста Kruskal-Wallis. Было показано, что численность лесных видов увеличивается с увеличением степени деградации, то есть, чем более деградировано болото, тем выше численность лесных видов. Численность видов типичных для олиготрофных болот или тех, которые классифицируются как гидрофильные, была наибольшей на средний стадиях деградации (D2 и D3). Метод DFA выявил, что все стадии деградации могут быть дискриминированы исходя из структуры сообществ пауков. Поэтому сообщества пауков могут быть использованы в качестве индикаторов для опеделения стадии деградации болота.

KEY WORDS: Araneae, bioindication, biostatistics, moor, ordination, wetland ecology.
КЛЮЧЕВЫЕ СЛОВА: Araneae, биоиндикация, биостатистика, болото, ординация, экология зоболоченных мест.

Introduction

The lowering of the ground water table primarily due to anthropogenic influence, means that oligotrophic moors and fens in Germany have undergone a rapid succession [Overbeck, 1975; Göttlich, 1990; Succow & Joosten, 2001]. Grasses outcompete peat mosses and therefore moss associations are replaced by wet meadows or shrubby sites. In the course of eutrophication, the latter are further replaced by woods of pine, birch or alder [Sukopp, 1959/60]. This process is called moor degradation, though for a long time no precise definition of what constitutes a degraded moor has been provided. The moors considered in this paper actually are, or formerly were oligotrophic moors; both kettle-hole mires (= Kesselmoore in German) and fens were studied, some of which were degraded [Sukopp, 1959/60; Succow & Joosten, 2002].

Generally, the degradation of oligotrophic kettle-hole mire and fen is caused by the lowering of the ground-water table and the subsequent contact of the peat with oxygen and leads to peat mineralization [Succow & Joosten, 2001]. This process can be enhanced by human activity (e.g., by drainage or by deposition of nutrients), but can also occur in a natural succession series, i.e., when the moor surface reaches its maximum height above the groundwater table (*c*. 10 m) caused by the limited capillary power of the peat moss. The moor degradation is characterized by directional changes of vegetation and physico-chemical parameters which permits assignment of the kettle-hole mires to six stages of degradation.

Here, I regard 'the degradation of moors' as a non-reversible process induced (naturally or through anthropogenic influence) by external factors. This process concerns the changing of water regime, microclimatic factors, physical and chemical parameters of the peat, as well as the quantitative and qualitative composition of phyto- and zoocoenoses.

Spiders respond to changes in abiotic conditions of moors in a very subtle way. In an 11 year study, Platen [1989] showed that if moors were drained or the groundwater table was sinking in their surroundings, the moor changed, for instance, to a wet meadow and the typical animal dwellers of *Sphagnum*-dominated sites were replaced by those typical for the replacing habitat. A similar process was observed when the moor was replaced by wet woods [Platen, 1991].

The goals of this paper are: (1) to relate spider species to 'ecological groups' and 'preferred habitat types' from field data; (2) to define different stages of degradation of moors in north-east Germany by the use of measured physico-chemical soil parameters; (3) to relate spider assemblages to the defined degradation stages by means of statistical analyses; and (4) to demonstrate that moor degradation may be described through changes in observed spider assemblages, as quantified using various statistical analyses (Kruskal-Wallis test, classification and ordination techniques) in an objective way.

Material and methods

Definition of the stages of degradation

The stages of degradation are primarily defined by rising pH-values, electric conductivity and a degree of humification from stage 1 to stage 9 (see Table 1). Nutrients seem to be less suitable for defining the stages of degradation. Physico-chemical soil data were taken from Linder [1995] and Rowinsky [1998].

Degradation stage 0 (D0): no degradation.
Degradation stage 1 (D1): very little degradation.
Degradation stage 2 (D2): slight degradation.
Degradation stage 3 (D3): medium degradation.
Degradation stage 4 (D4): strong degradation.
Degradation stage 5 (D5): total degradation.

Data collection

Spiders were collected by pitfall trapping [Barber, 1931] at 29 sampling plots in 19 moors in north-east Germany. Each plot covered an area of 0.2–2 ha and was assigned to a defined degradation stage. The locations, site names (abbreviations), as well as the number of species and individuals collected, are listed in Table 2.

In each moor, six pitfall traps (each with an upper diameter of 7.5 cm) were operated in a line from 1 April – 31 October (1982–1998). The pitfall traps were one-third filled with 4% formalin, to

Table 1.

Mean values of soil physical and chemical data at the sites investigated: pH = soil acidity, ec = electric conductivity, Ca^{2+} = calcium, Mg^{+} = magnesium, SO_4^{2-} = sulfate, Cl^{-} = chloride, NO_3^{-} = nitrate, NH_4^{+} = ammonium, PO_4^{3-} = phosphate, DoH = degree of humification (after von Post), D = stage of degradation. No data for D0 exist.

Таблица 1.

Средние значения почвенных физических и химических характеристик исследованных мест: pH = почвенная кислотность, ec = электропроводимость, Ca^{2+} = кальций, Mg^{+} = магний, SO_4^{2-} = сульфат, Cl^{-} = хлор, NO_3^{-} = нитрат, NH_4^{+} = аммиак, PO_4^{3-} = фосфат, DoH = уровень гумидизации (по von Post), D = стадия деградации. Данных для D0 нет.

Sites	**pH**	**ec** µS/cm	**Ca^{2+}** mg/l	**Mg^{+}** mg/l	**SO_4^{2-}** mg/l	**Cl^{-}** mg/l	**NO_3^{-}** mg/l	**NH_4^{+}** mg/l	**PO_4^{3-}** mg/l	**DoH** 0–10 cm
Mean D1	5.3	81.3	7.9	2.2	27.8	10.4	0.62	0.62	0.35	1.9
Mean D2	5.7	189.3	19.6	3.9	42.6	27.7	0.78	1.46	0.19	6.8
Mean D3	6.2	183	13.1	3.2	<30	13.7	1.40	3.33	0.28	5
Mean D4	6.3	204.2	23.1	4.3	51.7	23.0	0.82	2.93	0.18	7.1
Mean D5	6.6	555.6	86.0	9.14	114.0	31.3	0.91	6.39	0.14	8

Table 2.

Locations, site-abbreviations (site name), number of species and individuals caught during the trapping periods (1 April – 31 October). The last number of the site name indicates the stage of degradation (0–5). In the column 'Location' the locality is given first, the name of the federal county is noted after the comma. M.-V. = Mecklenburg-Vorpommern.

Таблица 2.

Местоположение, сокращение места (название), количество видов и особей, пойманных во время исследований (с 1 апреля по 31 октября). Цифры в конце наваний мест обозначают стадию деградации (0–5). В колонке «Местоположение» название локалитета дано в начале, после запятой название федерального округа. M.-V. = Mecklenburg-Vorpommern.

Location	**Site name**	**No. of species**	**No. of individuals**
Uckermark, Brandenburg	PD0	39	343
Müritz, Mecklenb.-V.-Pommern	KM0	54	1 674
Uckermark, Brandenburg	HD0	46	444
Müritz, Mecklenb.-V.-Pommern	KB0	57	1 247
Müritz, Mecklenb.-V.-Pommern	SB0	90	3 093
Grunewald, city of Berlin	LLO1	45	1 053
Grunewald, city of Berlin	PS1	32	399
Schlaubetal, Brandenburg	OD1	52	752
Müritz, Mecklenb.-V.-Pommern	KM1	50	994
Grunewald, city of Berlin	HKF1	57	1 025
Forst Düppel, city of Berlin	GF2	89	4 244
Spandauer Forst, city of Berlin	TB2	72	2 943
Forst Köpenick, city of Berlin	LLO2	28	698
Grunewald, city of Berlin	BS2	55	670
Grunewald, city of Berlin	LLW3	46	2 704
Forst Düppel, city of Berlin	GF3	80	2 253
Uckermark, Brandenburg	HD3	59	599
Uckermark, Brandenburg	PD3	53	534
Grunewald, city of Berlin	PF3	74	1 224
Grunewald, city of Berlin	TF14	52	631
Grunewald, city of Berlin	TF24	45	814
Spandauer Forst, city of Berlin	TB4	63	1 995
Schwinzer Heide, M.-V.	BB4	65	1 343
Spandauer Forst, city of Berlin	RP4	55	942
Spandauer Forst, city of Berlin	RP5	55	1 038
Spandauer Forst, city of Berlin	TB5	63	954
Grunewald, city of Berlin	PF25	89	2 375
Grunewald, city of Berlin	PF15	81	1 309
Spandauer Forst, city of Berlin	HL5	120	1 324
Totals:	29	298	39 618

which was added a detergent solution (Pril; 50 ml/5 l of formalin) to decrease the surface tension. The traps were emptied every fortnight, all six samples were placed in a single glass jar. Species were collected by the following authors: Barndt [unpubl. data from 1997], Bruhn [1995], Hiebsch [1985], Platen [1989, 1991, 1996]. Spiders were identified to species using Locket & Millidge [1951, 1953], Locket *et al*. [1974], Roberts [1985, 1987], Wiehle [1956, 1960] and Heimer & Nentwig [1991].

Ecological groups

Each spider species was related to an ecological group and a preferred habitat type as a starting point for subsequent analyses. Many of the ecological field studies had been completed before this work began so most of the classification concerning ecological groups and preferred habitat types was already established. Consequently, the most relevant data were adopted from Platen *et al*. [1999].

While each ecological group reflects the abiotic factors, such as light, moisture and temperature at a site, the preferred habitat type is a vegetation unit, i.e., where the species was caught most frequently compared to all other defined habitat types [Martin, 1993; Platen *et al*., 1991, 1999]. Three examples are given to describe the adopted system more precisely.

1. *Gnaphosa nigerrima* L. Koch, 1877.

In Germany this species is almost exclusively confined to the *Sphagnum*-dominated moors [Blick & Scheidler, 1991; Platen *et al*., 1991, 1999; Renner, 1992a; Martin, 1993; Fründ *et al*., 1994; Tolke & Hiebsch 1995; Malt & Sander, 1996; Platen, 1996; Finch, 2001; Otto *et al*., 2001; Sacher & Platen, 2001]. For 25 (83.3%) of the 30 sites in Germany, where data could unequivocally be related to a defined locality, the habitat of this species was described as the peatmoss-carpets. Consequently, the spider was treated as hygrophilic and as having 'oligotrophic moors' as the preferred habitat type. See Platen *et al*. [1999] for a complete description of the key to ecological groups and preferred habitat types.

2. *Trochosa robusta* (Simon, 1876).

This species is often mentioned in the literature [e.g., Otto *et al*., 2001] as being extremely rare in Germany. However, it is rather widespread throughout the country. It has been recorded in 12 of the 13 German federal counties for which checklists are available [Blick & Scheidler, 1991; Renner, 1992a; Martin, 1993; Fründ *et al*., 1994; Tolke & Hiebsch, 1995; Malt & Sander, 1996; Staudt, 1996; Reinke *et al*., 1998; Kreuels & Platen, 1999; Platen *et al*., 1999; Finch, 2001; Sacher & Platen, 2001]. From the 43 sites where the data are reliable, 30 (69.8%) were referred to as dry grassland, predominantly on limestone. Thus, this species was assigned to the 'xerophilic in dry, open grassland' ecological group and to the preferred habitat type of 'grassland, growing on limestone'.

3. *Histopona torpida* (C.L. Koch, 1834).

In the plains and highlands of the southernmost federal counties of Germany, this species is rather common in all forest types. It appears in nine out of the 13 federal counties for which checklists are available [Blick & Scheidler, 1991; Renner, 1992b; Martin, 1993; Fründ *et al*., 1994; Tolke & Hiebsch, 1995; Malt & Sander, 1996; Staudt, 1996; Kreuels & Platen, 1999; Sacher & Platen, 2001; Barndt *et al*., 2002]. For 59 (80.8%) out of 73 sites where the data are reliable, the habitat for this species is referred to as moderately moist coniferous and deciduous forests. Thus, the species was assigned to the 'in forests with moderate humidity' ecological group and to the preferred habitat type 'forests and woods with moderate humidity'.

Besides the species for which ecological groups could clearly be defined from their most frequent occurrence in defined habitat types, others show 'eurytopic' distributions in open sites, forests or both. For these species an ecological group and preferred habitat type may only be fixed statistically, if at all. This holds for species found in low numbers all over the country.

Statistical Analyses

To relate a species to particular stages of degradation, the percentage values of individuals of preferred defined habitat types was calculated [see Platen *et al*., 1999]. A Kruskal-Wallis-Test [Köhler *et al*., 1996] was performed with the sum of individuals from each stage of degradation to test whether spiders of a certain preferred habitat type differed between the stages of degradation. A Nemenyi-Nuy Test [Sachs, 1997] was then performed to test if the differ-

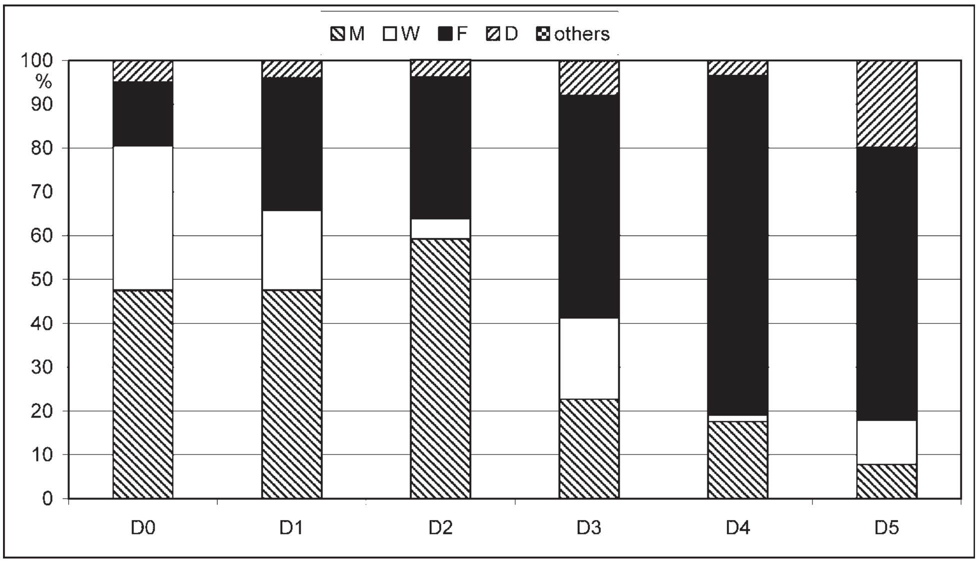

Fig. 1. Percentage values of spider individuals related to preferred habitat types for each stage of degradation: M — oligotrophic moor species, W — wetland species, F — forest species, D — dry grassland species, others — species with other preferred habitat types (not visible, as their percentage values were < 0.5%).

Рис. 1. Процентные значения экземпляров пауков относительно предпочитаемых местообитаний для каждой стадии деградации: M — виды олиготрофных болот, W — виды заболоченных мест, F — лесные виды, D — виды суходольных лугов, другие — виды с другими предпочтениями (незначительное количество, так как их процентные значения были меньше 0,5%).

ences between the stages of degradation were statistically significant.

To determine whether the whole spider assemblages discriminated between the six stages of degradation, a Detrended Correspondence Analysis (DECORANA) was performed including all species and sites. The DECORANA was calculated using the program CANOCO v. 4.0 [Braak & Smilauer, 1998].

In addition, a Discriminant Function Analysis (DFA) was calculated to reveal which spider species discriminated most between the stages of degradation [Backhaus *et al*., 1996]. The classes (stages of degradation) were defined '*a priori*'. The computer program Statistica v. 5.0 was used for the DFA and the Kruskal-Wallis test.

Results

Number of spider individuals related to preferred habitat types

As illustrated in Fig. 1, the percentage value of individuals of hygrophilic spider species, which are typical for open, oligotrophic moors (M), does not culminate in the stages D0 and D1, but does so in D2. From D3 to D5 the percentage values decrease continuously. The percentage value of individuals belonging to forest species (F) first increases continuously from D0 to D4 but then decreases again in D5. The individuals of wetland species (W) oscillate from one stage of degradation to another. The percentage value of individuals of species typical for dry grassland (D) remains nearly constant up to D4 and increases in D5, whereas the proportion of those belonging to other habitat types is negligible.

Composition of ecological groups vs. preferred habitat types

The median values of spider individuals belonging to species typical for dry forests ((x) f) are significantly lower in D0 than in D5 ($P < 0.05$) (Fig. 2).

The median values of individuals of spider species typical for moist forests ((h) f) are significantly higher in D5 compared to D2, D1 and D0 at the 5% level (Fig. 3).

The median values of spider individuals of species occurring predominantly in arable land differ significantly between the six stages of

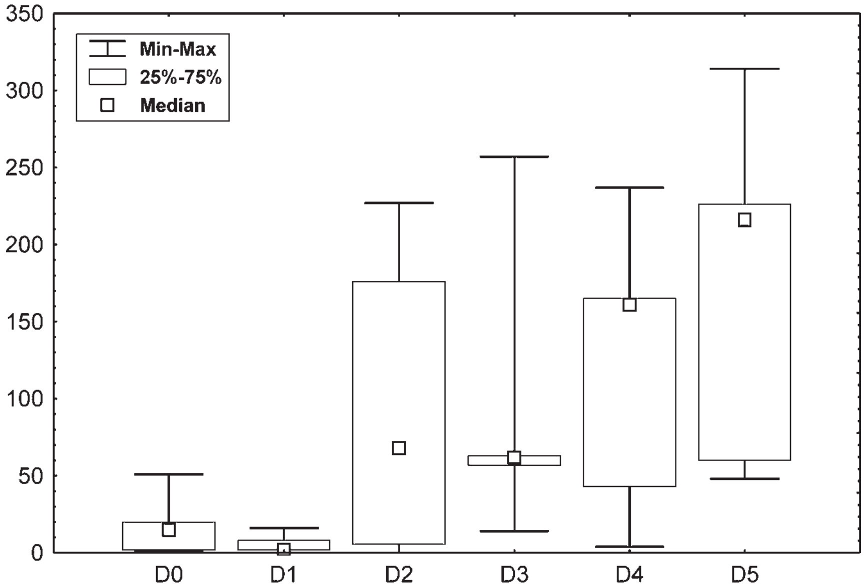

Fig. 2. Median values of spider individuals of the ecological group 'dry forests'.

Рис. 2. Средние значения численности пауков из экологической группы 'сухие леса'.

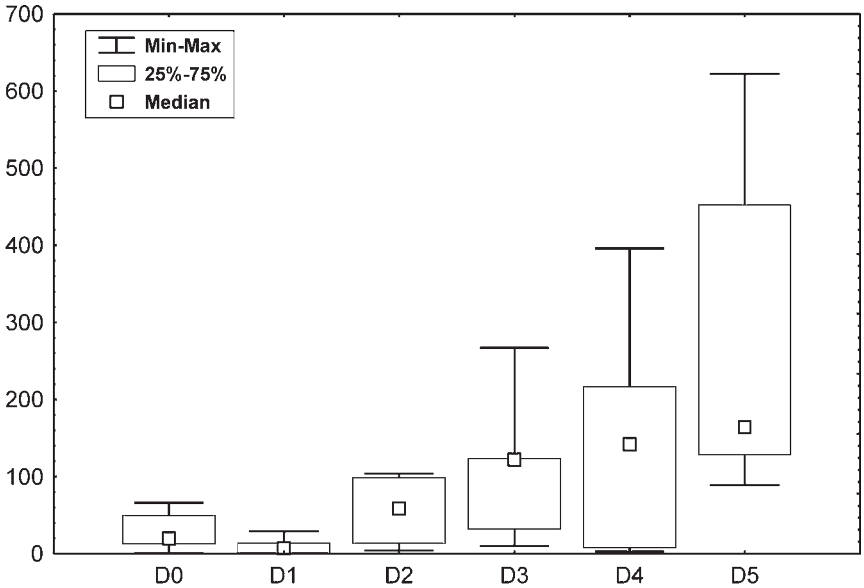

Fig. 3. Median values of spider individuals of the ecological group 'moist forests'.

Рис. 3. Средние значения численности пауков из экологической группы 'влажные леса'.

degradation. They are significantly lower in stages D0, D1 and D4 than in D5 with $P < 0.01$ (Fig. 4). As seen in Figs 2–4, except for the outlier D4 in Fig. 4, the median values rise from D0 to D5 in a curvelinear relationship. However, the equation of the graph could not be determined by performing a Kruskal-Wallis test.

Spatial distribution of spider assemblages over different stages of degradation

As illustrated in Fig. 5, all the sites of different degradation stages are shown in a two-dimensional ordination plot; the species have been omitted for clarity.

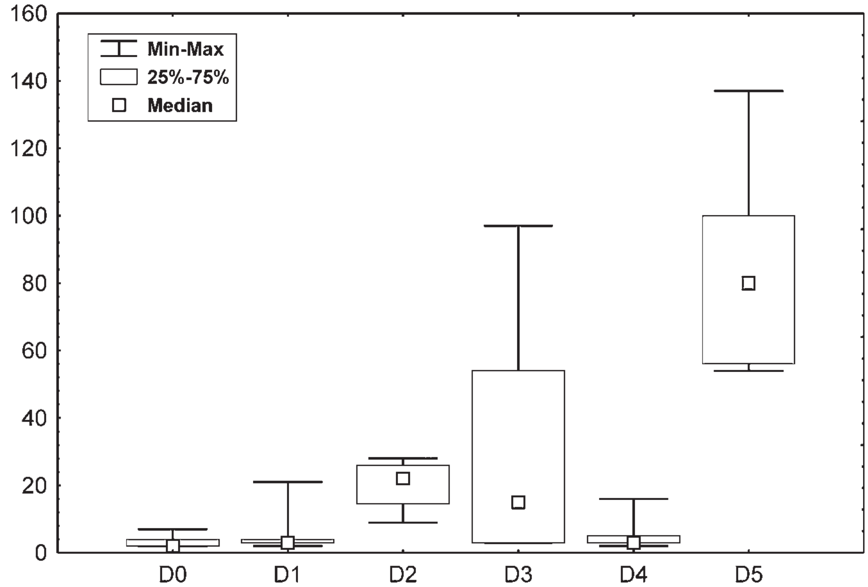

Fig. 4. Median values of spider individuals of the ecological group 'arable land'.

Рис. 4. Средние значения численности пауков из экологической группы 'пахота'.

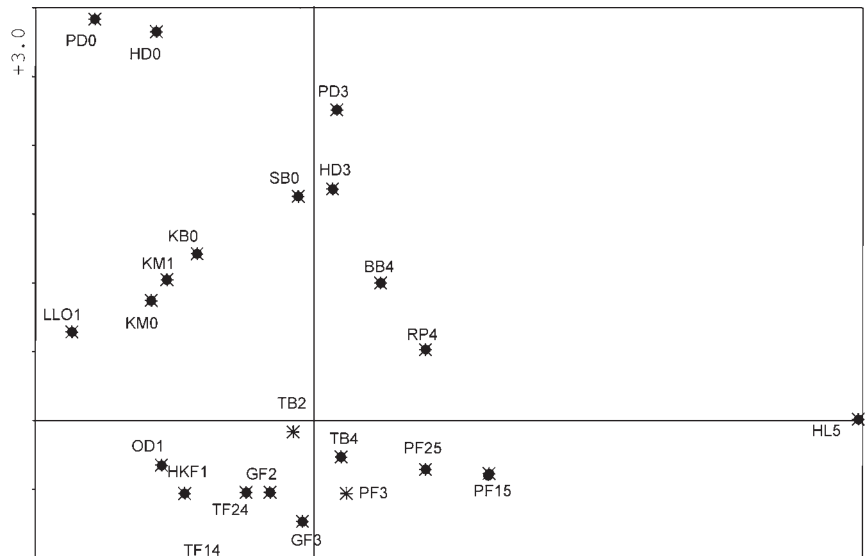

Fig. 5. Ordination diagram for both the sampling plots and spider species (not shown) based on the DECORANA. Abbreviations of the sites as given in Table 2. The different stages of degradation are indicated by the last numbers of the site labels.

Рис. 5. Ординационная диаграмма для исследованных мест и видов пауков (не показаны), посчитанная методом DECORANA. Сокращения мест как в Таблице 2. Различные стадии деградации обозначены последней цифрой в аббревиатуре точки.

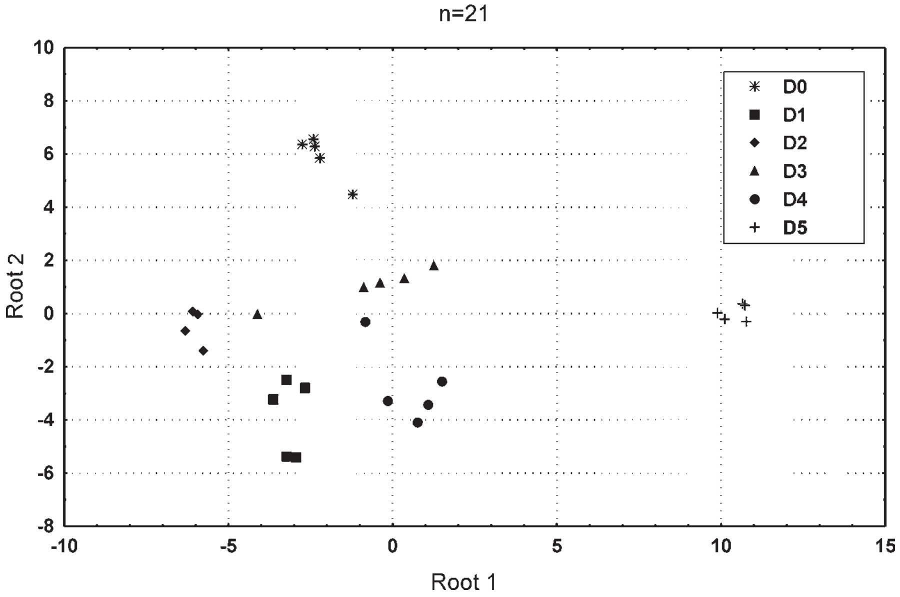

Fig. 6. Ordination diagram for spiders, calculated from the result of a multivariate DFA. Root 1 — first canonical axis, Root 2 — second canonical axis.

Рис. 6. Ординационная диаграмма для пауков, посчитанная методом DFA. Root 1 — первая каноническая ось, Root 2 — вторая каноническая ось.

The eigenvalues are 0.396 for the first axis and 0.274 for the second axis. The cumulative percentage variance is 12.7, 22.3, 31.2 and 37.4 in order of axis 1 to 4. Roughly speaking, that means slightly more than one third of the total variance is explained by the first four axes.

All low degraded sites (D0 to D2) can be found in the left part of the diagram with the sites of D0 plotted closely together in the upper left side. The D1 sites are scattered all along the second axis, which means that they don't share many species. This is true for sites D3 to D5, but they differ in that they tend to drift to the right, i.e., 'the drier side' of the diagram, if one supposes that a moisture gradient runs parallel to the first axis.

Unfortunately, no measurements of moisture, light or temperature were taken at any of the sites, so a Canonical Correspondence Analysis (CCA) could not be performed with these abiotic factors. Consequently, the description of the abiotic gradients have to be done only on the basis of site knowledge.

The D2 sites are restricted to the lower part of the left side. The open sites (e.g., GF2, HKF1, GF3, PS1) as well as the slightly shady sites (e.g., OD1, TF24, TB5, BS2) are plotted close together. A light gradient may be assumed to be present along the second axis. The sites of D3 are scattered all over the sheet. They are present near the D0 sites at the top, also in the middle near the D4 sites and at the bottom between a D2 and a D5 site. Their distribution is somewhat unclear.

The interpretation of moisture and light gradient results from measurements, which were taken at some of the sites [Platen, 1989, 1991].

Species discriminating between the stages of degradation

To recognize which species are best able to discriminate between the six stages of degradation, a Discriminant Function Analysis (DFA) was performed. The DFA is presented in a canonical way (Fig. 6), including 21 species. The results can also be seen in Tables 3 and 4.

As illustrated in Fig. 6, all stages of degradation are well separated from each other. In particular, species from the sites of stages D5, D2, D4 and D0 are plotted close together and, regarding them as a whole group, they are clearly separated from groups of other stages. Only species of D1 are tending slightly towards the direction of D2.

Table 3.
Preferred habitat types (PH) and characteristic statistical values of the DFA calculated for spiders: 2 = oligotrophic moors, 4 = wet meadows, 6 = wet forests*, 7 = moist forests**, 8 = dry forests, 9c = dry forest margins, 15 = arable land.

Таблица 3.
Предпочитаемые типы местообитаний (PH) и характерные статистические значения подсчитанные методом DFA для пауков: 2 = олиготрофные болота, 4 = сырые луга, 6 = сырые леса, 7 = влажные леса, 8 = сухие леса, 9c = края сухих лесов, 15 = пахота.

Species	pH	Wilk's Λ	Partial Λ
Ceratinella brevis (Wider, 1834)	7	0.000088	0.847029
Pirata piraticus (Clerck, 1757)	2	0.000106	0.709295
Pachygnatha clercki Sundevall, 1823	4	0.000107	0.696839
Pardosa pullata (Clerck, 1757)	2	0.000111	0.673764
Euryopis flavomaculata (C.L. Koch, 1836)	9c	0.000124	0.604177
Trochosa terricola Thorell, 1856	8	0.000124	0.601626
Pachygnatha listeri Sundevall, 1830	6	0.000132	0.566539
Oedothorax retusus (Westring, 1851)	2	0.000144	0.521173
Walckenaeria kochi (O. Pickard-Cambridge, 1872)	2	0.000147	0.508885
Pardosa lugubris (Walckenaer, 1802)	7	0.000160	0.469456
Oedothorax gibbosus (Blackwall, 1841)	2	0.000170	0.440407
Agroeca brunnea (Blackwall, 1833)	8	0.000173	0.432314
Erigone atra Blackwall, 1833	15	0.000177	0.639563
Walckenaeria alticeps (Denis, 1952)	2	0.000195	0.384721
Pardosa prativaga (L. Koch, 1870)	4	0.000199	0.375704
Pirata tenuitarsis Simon, 1876	2	0.000247	0.303506
Agyneta cauta (O. Pickard-Cambridge, 1902)	2	0.000307	0.244046
Centromerus sylvaticus (Blackwall, 1841)	7	0.000308	0.242903
Pirata latitans (Blackwall, 1841)	2	0.000330	0.227012
Lepthyphantes mengei Kulczyński, 1887	2	0.000343	0.218183
Trochosa spinipalpis (F.O. Pickard-Cambridge, 1895)	2	0.000356	0.210556

* = Wet forests are those of alder, where the water, as a rule, stands above the soil surface for several weeks; cf. moist forests.

* = Сырые леса — это леса из ольхи, которые, как правило, залиты водой в течении нескольких недель; ср. влажные леса.

** = Moist forests are the deciduous forests (e.g., consisting of oaks, ash and elm), where water never stands above the soil surface; cf. wet forests.

** = Влажные леса — это широколиственные леса (напр., из дуба, клена и ясеня), которые никогда не заливаются водой; ср. сырые леса.

Table 4.
Median canonical values for the six stages of degradation in the DFA, calculated for spiders.

Таблица 4.
Средние канонические значения для шести стадий деградации, посчитанные методом DFA для пауков.

Stages of degradation	Root 1	Group Root 2	Root 3
D0	-2.19016	5.90467	-0.91331
D1	-3.14296	-3.86127	-2.23792
D2	-6.02109	-0.50201	-1.20044
D3	-0.74974	1.05005	2.95535
D4	0.47227	-2.73572	2.47682
D5	10.42747	0.04387	-1.32058

The species best able to discriminate between the stages of degradation is *Ceratinella brevis* (Wider, 1834), the least able is *Trochosa spinipalpis* (F.O. Pickard-Cambridge, 1895) (Table 3). Roughly, one-third of the species included in the DFA are those living in forests, more than half of them are moor species, one-tenth of the species occur in wet meadows and a single species is found predominantly in arable land.

The measure to describe the strength of discrimination is Wilk's Λ. In this case, where the classes are defined '*a priori*', the species with the lowest Wilk's Λ discriminates most between the classes. Partial Λ describes the proportion of the discrimination power which contributes to overall discrimination. So, in contrast to Wilk's Λ, the species with the highest partial Λ discriminates best between the classes.

The median canonical values of the first three roots (canonical axes) are shown in Table 4. They denote the positive or negative deviation from the overall median value (coordinate 0/0 in Fig. 6).

Discussion

It is striking that moors of the lowest stages of degradation obviously do not include most of the moor species in the true sense. The percentage values of the individuals cumulate at stage D2. This may be because open, undisturbed moors with distinct tussock and hummock patches may be extremely hot and dry on the tussocks in summer. As the hummocks are flooded at least until late spring, pitfall traps can be set only in the tussocks. Consequently, only a few moor species with a low abundance are caught in favour of wetland, eurytopic and dry grassland species or even those living predominantly in the arable land [Platen, 1995; Schikora, 2003]. With progressing degradation of the surface, the moor becomes more plain, the hummock and tussock patches vanish and flooding events are more seldom because of desiccation [Succow & Joosten, 2001]. The remaining humidity of the peat still allows hygrophilc and typical moor spiders (not the moor specialists, which have already vanished) to exist and thus these are caught in the pitfalls. Spiders, and in particular Lycosidae, e.g., *Pardosa sphagnicola* Dahl, 1912, *Pirata uliginosus* (Thorell, 1856), etc., are present in huge numbers, even in wet, undisturbed moors [Schikora, 2003]. They are able to exist under these conditions because their offspring are not exposed continuously to the wet surface. In lycosid spiders, the mother carries her eggs in an egg sac and for a short while after hatching, the young are carried on her back. In the case of web-builders, the spiderlings live in cocoons attached to plants on higher ground.

The results of the DECORANA (where all species together with their abundances were included in the analysis) did not reveal clear differences between the stages of degradation. This may be because the entire spider assemblage is composed of species within all kinds of ecological groups. Many of them are eurytopic so that they occur in nearly all of the stages of degradation. They cause a 'smear' in the ordination diagram so that the sites of some stages are mixed. Only those of D0 are plotted close together because of their almost unique species composition. This may be because three of the plots of D0 are bog-like, rather than kettle-hole mires.

Medium stages of degradation cannot be discriminated by entire spider assemblages, as some species occurred both in undisturbed moors and in 'transition coenoses', i.e., the species preferring both wet meadows and wet forests. Furthermore, there are species typical for an actual stage of degradation (moist forests, pastures, etc.). Extremely degraded sites, which changed from wet to very dry conditions (i.e., the site 'HL5' in Fig. 6), appear as outliers. Thus, their spider assemblages differed greatly from those of other degradation stages.

When the median values of individuals of species belonging to the same type of preferred habitats are compared, all stages of degradation can be properly distinguished in most cases. Here, only a part of the whole coenosis is considered, focussing on a single ecological group and habitat type. In the example given above, the whole coenosis is considered, including species of all ecological groups and preferred habitat types. Thus, at the extremes (D0 and D5) only stenotopic (i.e., specified) species occur, whereas in the more moderate conditions within the D2 to D4 habitats species of many ecological groups/preferred habitat types are present. This causes a 'smear' effect which makes it somewhat difficult to distinguish these stages of degradation using spider assemblages. Moreover, the absence of typical species of oligotrophic moors in the more degraded sites may directly indicate the stage of degradation. The latter indication is rather subjective, but it can be more objective provided one counts the abundance of a species belonging to the defined ecological group and preferred habitat type. It should also be noticed that the ecological groups and preferred habitat types considered are themselves based on a subjective evaluation.

Of the different statistical methods used for discriminating spider assemblages between the different stages of moor degradation, the simultaneous consideration of ecological groups and preferred habitat types is clearly the best one. It is possible to visualize the development of the percentage values of individuals of each ecological group and preferred habitat type. Moreover, it is possible to perform objective statistical tests to show whether the differences between the median values of individuals belonging to a certain ecological group/preferred habitat type are significant.

The results presented by means of classification and ordination techniques including all the species found at the sites, can weakly relate spiders to the different stages of degradation. At some sites the animal assemblages showed distinct differences between the stages of degradation, at other sites they did not. This may have been due to the following reasons:

(1) Some of the sites were misclassified concerning their stage of degradation.

(2) The geographical location (i.e., neighbourhood) of the sites had a stronger effect than the stage of degradation, on the composition of the coenoses. This has to be considered, at least for the spider coenoses of the Uckermark-sites (PD + HD). However, this factor remains hypothetical, as no exact distances between the sites were surveyed.

(3) Spiders differ from plants in the way they react to moor degradation. Most animals can leave sub-optimal environments, whereas plants cannot. However, they may stay within the degraded moor as seeds without germinating.

(4) Regardless of exposure to light, the occurrence of most common species in wet places resulted in a similarity of all zoocoenoses, whereas less common or rare species, e.g., moor specialists, distinguished between the different stages of degradation. This even holds for the results of the DECORANA used here, when the abundance values were logarithmically transformed before the analysis.

(5) The moors studied were of different ages. It was not known when a moor developed for the first time or when the 'degradation' began. Anthropogenic impact on the moors differed and thus was also responsible for slower or quicker degradation.

Conclusions

(1) Spider assemblages can be related to the different stages of degradation; the best way to do this is to compare the median values ofcertain ecological groups and preferred habitat types.

(2) Entire spider assemblages only discriminate between the six stages of degradation at those sampling plots which are extremely low (D0) or very strongly degraded (some plots of D5).

(3) Medium stages of degradation (D2 and D3) show the highest abundance of hygrophilic species preferring the oligotrophic moors.

(4) Spider assemblages can be used as an indicator system for separating the six stages of degradation via simultaneous consideration of ecological groups and preferred habitat types. Additionally, the presence or absence of certain 'indicator' species regarded as specialists for oligotrophic moors can also be taken in account.

In conclusion, spider assemblages are suitable for use as indicators of moor degradation, depending on the level of interpretation.

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