Collembolan community structures in a continental psammic habitat of southwest Germany

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Abstract

The present study reports for the first time on the collembolan community composition and structure across a successional gradient in a continental sand habitat. Nine sites – ranging from open sands to a woodland site – in southwest Germany were sampled. Increasing vegetation corresponded significantly with increasing organic matter and nutrient content as well as decreasing pH of the sandy soils, showing a clear eutrophication of the sands along the gradient. Parallel to increasing successional status, the registered microarthropod densities increased and showed a strong shift in group composition. Specifically, the collembolan densities and species numbers also generally increased along the gradient. The open sands showed extremely species-poor communities and strong eudominances of single species, whereas up to 20 species in balanced community structures were found in the most developed sites. Specialised, psammophilous species were largely limited to the open sands and short-grass sites, whereas eurytopic, thermophilous species were for the most part limited to and were dominant in the more highly vegetated and eutrophied sites. Correlation analyses showed a significant connection between soil eutrophication and distribution of these species. Psammophilous taxa, on the other hand, were limited to the nutrient-poor, abiotically extreme sites, which also showed potentially low faunistic competition. These results can be related to theories of A-selection of arthropods from extreme habitats.

Key words: Collembola, psammophile, sand, succession

Zusammenfassung

In der vorliegenden Studie wurden die Zusammensetzung und Struktur der Collembolen-gemeinschaften von Binnendünen unterschiedlicher Sukzessionsstufen - von offenen Sanden bis Wald – in Südwest-Deutschland untersucht, Die neun Untersuchungsflächen wurden hierzu entlang eines Gradienten der Bodenentwicklung ausgewählt. Mit zunehmender Vegetationsdecke nahmen unter anderem auch der organische Kohlenstoffgehalt zu und der pH-Wert ab. Collembolendichten und –artenreichtum stiegen entlang des Sukzessionsgradienten. Die offenen Sande zeichneten sich durch artenarme Gemeinschaften mit Eudominanz einzelner Arten aus. Bis zu 20 Arten in homogenen Gemeinschaften wurden in den weitest entwickelten Flächen vorgefunden. Spezialisierte, psammophile Arten waren auf die frühen Sukzessionstadien beschränkt, während auf den weiter entwickelten Flächen v. a. euryöke, thermophile Arten dominierten. Besonderes letztere korrelierten signifikant mit dem organischen Kohlenstoffgehalt und dem pH-Wert des Bodens, während psammophile Arten eine starke Affinität zu nährstoffarmen, abiotisch extremen Flächen zeigten, die hier vermutlich unter anderem in einer geringen Konkurrenz durch andere Bodentiere begründet ist. Die Ergebnisse dieser Studie werden im Zusammenhang mit den A-Selektionstheorien diskutiert.

1. Introduction

Especially since the publications of Coineau and colleagues (Coineau & Massoud 1977, Coineau et al. 1978, Coineau & Seely 1983), soil zoologists around the world have become increasingly interested in the specialised microarthropod fauna occurring in sandy habitats. Early studies of Collembola in sand sediments took place in various continents (i.e., Schaller 1951, Delamare Deboutteville 1953, Poinsot 1966, Wood 1971), while systematic studies of psammic Collembola at the end of century have been mainly carried out in Europe and the Mediterranean region, for the most part by Christian, Thibaud, and colleagues (reviewed in Thibaud & Christian 1995, 1997). Recently, reports of psammophilous Collembola from various areas around the world have again been published (i.e., Lee & Kim 1994, Thibaud 1994, Barra 1995, Palacios-Vargas & Thibaud 1998, Thibaud & Diaz 1998, Thibaud & Palacios-Vargas 1999). All of these studies have revealed many new, un-described species occurring in psammic habitats (for just a few examples: Weiner & Thibaud 1991, Thibaud & Weiner 1994, Fjellberg 1995, Christian and Thibaud 1996, Thibaud & Peja 1996, Thibaud 1996) and have shown that many species and genera occurring in such habitats are very specialised for sand sediments.

The majority of published studies on Collembola from terrestrial sand sites has been of taxonomic nature, reporting the occurrence of psammophilic species or describing new taxa, or have dealt with the zoogeography and habitat preference at a large (continental) scale. Community-level studies – investigating the composition and community structure of sympatrically occurring species in dependence on habitat conditions at a small spatial scale – are markedly lacking for psammic habitats. Understanding of the community-level occurrence and distribution of microarthropod species in sandy habitats can help to understand the processes leading to the colonisation and inhabitation of such abiotically extreme habitats. The study of the community-level diversity at a small, local spatial scale was possible during investigations of the microarthropods in protected sand-meadows for the environmental authorities in Southwest Germany, which took place between 1993 and 1998 in sandy habitats exhibiting high small-scale heterogeneity (see Rohde 1994). The present report summarises the collembolan results of parts of these studies.

2. Materials and methods

The data presented here originated from two continental dune areas (named 'Pt' and 'PS' in the following), separated by approximately 2 km, in the Upper Rhine Valley in southwest Germany (in Sandhausen near Heidelberg), which were sampled regularly between 1993 and 1996. The two studied areas had a spatial expanse of approximately 4.5 and 2.5 ha, respectively. Within these areas, sampling sites were chosen in botanically well-defined plots, which represented relatively homogenous plant-sociological units (see Breunig 1994 for further details). Of these sampling sites, nine are presented here, representing a successional gradient ranging from open sands, short-grass (*Koeleria glauca* and *Corynephorus canescens* grasslands) and tall-grass (*Festuca guestfalica*) sand-meadows, to wooded (*Pinus sylvestris*) areas. The specific sites and the major abiotic soil parameters are listed in Tab. 1. The sands of all sites were aeolic of Pleistocene and Holocene origin and were exceedingly similar in composition, consisting of approximately 3 % rough sand and gravel (grain size > 0.63 mm), 47 % medium sand (0.2 – 0.63 mm), 48 % fine sand (0.063 – 0.2 mm) and 2 % silt and

clay (< 63 μm). Soil-organic-matter and plant-nutrient content increased and pH decreased significantly along the successional gradient (Tab. 1), indicating that the spatial chronosequence also represents a gradient of increasing soil (sand) eutrophication.

Within the botanical units, microarthropod sampling took place within plots measuring 5 × 5 m. The average distance between sampling plots of each dune area (also of different successional status) was 30 – 100 m. Due to the close spatial vicinity of the sampling areas and the absolutely protected legal status of the sand-meadows, sampling was restricted. Most sites presented here were only sampled in one year; the data from the open-sand site from one dune area ('Pt'), however, are presented here for two of a total of four sampling years to show successional tendencies. The plots were sampled three times per year (with 9 – 15 samples total, to a depth of 5 cm). Since quantitative data were desired, the microarthropods were extracted in a high-gradient extraction device as opposed to flotation methods. The animals thus obtained were sorted under the dissecting microscope into Collembola, the major acarological groups and remaining arthropods ('Other Groups'). Collembola and Actinedida were determined to species level; only major aspects of the collembolan results are presented here, for details of the acarological results see Russell & Alberti 2008.

Tab. 1   Studied sampling sites and selected abiotic soil (sand) parameters. Only the different plant-nutrient contents and pH were significantly different between sites (at at least $P<0.01$). Soil moistures and soil temperatures do not represent true field averages (i.e., surface temperatures > 50°C have been measured at irregular dates outside the sampling periods). Except for the open sands, the sites are named for the dominant plant species. 'Pt' and 'PS' designate the two dune areas, within which the different sampling sites were located. 'I', 'II', and 'III' designate different sampling areas within separate, but similar plant sociological units. 'Pt-Sand' was sampled in different years, of which 1993 and 1996 are presented here.

	Open sands			Short-grass sites			Long-grass sites			Woodland
Site	Pt-Sand (93)	Pt-Sand (96)	PS-Sand	Corynephorus	Koeleria I	Koeleria II	Festuca I	Festuca II	Festuca III	Pinus
C_{org} [%]	0.31	0.31	0.24	0.99	0.55	1.19	1.95	2.40	2.64	7.17
N_{tot} [%]	0.028	0.027	0.014	0.071	0.030	0.085	0.136	0.190	0.206	0.359
Na^+_{mobile} [mg/kg]	0.4	0.7	0.9	1.5	0.8	2.0	0.8	1.8	2.1	4.3
Ca^{++}_{mobile} [mg/kg]	675	738	603	774	714	912	1193	1408	1712	2205
pH	7.57	7.46	7.62	7.07	7.38	7.11	7.04	6.42	6.15	6.09
Soil moisture [%][a]	3.1	19.4	2.7	4.5	5.0	23.8	7.1	25.3	13.2	14.7
Soil temperature [°C][a]	18.1	15.9	20.2	19.6	17.7	19.6	18.3	14.2	15.1	16.5

The collected data, as yearly averages per sampling site, was analysed to obtain standard faunistical parameters: total microarthropod densities (in individuals m^{-2}), microarthropod group composition (in % relative abundance); total collembolan densities, recorded species number, relative abundances of each collembolan species (in % of total site abundances of Collembola = dominance) and sampling frequencies (% occurrence in individual samples). Due to sites being partly sampled in different years, it was abstained from carrying out quantitative statistics (i.e. ANOVAs of densities or species richness), since important statistical prerequisites could not be guaranteed (i.e. absolute independence of individual samples). Instead, statistical procedures were limited to correlative analyses of species abundances and environmental parameters of the individual sites, for which the data from all sampled sites of the area, some of which are not shown here, were used. The abundances of the recorded species were correlated with soil abiotic parameters (soil moisture, organic-C content, pH, etc.), individual numbers for each species and abiotic parameters having always been obtained from one and the same soil core, with a non-parametric Spearman rang correlation, performed with the program StatView (Abacus Concepts, Berkley, California) on a Macintosh computer. Only correlations with [C_{org}] and pH produced significant results and are presented here. Finally, a multivariat indirect gradient analysis (correspondence analysis) was carried out with CANOCO V. 4.5. on an IBM-compatible network system using the density data for the individual species as well as the vegetation-type and abiotic soil data for each sample.

3. Results

3.1. Microarthropods

To understand the occurrence of Collembola in the present sites, it is important to put them in relation with the total microarthropod assemblages. A general tendency for increasing total microarthropod densities with increasing vegetative cover (= increasing soil eutrophication) was found here (Fig. 1, top). There was also an obvious relationship between group composition and successional development of the sampling sites (Fig. 1). Except for the woodland site, Collembola occurred in comparatively low densities and did not constitute a dominant microarthropod group. In all sites, the Actinedida (here divided into Endeostigmata and Prostigmata including Heterostigmata) represented the most frequently registered microarthropod group. In the open sites, the microarthropod assemblages were strongly dominated by Endeostigmata, which have often been described, from all continents, as being dominant in sandy and xerotherm habitats (cf. cit. in Russell 2000, Russell & Alberti 2008). In the short-grass sites, prostigmatid species – often the dominant microarthropods in grassland soils (cf. Kethley 1990) – became dominant. In the tall-grass meadows, the Oribatida were found equally abundant, and, finally, in the woodland site, the Collembola first occurred in stronger relative abundances and the microarthropod communities were fairly balanced.
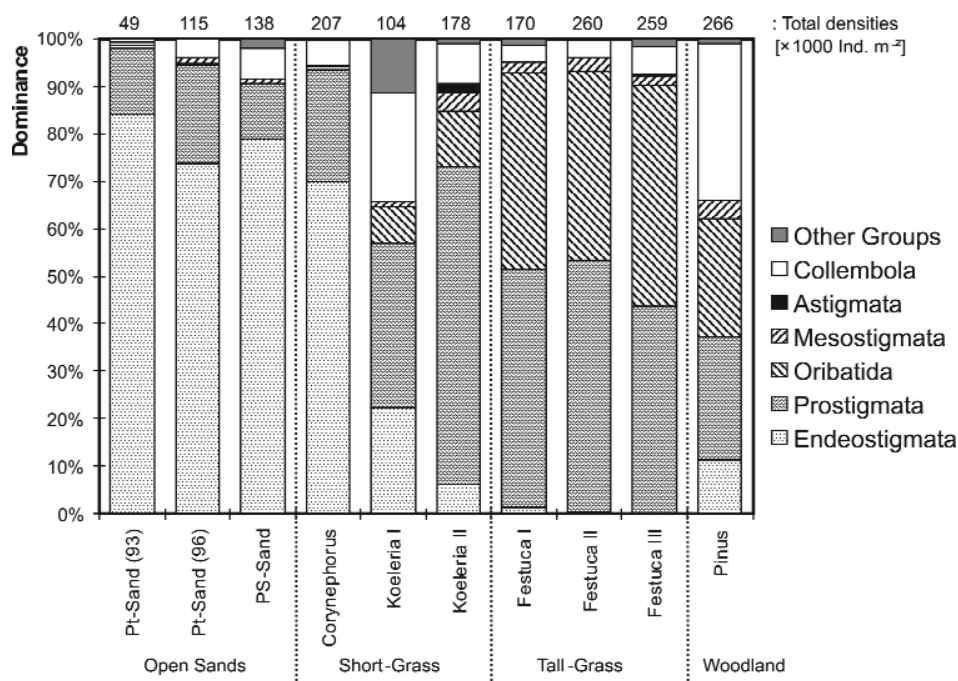
Fig. 1 Group composition (in % relative abundance) of the microarthropod fauna registered in the different sampling sites. Given above are the recorded total microarthropod densities (in 1000 individuals m^{-2}). Site designations as in Tab. 1.

3.2. Collembola

The Collembola were found in relatively low total densities (Tab. 2), only in the *Pinus* site did they show comparatively high total abundances, which were, however, attributable to the individual-rich occurrence of a few species. Although a tendency for increasing densities from the open sands, the meadows, to the woodland site was observed, higher total densities were actually found in the short-grass meadows than in the tall-grass sites. A clear tendency through the entire successional gradient was observed for species richness: very species-poor communities (as few as two species) being found, on average, in the open-sands and short-grass meadows and clearly increased numbers of species in the *Festuca* and *Pinus* sites (see Tab. 2).

Of the few species constituting the collembolan communities in the open-sands and short-grass sites, most were found consistently throughout all these sampling areas: *Brachystomella curvula*, *Micranurophorus musci*, *Scaphaphorura arenaria* and *Xenyllogastrura octoculata*. Besides these species, at most only sporadic individuals of other species were found occasionally in these sites. In the open sands, the observed species were usually registered in very low densities and in only few of the samples (see Tab. 2). In the short-grass sites, the densities of these species increased appreciably and they were apparently more broadly distributed throughout the sampling areas, as indicated in the higher sampling frequencies

Tab. 2 Collembolan taxa registered in the present study. For the individual species, the densities in the different sampling sites (yearly averages) (in 1000 individuals m⁻²) are presented as well as the within-site frequencies in the individual samples (= occurrence in per cent of samples, in brackets). Total densities in individuals m⁻². Site designations as in Tab. 1. Abbreviations of species' names given for Fig. 2.

Registered taxon	Abbreviation	Open Sands			Short-Grass Meadows			Tall-Grass Meadows			Woodland
		Pt-Sand (1993)	Pt-Sand (1996)	PS-Sand	Corynephorus	Koeleria I	Koeleria II	Festuca I	Festuca II	Festuca III	Pinus
Entomobryidae											
Entomobrya handschini Stach, 1922	E.h		0.03 (11%)		0.08 (25%)		0.12 (31%)	1.31 (66%)	0.62 (66%)		1.55 (50%)
Entomobrya multifasciata (Tullberg, 1871)	E.mf						0.16 (8%)	0.55 (44%)		0.13 (29%)	0.08 (25%)
Entomobrya quinquelineata Börner, 1901	E.q							0.59 (33%)			
Entomobrya spec. (juv.)			0.03 (11%)				0.59 (19%)	1.59 (55%)	3.21 (100%)	0.09 (29%)	1.09 (75%)
Lepidocyrtus lanuginosus (Gmelin, 1788)	L.la										7.23 (100%)
Lepidocyrtus spec. (juv.)	L.sp								1.45 (67%)		1.09 (75%)
Orchesella cincta (Linné, 1758)	Or.c										0.16 (25%)
Isotomidae											
Cryptopygus bipunctatus (Axelson, 1903)	Cr.b										56.50 (100%)
Cryptopygus thermophilus (Axelson, 1900)	Cr.th						1.74 (19%)				
Isotoma cf. agrelli Delamare, 1950	I.a									0.04 (14%)	
Isotoma viridis Bourlet, 1839	I.v						0.03 (11%)	0.83 (44%)	1.87 (100%)	1.15 (100%)	0.16 (50%)
Isotoma spec. (juv.)	I.sp						0.03 (11%)				
Isotomodes productus Axelson, 1906	Id.p	0.55 (22%)	1.97 (44%)	1.32 (100%)	7.07 (100%)	18.37 (78%)	5.69 (33%)	0.31 (44%)	0.31 (67%)	0.09 (14%)	0.16 (50%)
Micranurophorus musci Bernard, 1977	Mn.m							0.21 (44%)	0.73 (67%)		0.39 (25%)
Parisotoma notabilis (Schäffer, 1896)	P.n										11.81 (100%)
Hypogastruridae											
Hypogastrura s.l. spec. (juv.)	Hy.sp							0.03 (11%)		0.09 (14%)	0.08 (25%)
Willemia anophthalma Börner, 1901	W.a									0.04 (14%)	0.23 (25%)
Xenylla boerneri Axelson, 1905	X.b										0.23 (75%)
Xenylla maritima Tullberg, 1869	X.m							0.07 (11%)			0.16 (50%)
Xenylla tullbergi Börner, 1903	X.t										4.74 (100%)
Xenyllogastrura octoculata (Steiner, 1955)	Xg.o	2.25 (11%)	0.31 (75%)	2.72 (100%)			0.25 (31%)				

Registered taxon	Abbreviation	Open Sands			Short-Grass Meadows			Tall-Grass Meadows			Woodland
		Pt-Sand (1993)	Pt-Sand (1996)	PS-Sand	Corynephorus	Koeleria I	Koeleria II	Festuca I	Festuca II	Festuca III	Pinus
Neanuridae											
Brachystomella curvula Gisin, 1948	B.c				0.54 (100%)	0.76 (44%)	3.42 (19%)				0.39 (50%)
Brachystomella nubila Gisin, 1957	B.n										0.08 (25%)
Brachystomella parvula (Schäffer, 1896)	B.p							0.03 (11%)		0.31 (29%)	
Micranurida pygmaea Börner, 1901	Ma.p		0.03 (11%)				0.03 (11%)			40 (14%)	
Odontellidae											
Axenyllodes caeca (Gisin, 1952)	A.c							0.03 (11%)			
Onychiuridae											
Doutnacia xerophila Rusek, 1974	Do.x		0.03 (11%)				0.16 (11%)			1.33 (71%)	0.70 (50%)
Mesaphorura critica Ellis, 1976	M.c										
Mesaphorura hylophila Rusek, 1982	M.hl						0.56 (42%)	0.31 (44%)			230 (25%)
Mesaphorura krausbaueri Börner, 1901	M.k.							0.03 (11%)	0.21 (33%)	0.09 (14%)	
Mesaphorura macrochaeta Rusek, 1976	M.m							0.17 (11%)	0.93 (33%)	1.69 (43%)	3.34 (50%)
Mesaphorura spec. (juv.)	M.sp						0.03 (11%)	0.03 (11%)			0.16 (50%)
Protaphorura pannonica (Haybach, 1960)	Pr.p		0.03 (11%)							7.24 (100%)	
Protaphorura pseudocellata (Naglitsch, 1962)	Pr.ps										0.31 (50%)
Scaphaphorura arenaria (Petersen, 1965)	Sc.a	0.03 (11%)		2.56 (50%)	0.23 (75%)	5.84 (89%)	0.44 (19%)				
Symphypleona											
Bourletiella s.s. spec. (juv.)	Bo.sp					0.03 (11%)		0.10 (11%)			
Heterosminthurus spec. (juv.)	Hs.sp							0.03 (11%)			
Lipothrix lubbocki (Tullberg, 1872)	Li.l										0.93 (75%)
Sminthurinus aureus (Lubbock, 1862)	S.a								1.87 (100%)	0.67 (71%)	0.70 (75%)
Sphaeridia pumilis (Krausbauer, 1898)	S.p							0.31 (44%)	0.73 (100%)	0.18 (29%)	
Symphypleona spec. (juv.)	S.p						0.12 (25%)			2.09 (57%)	
Total Collembolan Densities		600	4,4	4,2	10,6	25	13,4	6,6	11,9	15,3	92,3
No. registered Species		2	6	3	5	4	12	16	9	14	21

(often in 100 % of the samples). Except for *M. musci*, which was found in almost all sites, albeit in low individual densities and in fewer samples in the successively further developed areas, these species were usually conspicuously missing in the samples from the tall-grass and woodland sites. Interesting is the second *Koeleria* meadow, which showed lower total collembolan densities than in the first *Koeleria* site, yet a much higher number of species. Although the psammobiontic taxa found in the other short-grass sites were also observed here and partly constituted the dominant species, these were generally found in lower abundances and were much more patchily distributed throughout the sampling area. Although no closer to or further from the *Festuca* areas than the other short-grass sites, many species were recorded here which were otherwise restricted to the tall-grass and woodland sites, thus indicating a further degree of faunistic succession.

The collembolan species assemblages recorded in the different *Festuca* sites were surprisingly similar (see Tab. 2); considering the fact that they were sampled in different years, this similarity is a strong indication of the general validity of these results. Except for *M. musci*, none of the psammobiontic taxa observed in the biotically less-developed sites were observed here. The communities found here were largely dominated by hemi- and epedaphic Entomobryidae, Isotomidae and Symphypleona (see Tab. 2). This tendency continued in the woodland site, which was dominated by more mesic woodland species, i.e., *Cryptopygus bipunctatus*, *Paristoma notabilis*, among others (see Tab. 2). Almost all of the species sampled from these sites were not found in the open-sands and short-grass sites. Surprising is the distribution of the registered *Mesaphorura* species, as an example of euedaphic forms, which were also limited to the successively further developed sites (including the second Koeleria site).

3.3. Correlative analyses

The correspondence analysis confirmed the associations of few specific species in the open sands and short-grass sites on the one hand and many, common species in the more eutrophied sites on the other hand. In this analysis, the two first axes had high eigenvalues (axis 1: 0.707; axis 2: 0.517) and together explained 53.6 % of the total species-environmental data variance. Axis 1 explained alone 30.7 % of the variance. This axis correlated strongly negative with nutrient status (r^2-values [C_{org}]: -0.673; [N_{tot}]: -0.776) as well as long-grass vegetation type (-0.553), but positive with open sands (0.531; Fig. 2). Axis 2 explained a further 23.6 % of the variance and also correlated strongly negative with nutrient status of the soils (r^2-values [C_{org}]: -0.643; [N_{tot}]: -0.501; C/N: -0.711) and the woodland vegetation (-0.781) but positive with long-grass vegetation type (0.529), thus separating the more heavily vegetated sites.

Loading positively onto both axes and grouped together were only a few taxa: *Brachystomella curvula*, *Micranurophorus musci*, *Scaphaphorura arenaria* and *Xenyllogastrura octoculata* (Fig. 2). Interestingly, the more eurytopic *Cryptopygus thermophilus* was included in this group. These species were widely restricted in their distribution to open-sands and short-grass sites. Almost all other species loaded negatively especially onto axis 1. Species dominating in the *Festuca* sites loaded somewhat positively onto axis 2. Interesting is the group of species (i.e., *Brachystomella parvula*, *Micranurida pygmaea*, *Protaphorura pannonica*, and *Doutnacia xerotherma*) that loaded strongly positive onto axis 2. These species were usually registered in disturbed short-grass and open sites in the present study area (data not shown). Loading negatively onto axis 2 were species also or exclusively found in the woodland site.
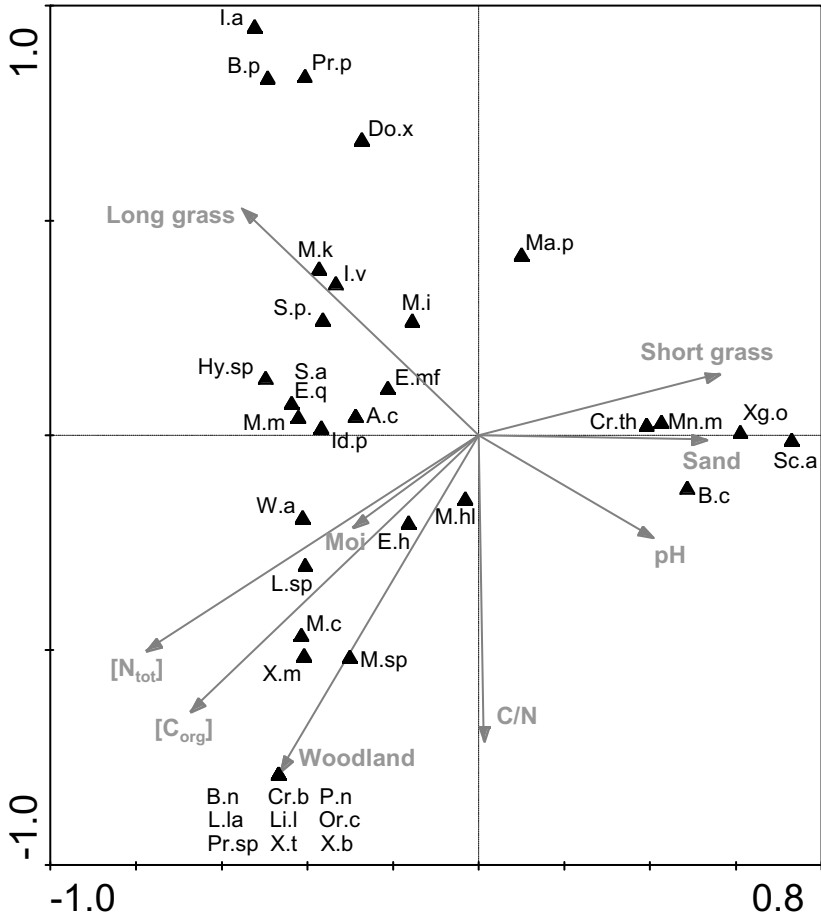
Fig. 2   Results of the correspondence analysis of the recorded abundances of all species registered in the Sandhausen study area. For eigenvalues and proportions of variance of the axes shown, see text. Species' scores plotted as small black triangles (for abbreviations of the species' names, see Tab. 2), vectors of important environmental variables as grey arrows.

    To see if these groupings and distributions were directly related to soil characteristics, the recorded species abundances were correlated with the major soil parameters, of which only [C_{org}] and pH showed significant correlations (Tab. 3). The species found exclusively occurring in the tall-grass and woodland sites were highly and significantly correlated with [C_{org}] (positively) and pH (negatively). The apparently psammobiontic species, however, were only non-significantly and in tendency negatively correlated with these soil parameters, indicating that a correlation with oligotroph sands probably only reflects an indirect consequence of their distribution.

Tab. 3   Correlations of selected species with soil abiotic parameters. Since only correlations with [C_{org}] and pH produced significant results, only these are shown here.

		r^2	
Species	[C_{org}]		pH
Xenyllogastrura octoculata	–0,283		0.236
Cryptopygus thermophilus	–0.059		0.023
Brachystomella curvula	–0.176		0.189
Micranurophorus musci	–0.251		0.236
Scaphaphorura arenaria	–0.259		0.314
Entomobrya quinquelineata	0.062		–0.017
Doutnacia xerophila	0.162		–0.521*
Protaphorura pannonica	0.172		–0.528*
Brachystomella parvula	0.180		–0.532*
Sphaerida pumilis	0.193		–0.484*
Mesaphorura krausbaueri	0.209		–0.575**
Entomobrya multifasciata	0.211		–0.215
Isotoma viridis	0.224		–0.603**
Mesaphorura hylophila	0.311		–0.193
Sminthurinus aureus	0.503*		–0.730***
Isotomodes productus	0.513*		–0.602**
Entomobrya handschini	0.740***		–0.514*
Xenylla maritima	0.874***		–0.539*
Orchesella cinta	0.899***		–0.563**
Parisotoma notabilis	0.899***		–0.563**
Cryptopygus bipunctatus	0.899***		–0.563**
Protaphorura pseudocellata	0.899***		–0.563**
Mesaphorura critica	0.899***		–0.563**
Xenylla tullbergi	0.899***		–0.563**
Lepidocyrtus lanuginosus	0.922***		–0.628**
Mesaphorura macrochaeta	0.956***		–0.868***
*$P<0.1$, **$P<0.05$, ***$P<0.001$			

4. Discussion

All of the species found primarily in the open sands and short grass sites (*B. curvula*, *M. musci*, *S. arenaria*, *X. octoculata)* can be considered psammobiontic or strongly psammophilic (cf. Thibaud & Christian 1997). Further species registered in disturbed short-grass and open sites (*B. parvula*, *M. pygmaea*, *P. pannonica*, *D. xerophila*) have also been shown to be at least psammophilous (Thibaud & Christian 1995, 1997). The occurrence of psammobiontic species in the present sites is not particularly surprising. While many obviously psammobiontic species appear to be endemic to specific areas, other such species are apparently widespread in Europe, if only in sandy habitats (i.e., *Micranurophorus musci*, *Scaphaphorura arenaria*: Thibaud & Christian 1991, 1995, Thibaud & Weiner 1994, Thibaud & Peja 1996, Sławska 1997, Sterzyńska & Ehrnsberger 1998, Koehler 1999). Coastal and inland sand habitats are not uncommon in Europe, leading to the somewhat widespread, yet

disjunct distribution of these taxa. Thus, although stenoecious, psammobiontic collembolan taxa can not necessarily be considered to be rare. Some collembolan genera also appear to be distributed at a global level only in psammic habitats (i.e., *Isotogastrura*, *Scaphaphorura*, *Xenyllogastrura*: Thibaud 1994, 1996, 2004, Palacios-Vargas & Thibaud 1998, Thibaud & Diaz 1998, Potapov & Thibaud 2003, Thibaud & Ndiaye 2006). Thus, further sampling of such habitats can quite likely bring forth such psammobiontic taxa.

In the sites studied here, these psammobiontic species occurred sympatrically, forming distinct psammophilous communities. These communities were species-poor and largely limited to the early successional stages. Except for *M. musci*, of which at least a few individuals were registered in almost all of the studied sites, psammobiontic species were not registered in the later successional stages. Species-poor communities, as found here in the open sands and short-grass meadows, are apparently common in oligotrophic sandy habitats, where typically <10 species have been recorded to date (i.e., Koehler et al. 1995, Thibaud & Christian 1995). The recorded collembolan densities were, however, generally higher in the short-grass sites than in the biotically more advanced tall-grass sites, showing that the few psammobiontic species can reach higher total densities than the species-richer communities in the more eutrophic sites. In the present sites, the psammobiontic Collembola occurred together with psammobiontic mite species (Russell et al. 1996, Russell & Alberti 2008), which for their part also constituted relatively species-poor communities. Most psammobiontic Acari showed a distribution that paralleled that of the collembolan species, so that one can speak of psammobiontic microarthropod communities in general.

Especially in the short-grass meadows, the psammophilous species were broadly distributed, as evidenced by the comparatively high frequencies of occurrence. In the open sands as well as more eutrophic soils (including *Koeleria* II), the populations were much more fragmented. Thus, in the sampling-site gradient *Corynephorus/Koeleria* I -> *Koeleria* II -> *Festuca* sites, an increase in total recorded species concurrent with a decrease in individual densities of psammobiontic species as well as an increased fragmentation of their populations was observed.

Taken together, these results indicate a strong habitat preference of the psammobiontic taxa, mostly for the short-grass sand-meadows. Although only these species were found in the open sands, only very few species were recorded and in very low densities and very patchily distributed, possibly attributable to the extreme abiotic conditions and/or limited resources due to lack of vegetation. In the more eutrophied tall-grass and woodland sampling sites, their occurrence approached null. These differences were observed in all studied sites; and it must be stressed that all sampling sites were in very close (at times < 50 m) spatial vicinity. Such a mosaic distribution of these specialised taxa in relation to habitat parameters is in accord with other studies of the distribution of microarthropods in xerothermic sand habitats (cf. André et al. 1997 and cit. therein).

Thus, psammobiontic collembolan taxa are, in climatically very different regions, obviously limited to species-poor communities occurring in oligotrophic, abiotically extreme sandy soils. Essentially nothing is known concerning physiological adaption of collembolan taxa to these conditions. One possibility allowing psammobiontic species to occur in such habitats may be an ability of anhydrobiosis (Poinsot 1974, Greenslade 1981, André et al. 1997), although this remains to be proven for the species registered in the present study. An indication of specific adaptation is the different species composition in the oligotrophic and

more eutrophic sites studied here. Psammobiontic taxa were conspicuously lacking in the species-richer communities of the biotically more developed sites (*Festuca* and woodland sites). Many of the species occurring in these later sites have also been found in sandy habitats (Thibaud & Christian 1995, 1997). However, they have a more eurytopic zoogeographic distribution than the stenoecious psammobiontic taxa and can therefore be considered to be simply xerothermic. Thus, psammobiontic taxa must have further adaptations that just to hot and dry habitat conditions.

Another difference between the collembolan species occurring in the different sampling sites regards their life-forms. The species occurring in earlier successional stages were advanced, euedaphic worm-like forms, whereas the later successional stages were dominated by hemi- and epedaphic forms. A worm-like life-form being a preadaptation for psammophily has already been postulated by others (i.e., Thibaud & Christian 1991, 1997). Although other, more eurytopically distributed euedaphic taxa were registered in the study area (i.e., Onychiuridae spp., *Isotomodes*), the psammobiontic species were solely of this life-form and mostly only these were registered in the open sands and younger short-grass sites. Psammobiontic acari show this adaptation to sand habitats to an extreme, with very elongated worm-like forms (e.g., Nematalycidae: Coineau et al. 1978, Haupt & Coineau 1999). Extremely small body size has been postulated to be another preadaptation for psammophily (André et al. 1994), as was also true for the psammobiontic collembolan species found here.

A different possibility is whether competition excludes psammobiontic species from biotically more developed sites. The (spatially regarded) sudden disappearance of psammobiontic taxa from the species-richer communities of the more eutrophied sites is conspicuous. In other studies, psammobiontic species have been found in deeper soil horizons in successionally more developed sites and in more surface layers in earlier, species-poorer stages (i.e., Thibaud & Christian 1991, André et al. 1997). In the present study the thermophilous, but not so exclusively psammobiontic taxa showed strong correlations to soil organic material, which could be an indirect effect (through resource availability or plant surface cover, alleviating extreme connections). The reduced biotic development in the early-successional sites could have set constrains on these species, allowing psammobiontic species to occur in the competition-free conditions. The truly psammobiontic taxa showed only a non-significant tendency towards oligotrophic sands, which may only reflect their limitations to these sites.

Yet another hypothesis is adversity (A-) selection of species occurring stenotopically in extreme habitats (Greenslade 1983). This author put forth certain life-history characteristics of species occurring in habitats of low favourableness, yet high (if variable) predictability, such as low migratory ability (as realised in euedaphic forms), high rates of parthenogenesis, low fecundity and slow development. Communities shaped under such conditions should display low diversity and low interspecific competition. Although some of these correlates must still be proven for psammobiontic Collembola, many have been shown for Acari, where meiotic thelytoky (automixis) appears to also have a genetic advantage for adaptation to competition-poor, highly variable extreme habitats and a 'generalist' genotype has been postulated for taxa occurring in such habitats (Lynch 1984, Norton & Palmer 1991, Palmer & Norton 1992, Wrensch et al. 1994).

5. Acknowledgements

6. References

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