Compositional patterns in Holarctic peat bog inhabiting oribatid mite (Acari: Oribatida) communities

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ABSTRACT

Soil inhabiting oribatid mites (Acari: Oribatida) are one of the most interesting groups of animals because of their ecological characteristics at the community level. However, existing knowledge does not provide comprehensive explanations of the mechanisms underlying their community or metacommunity structure. The aim of this study is to investigate peat bog inhabiting oribatid mite metacommunity distribution throughout the Holarctic region. Species incidence data was collected (mainly from published sources) for 46 peat bog localities, comprising a total of 410 species. Characteristics of species composition (coherence, turnover and boundary clumping) were analyzed to reveal patterns of peat bog oribatid metacommunity for different ecological guilds. We also applied correlation and regression analysis to detect whether peat bog oribatid communities show latitudinal gradient and distance decay in compositional similarity. Analysis of metacommunity structure showed non-random structure for all ecological guilds studied with dominating nested and Clementsian patterns. No significant evidence was found for latitudinal gradients in species composition whereas non-linear distance decay in compositional similarity is a common phenomenon for peat bog oribatid communities. We discuss these metacommunity patterns within the framework of existing hypotheses and conclude that the community level structure for peat bog oribatid species is largely determined by interspecific interactions and common biogeographical history, whereas metacommunity patterns are the result of postglacial colonization processes.

Introduction

Oribatid mites are one of the most abundant and important decomposers in soil (Schneider 2005; Maraun et al. 2007; Norton and Behan-Pelletier 2009). Despite much research on biogeography of Oribatida at different scales (Bernini 1984; Wallwork 1984; Niedbala 1991; Schatz 2004; Maraun et al. 2007; Schatz and Behan-Pelletier 2008; Behan-Pelletier and Schatz 2010), there remains much to be understood about their distribution patterns. More precisely, we still do not know how the contemporary biogeographical pattern has been shaped or what underlying mechanisms structure soil dwelling mite communities. One of the most intriguing facts associated with these arthropods is the very high number of coexisting species (up to 100 species in one locality) (Behan-Pelletier and Newton 1999; Schatz and Behan-Pelletier 2008). Several ideas have been proposed to explain this phenomenon but there is contention as to which is most explanatory, and what is more important, most of them lack empirical proofs (Schneider 2005).

Evidence showing differences in oribatid feeding habits which may support species coexistence was reviewed by Schneider et al. (2004). However, this and following works (papers cited in Maraun et al. 2011) provide compelling evidence that the interspecific differences in resource utilization between oribatid species alone are insufficient to achieve niche splitting and hence coexistence. Moreover, we know that many species of Oribatida are generalist feeders and some do not show habitat specialization (Aoki 1967; Behan-Pelletier and Eamer 2007; Maraun et al. 2007). It is increasingly evident that the high number of coexisting species has a scale component (Berg and Bengtsson 2007; Nielsen et al. 2012) and is the result of resource availability, variability in soil properties and vegetation, with the relative importance of these factors varying with habitat (Nielsen et al. 2012).

Soil oribatid mites have considerable passive dispersal abilities (Karasawa et al. 2005; Lebedeva and Lebedev 2008; Lebedeva 2012; Lehmitz et al. 2011, 2012). There is recent evidence that many active surface and litter dwelling species can be transported by wind and that some species actively disperse from surrounding source substrates into newly found habitats (Lehmitz et al. 2012). Given this, it could be hypothesized that the oribatid community has a random structure (resulting from random colonization and random

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extinction) or from a more idealized perspective, every species could live everywhere, with no gradients existing in community composition. But this is not the pattern seen frequently. First, there are many oribatid species with restricted ranges, and second, although many species can co-exist within localities (high α diversity), not all species can be found at all patches within localities (Lindo and Winchester 2009a,b). This led us to postulate that there are other kinds of structural mechanisms shaping oribatid communities.

In this paper we conduct a Holarctic scale investigation of peat bog inhabiting oribatid mites to analyze the patterns of their community composition. Peat bogs are useful for this analysis for several reasons: (a) Holarctic peat bogs are rather similar in their mode of development and almost similar in age; (b) they maintain a high humidity level throughout the year; (c) soil quality and humus content are usually high and similar between sites (i.e. peat bogs can be considered as homogenous habitat across any scale) and (d) they can be regarded as insulated systems within continents (Tjuremnov 1976; Lappalainen 1996; Rubec 1996; Parish et al. 2008; Joosten and Clarke 2002; Rydin and Jeglum 2006). For these reasons peat bog ecosystems can be considered as islands, and their investigation should provide insights into mechanisms driving oribatid community composition. We address the following questions: (1) is metacommunity composition non-random for peat bog inhabiting oribatid mites and if so, what kind of patterns can be observed? We expected oribatid metacommunity to have a random pattern or close to randomness driven by random ecological drift and dispersal (Hubbell 2001), since there is no compelling evidence of competition for food, habitat or other types of resources between peat bogs; (2) is there latitudinal gradient in oribatid species richness living in peat bog habitats? We hypothesized no latitudinal gradients to exist in species richness because of the homogeneity of the peat bog habitat; (3) whether there is distance decay in similarity in community composition? We hypothesized that more distant communities are not different in species composition or species richness, because of passive dispersal abilities and similar environmental requirements for oribatid mites in peat bogs.

Materials and methods

Study area and data collection

Faunal data of peat bog inhabiting oribatid mites from 46 localities in the Holarctic region were analyzed (Fig. 1). Species by site presence–absence matrix was compiled from published species lists and original data (for Colchis lowland). Only papers which included exact geographical locality, well defined soil habitat specificity, description of vegetation cover and complete faunal list of recorded Oribatida were used. We rejected published data where less than 10 oribatid species were recorded. We choose this arbitrary threshold as a measure of sampling completeness. Supplementary material (Appendix 1) is a list of studied localities and site names we used to simplify data handling.

In the Holarctic, publications on oribatid fauna of European bogs appeared most suitable for our purpose. Peat bog habitats of Germany were very well studied for Oribatida (Willmann 1939, 1942; Strenzke 1952; Weigmann and Kratz 1981; Weigmann 1991). Well defined faunal data are available also for the Czech Republic, Lithuania and Finland (Karppinen 1958; Halaškova and Kunst 1960; Eitminavichute 1966, 1968; Markkula 1986; Stary 2006). Bogs of Russia were studied mainly for tundra habitats in Murmansk and Arkhangelsk provinces (Laskova 1980; Sidorchuk 2008; Yudin 2008; Zenkova et al. 2011). Sporadic data were obtained for Austria, Poland, Norway and Sweden (Willmann

1939; Tarras-Wahlberg 1961; Borcard 1991a,b, 1992a,b, 1994, 1995, 1996; Borcard and von Ballmoos 1997; Seniczak et al. 2010; Seniczak 2011). The database on Georgian peat bog Oribatida was created using manuscripts of Murvanidze and Kvavadze (2010) and Murvanidze et al. (2011), with the addition of our unpublished data collected during field investigations in 2009–2010 years.

Species lists of several bogs from USA were created using works of Belanger (1976) and Donaldson (1996). There is additional data on USA wetlands in manuscripts of Banks (1895) and Behan-Pelletier and Bisset (1994), but there are no exact localities for mite species in these publications. However, well defined species lists were obtained for Canadian peat lands (Behan-Pelletier 1989; Behan-Pelletier and Bisset 1994; Behan-Pelletier 1997).

Total list of species (Supplementary material, Appendix 2) follows the classification of Schatz (2011). Synonyms of species were identified after Subias (2004, electronically updated in 2011). Estimating habitat preferences of oribatid species to separate different ecological guilds was based on works of Weigmann (2006) and Behan-Pelletier and Eamer (2007). Species were assigned to either eurybiont (i.e. species known to occur in different habitat types) or bog specific (i.e. species known from only bog habitats). We used Google Earth (Google Earth V. 6.2.2. CA: Google Inc. (2012). Available at http://google.com/earth/) to extract exact locations of several peat bog points for which GPS coordinates were not provided in the original source material.

Analytical techniques

To analyze bog inhabiting oribatid metacommunity structure we applied EMS (Elements of Metacommunity Structure) method sensu Leibold and Mikkelson (2002) and Presley et al. (2010). EMS integrates methods of multivariate ordination and null model testing and allows selection of which from the predetermined models fits best (Burnham and Anderson 2002; Gotelli and Ulrich 2010) to the given data set. The species-by-site presence–absence matrix is tested against five idealized models – Clementsian (Clements 1916), Gleasonian (Gleason 1926), checkerboards (Diamond 1975), evenly spaced gradients (Tilman 1982), and nested subsets (Patterson and Atmar 1986). EMS method analyzes three characteristics of a metacommunity: coherence, turnover and boundary clumping (detailed definition of concepts can be found in Leibold and Mikkelson 2002). According to this analytical protocol, the presence–absence data matrix should be ordinate (as usual using reciprocal averaging) in multidimensional space to extract orthogonal axes of variation. For each ordination axis, the data matrix is arranged along a gradient so that sites and species scores have maximal correspondence along the gradient without a priori knowledge of any environmental variable that may govern species distribution (Jongman et al. 1995). Reordered matrices for the respective axes are then used to assess coherence of species composition by counting embedded absences (i.e. sum of absences within presence ranges for each species). If the number of embedded absence equals to zero, then the community is perfectly coherent but this seldom (if ever) applies to the real data set. Compared to the average number of embedded absence generated by null models (null matrices must also be subjected to ordination), a given data set may be significantly coherent i.e. have a significantly lower number of embedded absences then expected by chance alone. Non-significant coherence indicates random occurrence of species with respect to given ordination axes (or latent environmental gradient). Negative significant coherence (observed > expected) indicates checkerboard distribution whereas significant positive coherence indicates other non-random species distribution along the respective axes. Magnitude of turnover is calculated as the number of substitutions when extreme presence for one species range is replaced by another between all possible pairs
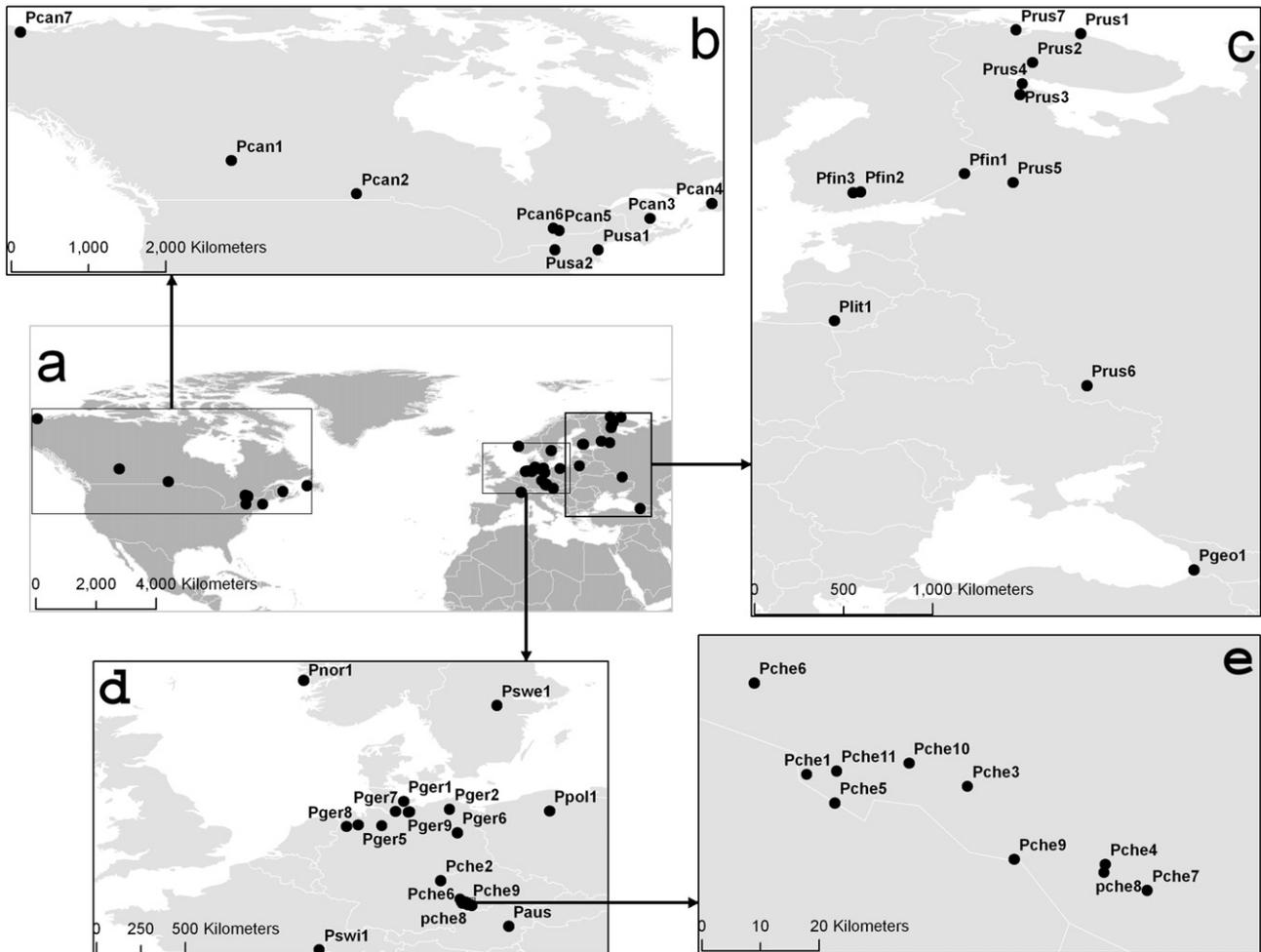
Fig. 1. Distribution of sampling localities using in this studies: (a) full view of sampling localities; (b) north American points; (c) north-eastern European and Georgian points; (d) central European points; and (e) Bohemian forest points (Czech republic).

Table 1

Results of analyses of coherence, species turnover and boundary clumping for oribatid mite communities. Analyses were performed for four guilds of species – all species combined, only bog specific, only eurybiont species and only rare species guilds. Significant results for each calculation are in bold–italics. *Abbreviation*: SD stands for standard deviation, *P* – significance level.

	Coherence				Turnover				Clumping		
	Observed	Expected	SD	*P*	Observed	Expected	SD	*P*	Morisita's *I*	*P*	
All species											
I axis											
All species	8501	12,155	422	***<0.001***	1,803,550	2,202,900	96,650	***<0.001***	2.23	***<0.001***	Nested
Bog specific species	800	1117	87	***<0.001***	48,107	31,653	4624	***<0.001***	2.4	***<0.001***	Clementsian
Eurybiont species	9944	9193	342	***0.028***	1,215,308	1,159,700	65,516	0.39	2.79	***<0.001***	Checkerboard
II axis											
All species	9922	12,078	456	***<0.001***	1,955,295	2,013,800	95,272	0.54	3.46	***<0.001***	Quasi-Nested
Bog specific species	1053	1117	74	0.38	32,074	25,308	3787	0.074	2.67	***<0.001***	Random
Eurybiont species	6287	9210	351	***<0.001***	1,108,052	1,321,300	66,125	***<0.001***	2.8	***<0.001***	Nested
Rare species removed											
I axis											
All species	5960	9600	282	***<0.001***	1,772,512	1,776,000	89,834	0.97	1.68	***<0.001***	Quasi-Nested
Bog specific species	624	912	60	***<0.001***	41,846	25,737	4300	***<0.001***	3.12	***<0.001***	Clementsian
Eurybiont species	4668	7293	221	***<0.001***	992,960	1,149,100	63,895	***0.0145***	1.89	***<0.001***	Nested
II axis											
All species	7225	9565	282	***<0.001***	2,003,668	1,426,500	80,047	***<0.001***	2.08	***<0.001***	Clementsian
Bog specific species	817	1205	65	***<0.001***	76,432	46,320	6810	***<0.001***	2.52	***<0.001***	Clementsian
Eurybiont species	5307	7300	227	***<0.001***	1,392,311	911,700	57,092	***<0.001***	2.21	***<0.001***	Clementsian
Rare species	1131	532	156	***<0.001***	5151	5330	15	***<0.001***	2	***<0.001***	Checkerboard

of sites. The observed result is then compared to the expected number of replacements generated by the null model which randomly shifts species ranges between iterations. If the observed turnover is significantly lower than expected, the community agrees with the nested pattern. In the opposite case (observed > expected) we evaluate boundary clumping to reveal other possible patterns. That is, evaluation of how frequently species ranges coincide to expectations generated by the null model. Morisita's Index (Morisita 1971) can be used for this comparison. When boundaries are arranged randomly, Morisita's I equals 1. If the observed value is not significantly different (Chi-square test), it indicates random boundary distribution and hence is consistent with a Gleasonian pattern. If the community has a significant positive (observed > 1) or negative (observed < 1) deviation then the community follows a Celementsian or evenly spaced distribution respectively. For each step of the analysis when observed results are different from expected generated by null models, but not significantly, patterns are assessed as quasi idealized models (Presley et al. 2010, 2011). EMS analysis was conducted for primary and secondary axes for each sub matrix (Table 1). Calculating significance statistics was based on a null model which maintains site richness fixed and species occurrence equiprobable, as this model has more acceptable type I and type II error rates simultaneously (Gotelli 2000; Presley et al. 2010). All above described comparisons are made at 5% significance level. EMS analysis was implemented in matlab scripts available at http://tarleton.edu/Faculty/higgins/EMS.htm (last accessed 02.12).

To determine whether the bog mite community reveals association with geographic or climatic constraints, we calculated Pearson's correlation between site scores for primary and secondary CA axes and also raw species richness values (measured as a species number at each site) and environmental variables (geographic – latitude, longitude and altitude; climatic – mean annual temperature and mean temperature of coldest month). Climatic variables where obtained from WorldClim Version 1.4 (http://www.worldclim.org/) with 2.5′ spatial resolution (Hijmans et al. 2005).

Mantel test (Smouse et al. 1986; Nekola and White 1999) with 1000 permutation was used to test the significance of regression models (as a measure of distance decay in similarity) between linear geographic or climatic distance and community similarity using IBD software (Bohonak 2002). Linear Euclidean distances and similarity values were calculated for each pair of sites using PAST (Hammer et al. 2001). As a community similarity measure we used Jaccard index which is one of the simplest and straightforward measures for presence–absence data (Nekola and White 1999; Magurran 2004). The same software was used for sample based rarefaction analysis to check the faunal completeness for the studied metacommunity.

To assess how geography or species functional composition is reflected in patterns of metacommunity structure, we applied EMS, environmental gradient and distance decay analysis to various subsets of the main data set. Six sub matrices were considered depended on species guilds included (Table 1). In addition, we applied EMS analysis to a group of rare species (we use the term "rare species" for those found in only one locality) to assess whether or not their distribution deviates from random or aggregate patterns.

Results

A total of 410 oribatid species distributed in 46 peat bog habitats were analyzed (Supplementary material, Appendix 2), of which 106 species are represented in only one locality. The most widespread species were *Tectocepheus velatus velatus* (Michael, 1880) (40 sites),

Oppiella nova (Oudemans, 1902) (39 sites) and *Limnozetes ciliatus* (Schrank, 1803) (34 sites). The first two are eurybiont species (species with very wide habitat spectrum), the latter is bog specific. In addition, two eurybiont (*Platynothrus peltifer* (C.L. Koch, 1839) and *Rhysotritia ardua* (C.L. Koch, 1841)) and one bog specific (*Nothrus pratensis* Sellnick, 1928) species occur in geographically most severe sites (Pcan7 and Pgeo1; Fig. 1). The most species rich bogs were Prus3, Prus4, with 180 and 171 species respectively, whereas several sites had less than 20 species. Rarefaction analysis showed that faunal completeness for each site is not perfect (Fig. 2) which may be an unavoidable confounding factor in metacommunity analysis.

Correspondence analysis (CA) ordination diagrams (CA1 vs. CA2 axes) did not reveal "arch effect" for any dataset (results not shown). Thus, derived ordered matrices were used for EMS analysis which were performed for three ecological guilds – all species, eurybiont species (326 species), bog specific (54 species), and the group of rare species (106 species). A second group of EMS runs was performed (for the guilds mentioned above) with removal of rare species. It was impossible to make an unambiguous classification of ecological preferences for about 30 species as they belong to neither eurybiont or bog specific guilds in the sense of Weigmann (2006) and Behan-Pelletier and Eamer (2007).

Contrary to our hypothesis 1, all analyzed matrices showed significant coherence (Table 1) along the first CA1 axis which means that oribatid mites do not distribute randomly. Nested pattern is evident in complete data sets with and without rare species for the first CA axis and it changes to Clementsian pattern for the second CA axis when rare species were removed. Correlation analysis generally shows weak but significant correlations between environmental variables (except altitude) and site scores for either or both CA axes (Table 2). Interestingly, species richness, CA1 and CA2 scores, all show significant correlations with longitude for all species guilds, with the strongest associations between longitude and CA1 site scores with and without rare species.

No significance coherence (random metacommunity pattern) along the second ordination axis characterizes the peat bog specific mite guild. This guild shows Clementsian structure with strongest correlation between CA1 (with or without rare species) and longitude (Tables 1 and 2), indicating that this guild may respond to no more than one latent environmental variable.

The eurybiont species guild showed checkerboard pattern for the first CA axis when rare species were included. However exclusion of rare species resulted in a nested structure. The rare species group alone also showed a checkerboard pattern indicating that the presence of rare species significantly affects the structure of the eurybiont species guild. The CA1 for the eurybiont species guild (with or without rare species) is significantly associated with all variables except altitude whereas species richness is not related to any variable used. After removal of rare species, a weak correlation appears between species richness and altitude and the negative correlation between CA1 and longitude decreased from −0472 to −0.826 ($P < 0.001$) (Table 2).

Overall, rare species have a noticeable influence on structuring bog oribatid metacommunity. With removal of rare species – 4 out of 6 cases changed the pattern of their structure, but associations of species richness with environmental variables and similarity decay with geographical distances changed insignificantly.

From 1035 pairwise combinations of sites only four of them do not have species in common. Linear regression showed significant (after mantel tests) decrease in community similarity with increasing geographic distance (Table 3). The decay rate in similarity (slope of regression line) for all data sets was approximately the same and the r^2 values ranged between 0.211 and 0.221 ($P < 0.001$ for all cases). Removal of rare species had very little effect on change of similarity decay rates and associated r^2 values but in all cases,
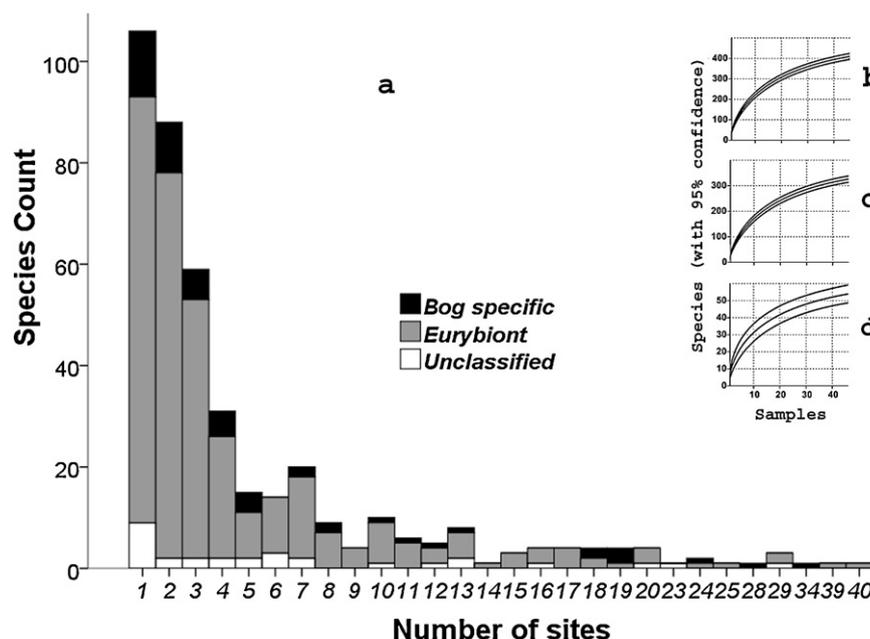
Fig. 2. The histogram (a) shows occurrence frequencies of species. Left sided bins showing that most of the species are represented in only 1–4 sites whereas a small number of species are represented in many (5 or more) sites. Right sided graphs represent sample based rarefaction curves: for all species (b), for eurybiont species (c) and for bog specific species (d).

Table 2
Pearson's correlation coefficients and associated *P* values are shown for three species guilds with and without rare species. Correlation was calculated between species number and site scores on the first and second CA axes (for respective matrices) and environmental variables. Bold–italic denotes significant associations.

	All species			Bog specific species			Eurybiont species		
	Species number	CA1	CA2	Species number	CA1	CA2	Species number	CA1	CA2
All species									
Latitude	0.235	0.149	−0.507	0.119	−0.340	−0.339	0.250	0.340	−0.394
P	0.116	0.322	*<0.001*	0.43	*0.021*	*0.021*	*0.094*	*0.021*	*0.007*
Longitude	0.302	−0.771	−0.571	0.21	−0.758	0.054	0.277	−0.472	−0.718
P	*0.041*	*<0.001*	*<0.001*	0.16	*0.000*	0.724	0.062	*0.001*	*0.000*
Altitude	0.223	−0.045	−0.186	0.368	−0.105	−0.159	0.182	0.005	−0.207
P	0.137	0.768	0.217	*0.012*	0.489	0.292	0.227	0.975	0.168
Mean annual *T*	−0.257	−0.576	0.285	−0.257	−0.092	0.457	−0.268	−0.624	0.102
P	0.084	*<0.001*	0.055	0.085	0.545	*0.001*	0.071	*0.000*	0.502
Mean *T* of coldest month	0.037	−0.693	−0.202	−0.019	−0.477	0.281	0.010	−0.528	−0.349
P	0.806	*<0.001*	0.179	0.899	*0.001*	0.058	0.946	*0.000*	*0.017*
Rare species removed									
Latitude	0.228	−0.379	0.287	0.095	0.355	−0.018	0.245	−0.400	0.338
P	0.128	*0.009*	0.053	0.530	*0.016*	0.904	0.101	*0.006*	*0.022*
Longitude	0.338	−0.838	−0.384	0.243	0.726	0.058	0.315	−0.826	−0.406
P	*0.021*	*0.000*	*0.008*	0.103	*0.000*	0.704	*0.033*	*0.000*	*0.005*
Altitude	0.220	−0.181	−0.266	0.378	0.126	−0.142	0.180	−0.198	−0.310
P	0.141	0.229	0.074	*0.010*	0.403	0.348	0.232	0.188	*0.036*
Mean annual *T*	−0.230	−0.013	−0.468	−0.219	0.057	0.176	−0.244	0.052	−0.492
P	0.123	0.930	*0.001*	0.143	0.709	0.241	0.102	0.731	*0.001*
Mean *T* of coldest month	0.069	−0.499	−0.506	0.014	0.448	0.186	0.041	−0.466	−0.521
P	0.650	*0.000*	*0.000*	0.925	*0.002*	0.216	0.784	*0.001*	*0.000*

Table 3
Results of distance decay analyses. Regression slopes, r^2 values and associated significance level are shown.

Pairwise similarity distance	Geographic distance					
	All sites			Without American sites		
	Reg. slope	r^2	*P*	Reg. slope	r^2	*P*
All species	0.5862	0.219	0.001	1.045	0.468	<0.001
Bog specific species	0.5877	0.212	0.001	1.049	0.431	<0.001
Eurybiont species	0.5858	0.221	0.001	1.380	0.459	<0.001
All species without rare	0.586	0.217	0.001	1.045	0.465	<0.001
Bog specific species without rare	0.5878	0.211	0.001	1.050	0.427	<0.001
Eurybiont species without rare	0.05845	0.219	0.001	1.042	0.475	<0.001

except the bog specific species guild, decay and r^2 decreased. After removing North American sites (this was done to analyze the effect of intercontinental differences) results of decay analysis changed unexpectedly: decay rate and r^2 values were much higher (Table 3).

Discussion

The composition of isolated communities of the same ecological guilds of species should have predictable patterns, as the main factors affecting community are considered to be species interactions, multiple environmental drivers and common biogeographical history. Environmental correlates and species interactions are more frequently studied in searching for mechanisms to explain composition of soil oribatid communities (Maraun and Scheu 2000). Our results show that peat bog inhabiting oribatid metacommunities do not have a random pattern. Many oribatid species have relatively high passive dispersal ability, including litter species (Karasawa et al. 2005; Lebedeva and Lebedev 2008; Lehmitz et al. 2011; Lebedeva 2012; Lehmitz et al. 2012). Colonization of new habitats from source territories can also be by active dispersal and pioneer species apparently have the ability to easily occupy different kind of habitats (Skubala 1999; Skubala and Gulvik 2005; Lindo and Winchester 2009a,b; Lehmitz et al., 2012). Despite this, species ranges are not equally large. Only a small number of species can be considered truly cosmopolitan (Fig. 2); most species are restricted to relatively small areas. What kinds of forces limit the distribution of oribatid mites?

Modern metacommunity theory follows two main approaches. The first are niche based models, where species differ in life history traits, providing niche diversity and thus avoiding competition for resources (Chase and Leibold 2003; Tilman 2004). Second is Hubbell's (2001) neutrality theory, which assumes that species do not differ from each other (ecologically) and that dispersal and random ecological drift are factors determining community structure. It is increasingly evident that metacommunities can be better characterized by applying elements of both approaches (Leibold et al. 2004; Alonso et al. 2006; Leibold and McPeek 2006; Adler et al. 2007; Rosindell et al. 2011). It seems that compositional mechanisms based on niche differentiation are most frequently found in oribatid communities (Schneider et al., 2004; Caruso et al. 2012; Ingimarsdóttir et al. 2012), however dispersal and random drift also play important roles in community structuring (e.g. Ingimarsdóttir et al. 2012). Here we discuss our results within the framework of the major hypotheses: postglacial colonization, ecological disturbance and niche specialization, which may be shaping oribatid communities in Holarctic peat bogs.

A dominant hypothesis about shaping modern distribution ranges of species is the process of postglacial colonization. Frequently, recolonization from glacial refugia results in nested patterns when an area more distant from the respective refugium is occupied by species which comprise a nonrandom subset of the species pool inhabiting areas more adjacent to the refugium (Patterson and Atmar 2000; Hausdorf and Hennig 2003). Our results are consistent with this hypothesis. EMS analysis of bog mite metacommunity detected a nested pattern for all species and for the eurybiont species guild with or without rare species. The latent environmental variable (CA1) is negatively correlated with geographical and climatic variables (Table 2). Bog specific species showed a Clementsian pattern with strong negative correlation between CA1 and longitude which can also be explained by postglacial dispersal (but from multiple refugia rather than a single refugium) or by other historical events. The postglacial colonization hypothesis assumes that not enough time has passed post-glaciation, thus preventing all species achieving maximal extension of their range. However, this assumption may not be applicable to oribatid mites because of their considerable dispersal abilities. The fact that the oribatid communities of Pgeo1 (peat bogs in Colchis lowland which existed at least 18 kyr before present (Maruashvili 1971; De Klerk et al. 2009) are not significantly richer then more northern communities suggests that oribatid mites quickly dispersed to available bog habitats postglaciation, or that there were several regional glacial refugia in the Holarctic. In bog inhabiting mites 87% represents eurybiont species (Supplementary material; Appendix 2) meaning that their immigration to particular bog habitats was possible immediately from adjacent areas (Ingimarsdóttir et al. 2012). In contrast, bog specific oribatids are likely to survive only in bog habitats and hence their colonization was possible only from the other nonglaciated bogs. If postglaciation dispersal alone from southern refugia shaped bog specific oribatid guilds then we would predict either nested guild patterns, or species richness decreasing from south to north. However, neither of these is evident (Tables 1 and 3). Instead there is a Clementsian structure for the bog specific oribatid guilds which is not consistent with the assumptions of that pattern (namely the differences in local environmental conditions drive a species composition) (Clements 1916; Chase 2003). It is clear that one should consider the influence of other factors like an interaction with eurybiont species. In contrast to bog specific oribatid guild, eurybiont species distribution is intuitively predicted by the mass effect model (Leibold et al. 2004) which would strongly affect the dynamics of local populations of bog specific oribatids. Our results do not provide unambiguous evidence of ordered colonization from an assumed species pool (any glacial refugia) but a more detailed study incorporating multiple refugia in nested pattern analysis (e.g. Hausdorf and Hennig 2003) may provide much stronger argumentation.

As another major contributor in structuring oribatid communities is considered ecological disturbance (Maraun and Scheu 2000 and references therein). Indeed, physical destruction of oribatid habitats reduces their abundance and results in random local extinctions. Sudden decrease of abundance and species richness provides niche or space opportunities for new colonizers. Thus, the result of regular extinction and colonization can be high diversity and heterogeneity within and between communities (Adams 2009). However, several studies on the responses of oribatid mites to fire disturbance showed that oribatid densities decreased significantly after fire, but post-fire recovery did not lead to an increase in species richness (Murvanidze et al. 2008; Hugo-Coetzee and Avenant 2011). There is no evidence that disturbance is an actor in peat bog habitats. Normally biotic and abiotic disturbances are low in peat lands (because of stable environmental conditions) (Rydin and Jeglum 2006; Parish et al. 2008). Furthermore, assuming that oribatid mites are good dispersers, we would expect a randomized metacommunity structure and not similarity decay with distance if ecological disturbance is a leading factor in structuring peat bog oribatid communities. Although the guild of bog-specific oribatid mites shows random metacommunity structure at the second CA axis (later expectation), overall our results suggest that disturbance is not a leading factor for structuring peat bog oribatid metacommunity.

Food niche differentiation can play an important role in the composition of oribatid mite community at the local scale (Hansen 2000; Caruso et al. 2012). Similarly, heterogeneity at a small scale, providing more patches and different foods for animals, can support high diversity of intermediate-size soil fauna (such as oribatid mites) (Nielsen et al. 2010, 2012). Rare species in peat bog communities we analyzed showed a checkerboard pattern which is consistent with niche splitting and strong interspecific competition; however specific drivers need to be investigated further.

As we expected, there are no clear gradients in species richness for peat bog oribatid mites (hypothesis 2), whereas contrary to our expectation, dissimilarity (hypothesis 3) significantly increases with increasing distances. Although distance decay in similarity is significant, there is no linear relationship, *i.e.* between continental differences is relatively smaller than within continental differences in community composition, indicating that intercontinental distance cannot be considered as a dispersal barrier for peat bog oribatid mites. This pattern of decay in community similarity may be due to spatial dependence on some factors but it is not the result of limited dispersal (passive) abilities or barriers at a broadest scale. Future testing of the role of spatial autocorrelation processes in structuring bog oribatid community could provide important additions to our knowledge. Non-random metacommunity composition – nested, Clementsian and checkerboard pattern for different ecological guilds are significantly correlated with latitude, longitude and the minimal temperature (Table 2), which implies complex underlying mechanisms driving bog mite community composition.

In conclusion, our analysis suggests that the composition of the peat bog oribatid community at a local scale is a function of interspecific interactions (particularly food niche differentiation) and common biogeographical history, whereas the structure of peat bog oribatid metacommunity seems to be largely driven by the postglacial dispersal processes.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pedobi.2012.10.001.

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