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Positive correlation between density and parthenogenetic reproduction in oribatid mites (Acari) supports the structured resource theory of sexual reproduction

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ABSTRACT

Question: A number of theories have been proposed to explain the dominance of sexual reproduction in Metazoa. Using oribatid mites (Acari, Oribatida) as model organisms, we test the validity of the structured resource theory of sexual reproduction (SRTS), which suggests that limited resources result in the dominance of sexual processes, whereas ample resources favour parthenogenesis. Oribatid mites are mainly soil-living animals that reproduce either sexually or by thelytoky.

Key assumptions: Resource supply is reflected by animal density. Populations are controlled predominately by bottom-up rather than top-down forces, such as predation, which is likely true for oribatid mites.

Data studied: The relationship between oribatid mite density and the frequency of parthenogenetic reproduction was investigated at two spatial scales: (1) regionally, using data on oribatid mites from two different forests in Germany, and (2) globally, by compiling data on 38 oribatid mite communities from different habitats.

Conclusions: Predictions of the SRTS were supported at both scales, indicating that ample resources (as indicated by high population densities) in fact favour parthenogenetic reproduction.

Keywords: evolution of sex, Oribatida, parthenogenesis, structured resource theory of sexual reproduction.

INTRODUCTION

The perceived disadvantages of sexual compared with parthenogenetic reproduction are manifold and include, for example, the break-up of favourable gene combinations and the need to both find mating partners and produce male offspring (Maynard Smith, 1978). Despite

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these disadvantages, most species of animals reproduce sexually (Bell, 1982). Theories proposed to explain the advantages and disadvantages of parthenogenetic and sexual reproductive modes might be viewed as either genetic (based on mutations) or ecological (based on species–environment interactions, including those with other species). Mutational theories state that parthenogens either accumulate detrimental mutations [Kondrashov's hatchet (Kondrashov, 1988)], or that in parthenogenetic populations mutation-free genotypes are more quickly lost than in sexual populations [Muller's ratchet (Muller, 1964)]. Another genetic theory assumes beneficial mutations to spread more quickly in sexual than in parthenogenetic populations [Fisher-Muller-accelerated-evolution (Fisher, 1930; Muller, 1932)]. Ecological theories propose that strong biotic interactions foster sexual reproduction [Red Queen hypothesis (Jaenicke, 1978; Hamilton, 1980)], or that spatially variable niches favour sexually produced offspring [Tangled Bank hypothesis (Ghiselin, 1974; Bell, 1982)].

These different and mutually exclusive theories led some authors to propose that multiple theories are needed to explain the various aspects associated with sexual reproduction (West *et al.*, 1999). However, the recent structured resource theory of sexual reproduction (SRTS) (Scheu and Drossel, 2007) proposes an overarching explanation, that sexual reproduction favours the exploitation of complex resources that are in short supply. According to the SRTS, outcrossing and mixing shuffle new genotypes, allowing a more complete exploitation of local resources. Conversely, it predicts that the availability of ample resources favours parthenogenetic reproduction, since parthenogenetic species exploit these resources more quickly. The SRTS resembles the Tangled Bank theory in that it relates advantages of sexual reproduction to variations in niche space, but it focuses on food resources rather than on abiotic conditions (Song *et al.*, 2011). Thus, the SRTS incorporates sib-competition models in which sexually produced offspring benefit from being genetically different by relaxing intraspecific competition (Williams, 1966, 1975; Bell, 1982). In addition, the SRTS integrates aspects of the Red Queen theory, since parasites may be experienced by the host as an aggravation of shortage of resources (Scheu and Drossel, 2007). Whether or not the SRTS is sufficient to explain all evolutionary aspects of these issues, we believe that it is a powerful predictor of the local distribution of reproductive modes – that is, of the relative dominance of sexual and parthenogenetic reproduction in local communities. This idea is best tested in environments where parthenogenetic taxa are frequent and widespread, where we can assume that mechanisms promoting the general dominance of sexual reproduction are more relaxed.

Below-ground communities are ideally suited for investigating the relative merits of sexual and parthenogenetic reproduction, since parthenogenetic or asexual reproduction is common in protozoans, nematodes, enchytraeid worms, earthworms, collembolans, isopods, and oribatid mites (Bell, 1982, 1988; Palmer and Norton, 1991; Christensen *et al.*, 1992; Sbordoni *et al.*, 1997; Doroszuk *et al.*, 2006; Terhivuo and Saura, 2006; Chahartaghi *et al.*, 2009; B.M. Fischer *et al.*, 2010). Sexual taxa are also common, and often co-exist with parthenogenetic taxa that are both closely related and ecologically similar. Thus understanding the high incidence of parthenogenetic reproduction in soil may help to identify unifying concepts responsible for the maintenance and general dominance of sexual reproduction.

Oribatid mites are among the most suited animal groups for investigating the mechanisms responsible for the maintenance of sexual reproduction in soil animal taxa. They are ubiquitous, occurring in high numbers in virtually all ecosystems (Maraun and Scheu, 2000). Of the approximately 10,000 species described to date, nearly 10% reproduce by parthenogenetic development of females, i.e. by thelytoky (Norton and Palmer, 1991; Palmer and Norton, 1991;

Norton, 1994), and parthenogenetic species can comprise up to 80% of oribatid mite individuals in local faunas (B.M. Fischer *et al.*, 2010).

Using oribatid mites as model organisms, we tested the prediction of the SRTS that the proportion of parthenogenetic individuals is positively correlated with resource availability. The prediction was investigated at two spatial scales: regional (two forest systems in Germany) and global. Oribatid mite density was taken as a proxy for resource availability, since all current information shows that oribatid mites are controlled predominately by bottom-up forces. Indeed, due to an array of defence mechanisms, including a strong cuticle, protective structures and body forms, and chemical repellants (Sanders and Norton, 2004; Heethoff *et al.*, 2011), oribatid mites have been shown to be resistant to predation (Peschel *et al.*, 2006).

Using density as a proxy for resource availability is too simplistic, as it ignores changes in metabolism with body size. Allometric scaling predicts that smaller organisms have higher metabolic rates per unit body mass (Brown *et al.*, 2004) and reach higher densities than larger organisms (Damuth, 1981). Therefore, at the regional scale we also investigated the relationship of oribatid mite reproductive mode to metabolism (i.e. respiration). The respiration of oribatid mites has been estimated to be equivalent to 16% of the energy ingested (Luxton, 1975; Wallwork, 1983).

Our regional sites comprised mull (Swabian Alb) and moder forests (Schorfheide) varying in macrofaunal density (Schaefer and Schauermann, 1990). The soil macrofauna is known to affect mesofauna (including oribatid mite) communities through mechanical disturbance, resource competition, predation, and destruction of habitable space (Maraun *et al.*, 2003; Eisenhauer, 2010; Erdmann *et al.*, 2012). Therefore, we expected the relationship between reproductive mode of oribatid mites and density and/or respiration to be most pronounced in the macrofauna-poor moder systems of the Schorfheide. On the global scale, we compiled data on the density of parthenogenetic oribatid mite species from 38 sites ranging from temperate and tropical forests, to fields and meadows, to the bark of trees. According to the SRTS, we expected the density of oribatid mites to be positively correlated with the frequency of parthenogenetic individuals in both datasets.

MATERIALS AND METHODS

Regional scale

The sites of the regional dataset comprised forests in the southwest (Swabian Alb; 460–860 m above sea level) and the northeast (Schorfheide; 3–140 m above sea level) of Germany. They form part of the 'Biodiversity Exploratories', a long-term monitoring and experimental study project (M. Fischer *et al.*, 2010). The Swabian Alb is dominated by European beech (*Fagus sylvatica*) growing on Jurassic limestone parent rock; the sampled forest types were on cambisols or leptosols (pH of 4.51 ± 0.72) at about 700 m above sea level. The Schorfheide is located on glacial till, which often is covered by sand; the accompanying soil types are mostly dystric cambisols (pH of 3.3 ± 0.19), but occasionally podsols occur (for details, see M. Fischer *et al.*, 2010). Mean annual precipitation in the Swabian Alb is 700–1000 mm and in the Schorfheide 500–600 mm, with a mean annual temperature of 6.0–7.0°C and 8.0–8.5°C, respectively (M. Fischer *et al.*, 2010). Four forest types were studied in each region: 30-year-old beech forests, 70-year-old beech forests, 120-year-old unmanaged beech forests, and 70-year-old coniferous forests (consisting of *Picea abies* in the Swabian Alb and *Pinus sylvestris* in the Schorfheide).

In spring 2008, four soil samples were taken from each forest in each of the two regions. The 32 samples were taken with a corer (5 cm diameter) each separated into organic (L/F material) and soil (4 cm thick) layers, from which soil arthropods were extracted by heat (Macfadyen, 1961); mite data from these two layers were subsequently pooled for all analyses. Adult oribatid mites were identified following Weigmann (2006) and the gender of each individual was determined by examining genitalia (Grandjean, 1955, 1956). Suctobelbidae and Brachychthoniidae were identified only to family level. The mode of reproduction (sexual or parthenogenetic) was inferred from sex ratios in combination with data in the literature (Palmer and Norton, 1991; Cianciolo and Norton, 2006).

For each species, fresh weight (M) was calculated from dry weight (dry$M$) of individuals (Hadley, 1994) as $M = 4 \times \text{dry}M$, or from the mean body length L (mm) given in Weigmann (2006) and the correlation constants a and b given in Huhta and Koskenniemi (1975) as $\log M = b \log L + a$, with $a = 2.386$ and $b = 2.519$. Respiration I ($J \cdot h^{-1}$) was calculated from fresh weight M (mg) using a linear model (Brown *et al.*, 2004; Downs *et al.*, 2008). The values i_0, a, and E are specific for oribatid mites and were adopted from Ehnes *et al.* (2011):

$$I = i_0 M^a e^{\frac{-E}{kT}}$$

with the normalization constant $i_0 = e^{22.02277}$ $J \cdot h^{-1} \cdot mg^{-1}$, the allometric exponent $a = 0.6793706$, the activation energy $E = 0.7060855$ eV, Boltzmann's constant $k = 8.62 \times 10^{-5}$ $eV \cdot K^{-1}$, and T = mean annual temperature (Swabian Alb = 279.7 K; Schorfheide = 281.4 K).

The calculated respiration per individual was multiplied by the density per square metre of each species; summing the respiration rates of all species present per square metre resulted in an estimate of the energy use of the whole oribatid mite community ($J \cdot h^{-1} \cdot m^{-2}$).

Global scale

The 38 sites investigated included a wide range of habitats: raw humus forests, moder forests, mull forests, riparian forests, peat bogs, meadows, fields, and lichen patches on the bark of trees (for details, see Table 1; for references, see evolutionary-ecology.com/data/2744Appendix.pdf). Most habitats were from temperate regions but we also included tropical forest sites. Sites strongly influenced by man such as agricultural systems were not included, as in such systems oribatid mites are unlikely to be controlled by resource availability.

Statistical analysis

The data (oribatid mite density, respiration, proportion of parthenogenetic individuals, and the respective residuals) were inspected using the Kolmogorov-Smirnov test. Data were normally distributed ($P > 0.2$). For the regional scale dataset, the relationships between the proportion of parthenogenetic individuals and oribatid mite density, oribatid mite respiration, and site (Schorfheide and Swabian Alb) were examined using stepwise linear regression. Similarly, for the global scale dataset, the relationships between the proportion of parthenogenetic individuals or taxa and oribatid mite density or habitat type (the seven different habitats where the oribatid mites were collected; see Table 1) were examined with stepwise linear regression. Prior to the analysis, data on the proportion of parthenogenetic

individuals and taxa were arcsin square-root transformed. Regressions between the proportion of parthenogenetic individuals and oribatid mite density were calculated with untransformed and log-transformed data; only results of the latter are presented, as the logarithmic regression explained more variation in the dataset. Statistical analyses were carried out using STATISTICA v.9 (StatSoft Inc., Tulsa, OK) and SAS 9.13 (SAS Institute, Inc., Cary, NC).

RESULTS

Regional scale

There were more parthenogenetic individuals in the Schorfheide than in the Swabian Alb (stepwise linear regression; $r^2 = 0.65$, $F_{2,29} = 56.24$, $P < 0.0001$). Furthermore, the proportion of parthenogenetic individuals correlated positively with oribatid mite density ($r^2 = 0.76$, $F_{2,29} = 14.82$, $P = 0.0006$), which was significant in the Schorfheide ($r^2 = 0.37$, $F_{1,14} = 8.12$, $P = 0.013$) and marginally significant in the Swabian Alb ($r^2 = 0.21$, $F_{1,14} = 3.72$, $P = 0.074$) (Fig. 1a). The proportion of parthenogenetic individuals also correlated positively with community respiration of oribatid mites (Fig. 1b), which was significant in the Schorfheide ($r^2 = 0.25$, $F_{1,14} = 4.68$, $P = 0.048$) but not in the Swabian Alb ($r^2 = 0.17$, $F_{1,14} = 2.92$, $P = 0.109$). However, including community respiration did not markedly increase the explained variance in the stepwise regression analysis, which was due to the high correlation between oribatid mite density and community respiration ($r^2 = 0.85$).

Global scale

The density of oribatid mites was significantly positively correlated with the percentage of parthenogenetic species and also with the percentage of parthenogenetic individuals (stepwise linear regression with log-transformed data; $r^2 = 0.61$, $F_{1,36} = 57.93$, $P < 0.0001$ and $r^2 = 0.66$, $F_{1,36} = 72.90$, $P < 0.0001$, respectively) (Fig. 2). Including habitat type did not increase the explained variance significantly.

DISCUSSION

Parthenogenetic reproduction in oribatid mites

Results of our study suggest that the percentage of parthenogenetic individuals in oribatid mite communities is positively correlated with density, at both the regional and global scale. The relationship also holds for metabolism as indicated by our regional scale dataset. Assuming that density and metabolism reflect the availability of resources, these relationships are consistent with predictions of the SRTS (Scheu and Drossel, 2007; Song *et al.*, 2011). Oribatid mites were considered especially well-suited to test predictions of the SRTS, as they are little affected by top-down forces and therefore their density likely reflects resource availability (Schneider and Maraun, 2009; Heethoff *et al.*, 2011). Although this may apply less strictly to soil invertebrates that are more subject to predation (Salamon *et al.*, 2006; Schneider and Maraun, 2009), it would be interesting to investigate correlations between density and reproductive mode in a wide range of soil invertebrate taxa, but nematodes and collembolans in particular.

Table 1. Habitat type, site characteristics, soil type (if known), country of the study site, oribatid mite abundance (individuals per m^2), percentage of parthenogenetic individuals of oribatid mites, percentage of parthenogenetic taxa of oribatid mites, and references for the 38 sites used for the meta-analysis of this study (references at evolutionary-ecology.com/data/2744Appendix.pdf)

Site no.	Habitat type	Site characteristics	Humus form (if known)	Country of study	Abundance (ind./m^2)	% Parthen. individuals	% Parthen. taxa	Publication
1	bark	Western red cedar trees (*Thuja plicata*)		Canada	323	27	18	Lindo and Winchester (2007)
2	meadow	brown earth on loess		Germany	1482	8	27	Toschki (2008)
3	bark	oak trees (*Quercus robur*)		Germany	1940	2	13	Woltemade (1982)
4	bark	lime trees (*Tilia cordata*)		Germany	5000	1	19	Weigmann and Jung (1992)
5	forest soil	tropical montane rainforest (3000 m)	raw humus	Ecuador	5769	4	17	Eissfeller (2007)
6	bark	oak trees (*Quercus robur*)		Poland	6000	2	15	Erdmann (2004)
7	forest soil	tropical montane rainforest (3000 m)	raw humus	Ecuador	6004	25	18	Fronszek (2010)
8	field	brown earth on loess		Germany	6179	23	35	Hülsmann and Wolters (1998)
9	forest soil	beech forest (Carpathians)	mull	Romania	9200	6	21	Fabian (1997)
10	riverine forest	sandy soils with mainly grey alder (*Alnus incana*)		Austria	11100	17	13	Totschnig and Schatz (1997)
11	peat bog	Ledo-Spagnetum with *Calamagrostis stricta*	mor	Germany	12200	43	35	Kehl (1997)
12	forest soil	tropical montane rainforest (1000 m)	moder	Ecuador	13677	43	31	Fronszek (2010)
13	forest soil	tropical montane rainforest (1000 m)	moder	Ecuador	15015	36	35	Eissfeller (2007)
14	forest soil	beech forest on limestone	mull	Germany	22134	36	44	Schulz (1991)
15	lichens	on limestone walls		Sweden	23500	24	50	Fröberg *et al.* (2003)
16	forest soil	beech forest	mull	Denmark	34515	38	40	Luxton (1981)
17	forest soil	beech forest	mull	Germany	40373	19	23	Alberti (1996)
18	forest soil	Scots pine forest	moder	France	42400	65	40	Garay (1981)
19	forest soil	mixed hardwood forest	moder	USA	44200	37	59	Lamoncha and Crossley (1998)

20	forest soil	mixed beech/spruce (Swabian Alb)	mull	Germany	53451	55	73	Erdmann (2012)
21	forest soil	mixed beech/spruce (Hainich)	mull/moder	Germany	59814	43	68	Erdmann (2012)
22	forest soil	beech forest	moder	Germany	61981	68	40	Wunderle (1992)
23	peat bog	Ledo-Spagnetum magellanici	mor	Germany	65000	77	43	Kehl (1997)
24	forest soil	beech forest, limed (Solling)	moder	Germany	66277	72	67	Heiligenstadt (1988)
25	forest soil	beech forest (Hainich)	moder	Germany	73980	68	58	Bayer (2008)
26	forest soil	mixed beech/pine (Schorfheide)	moder	Germany	84690	82	77	Erdmann (2012)
27	forest soil	coniferous forest	hemimor	Canada	91904	87	75	Berch *et al.* (2007)
28	meadow	Galio-Molinetum		Germany	95500	80	42	Kehl (1997)
29	forest soil	beech forest, not limed (Solling)	moder	Germany	101301	84	77	Heiligenstadt (1988)
30	forest soil	pine forest with earthworms	moder	Canada	102013	45	54	McLean and Parkinson (1998)
31	forest soil	mixed oak, beech and hornbeam forest	moder	Germany	133000	74	51	Schneider (2001)
32	forest soil	pine forest without earthworms	mull	Canada	150447	50	56	McLean and Parkinson (1998)
33	forest soil	120-year-old spruce forest (Solling)	moder	Germany	165264	85	62	Migge (1996); Migge *et al.* (1998)
34	forest soil	Sesslle oak forest	moder	France	182900	87	40	Garay (1981)
35	forest soil	coniferous forest (Tuusula)	raw humus	Finland	185800	85	71	Huhta *et al.* (1986)
36	forest soil	mixed beech and spruce stand (Solling)	moder	Germany	196137	90	60	Migge (1996); Migge *et al.* (1998)
37	forest soil	coniferous forest (Tammela)	raw humus	Finland	276700	79	67	Huhta *et al.* (1986)
38	forest soil	coniferous forest (Saarijärvi)	raw humus	Finland	351500	78	66	Huhta *et al.* (1986)

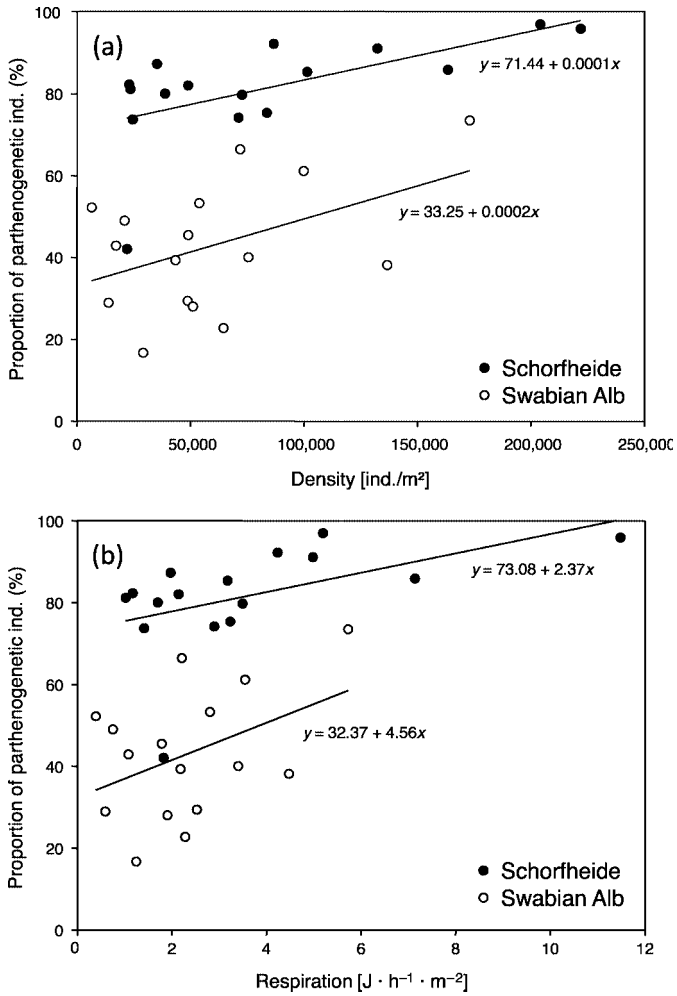

Fig. 1. Relationship between the proportion of parthenogenetic individuals and oribatid mite density (a) and oribatid mite respiration (b) in Swabian Alb and Schorfheide.

Regional scale

Irrespective of the indicator of the resources available to oribatid mite communities (density or respiration), or of the soil type at the two sites (mull or moder), the proportion of individuals of parthenogenetic oribatid mite species correlated positively with the resource proxy. However, the correlation was weaker in the mull (Swabian Alb) than in the moder forests (Schorfheide) and less strong for respiration than for density.

The mull and moder forests studied differed both in the proportion of individuals of parthenogenetic oribatid mite species and in oribatid mite density (43% vs. 82% and 59,800 vs. 84,700 individuals per m^2, respectively). The lower proportion of individuals of parthenogenetic species in the mull forests of the Swabian Alb, where oribatid mite density was lower, conforms to our expectations and is consistent with predictions of the SRTS.

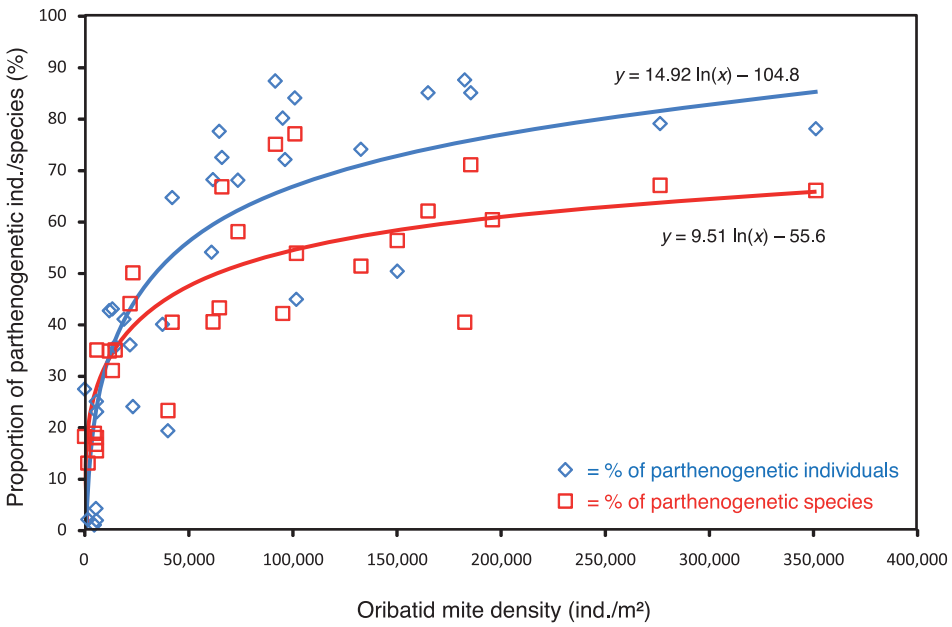

Fig. 2. Relationship between the proportion of parthenogenetic individuals/proportion of parthenogenetic species and oribatid mite density on a global scale. For details, see text.

However, differences in habitat characteristics may also have contributed to the lower proportion of individuals of parthenogenetic oribatid mite species, since at this site the parthenogenetic Brachychthoniidae were rare. Low abundance of Brachychthoniidae is typical for mull forests and is likely to be due to disturbances by earthworms (Maraun and Scheu, 2000; Eisenhauer, 2010). Macrofauna activity, in particular that of earthworms, has a detrimental effect on mesofauna communities, including those of the slow-developing, long-lived oribatid mites, weakening bottom-up control via resource availability.

Global scale

On the global scale, the proportion of parthenogenetic taxa (as well as parthenogenetic individuals) fitted best with density on a logarithmic scale. This reflects the high proportion (typically > 60%) of parthenogenetic taxa in temperate and boreal forests where the density of oribatid mites spans a wide range from moderate to high (Behan-Pelletier, 1999). The shape of the curve further shows that the high incidence of parthenogenetic species (and individuals) in temperate forests is in contrast with that elsewhere, where parthenogenetic species are much less abundant, such as tropical forests, meadows, and the bark of trees. According to the SRTS, the high proportion of parthenogenetic oribatid mites in temperate forests should be due to the high availability of resources. Both above- and below-ground inputs of resources (i.e. leaf litter and root-derived resources) are likely to contribute to this high resource pool (Pollierer *et al.*, 2007). Low densities of oribatid mites in tropical systems are probably related to poor litter quality; indeed, it is increasingly recognized that, compared with temperate and boreal forests, litter in tropical forests decomposes slowly (Haettenschwiler *et al.*, 2011). This is consistent with the finding that tropical forests lack true decomposer

animal taxa (Illig *et al.*, 2005). The low density of oribatid mites on the bark of trees (and associated high proportion of sexual species) presumably relates to the fact that many bark-living oribatid mites feed on lichens, which are well defended by secondary compounds (B.M. Fischer *et al.*, 2010).

Overall, the results indicate a somewhat counterintuitive interrelationship, i.e. with increasing oribatid mite density, the importance of resource limitation declines. Presumably, in temperate and boreal forests oribatid mites are structured predominantly by density-independent factors such as cold winters but also by pulsed resource inputs via litter and root deposits. In contrast, in habitats where sexual reproduction of oribatid mites dominates, i.e. on the bark of trees and in soil of tropical forests, resources likely are limiting. Again this is counterintuitive, as animal communities on the bark of trees are exposed to harsh environmental conditions, suggesting that bark-living communities are structured by density-independent factors. In fact, oribatid mites are well adapted to cold winter conditions and, by feeding predominantly on lichens, presumably are regulated by the availability of food resources that are well defended (e.g. by producing secondary compounds such as usnic acid) (Seyd and Seaward, 1984). Also, the low density of oribatid mites in tropical forest soils suggests a predominance of resource control, reflecting that tropical soils are poor in nutrients and leaves of tropical trees are of low food quality. Low densities of oribatid mites on the bark of trees and in tropical forests therefore also conform to the predictions of the SRTS.

The structured resource theory of sexual reproduction as an integrative theory

Compared with other theories that attempt to explain the predominance of sexually reproducing species, the SRTS focuses on resource availability as the main factor responsible for the mode of reproduction (Scheu and Drossel, 2007; Song *et al.*, 2011). Results of the present study support this view by providing evidence that oribatid mite communities of low density and with a high proportion of sexual species are controlled predominantly by density-dependent factors (i.e. the availability of food resources). In contrast, resources presumably are of limited importance as a regulating factor of oribatid mite populations in soils of temperate and boreal forests where they reach high densities and where parthenogenetic species and individuals prevail. We propose that these somewhat counterintuitive relationships explain one of the most striking patterns in oribatid mite ecology, i.e. the dominance of parthenogens in certain ecosystems, such as temperate and boreal forests. This view is consistent with the assumption that the reproductive mode in oribatid mites is not controlled by biotic interactions (Cianciolo and Norton, 2006).

Overall, both the regional and global scale datasets analysed in this study are consistent with predictions of the SRTS, suggesting that the high incidence of parthenogenetic reproduction in soil animal taxa is related to periods of relaxed resource competition allowing parthenogenetic taxa to outgrow sexual ones. Experiments manipulating the resource supply of soil animal communities are needed to provide support for these conclusions. Soil animal communities are well suited for such experiments, as many parthenogenetic species of different taxonomic affiliation co-exist on small spatial scales, allowing tests of the generality of the SRTS in explaining sexual versus parthenogenetic reproduction in Metazoa.

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