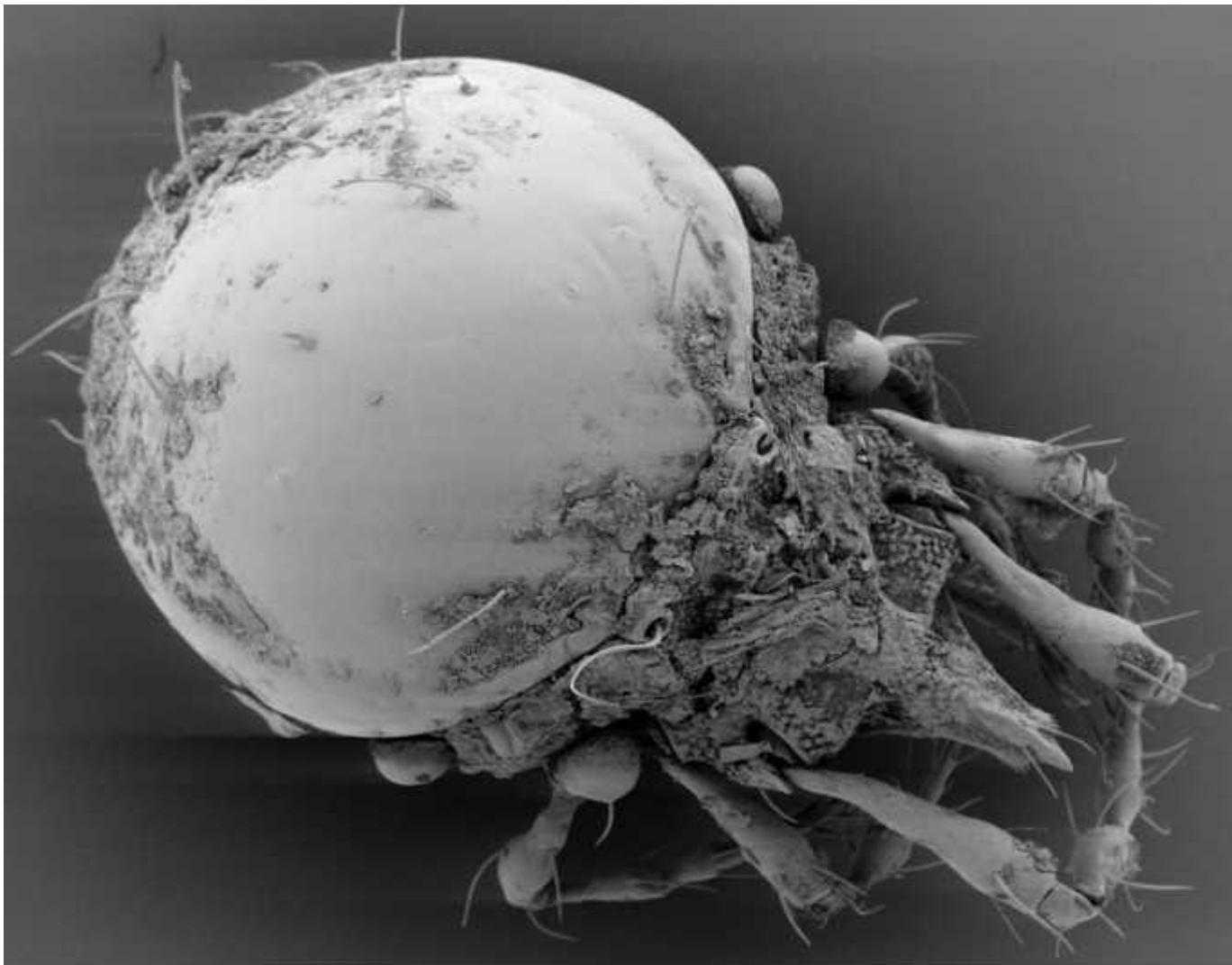




# Das ungelöste Rätsel der Boden-tier-Diversität

Mark Maraun  
University of Göttingen

## Oribatid mites as model organisms



### (1)The enigma of soil animal species diversity (1975)

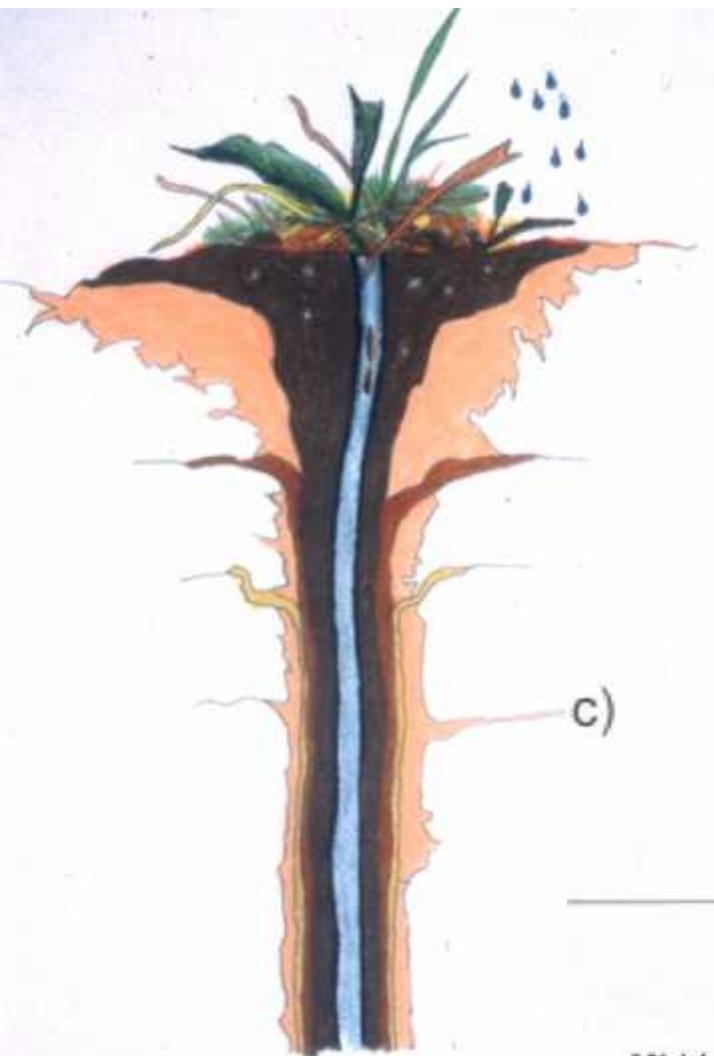
J. M. ANDERSON

Department of Zoology, Animal Ecology Research Group,  
Oxford

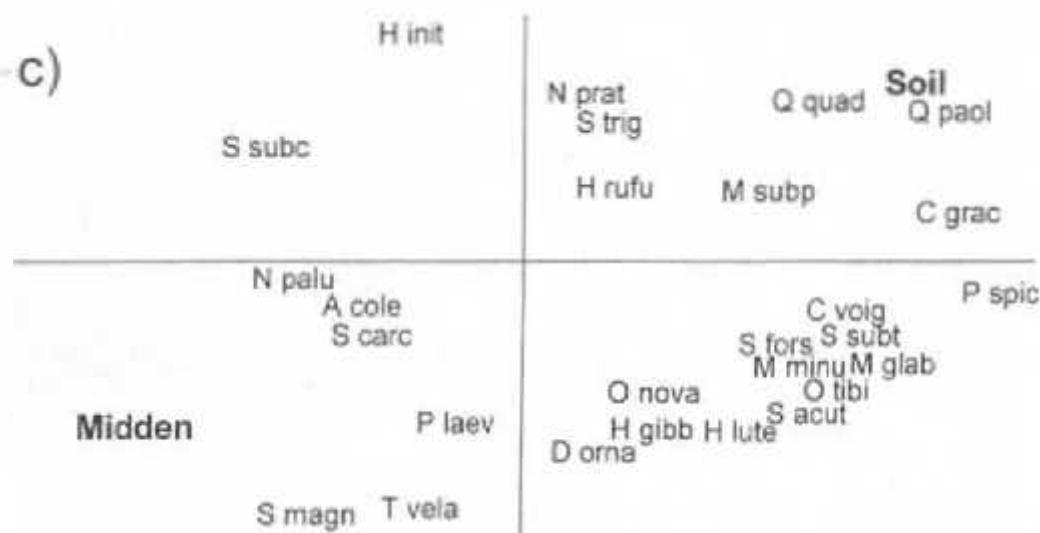
Why are there so many species ?

Germany : ~ 550

Worldwide: ~ 11,000



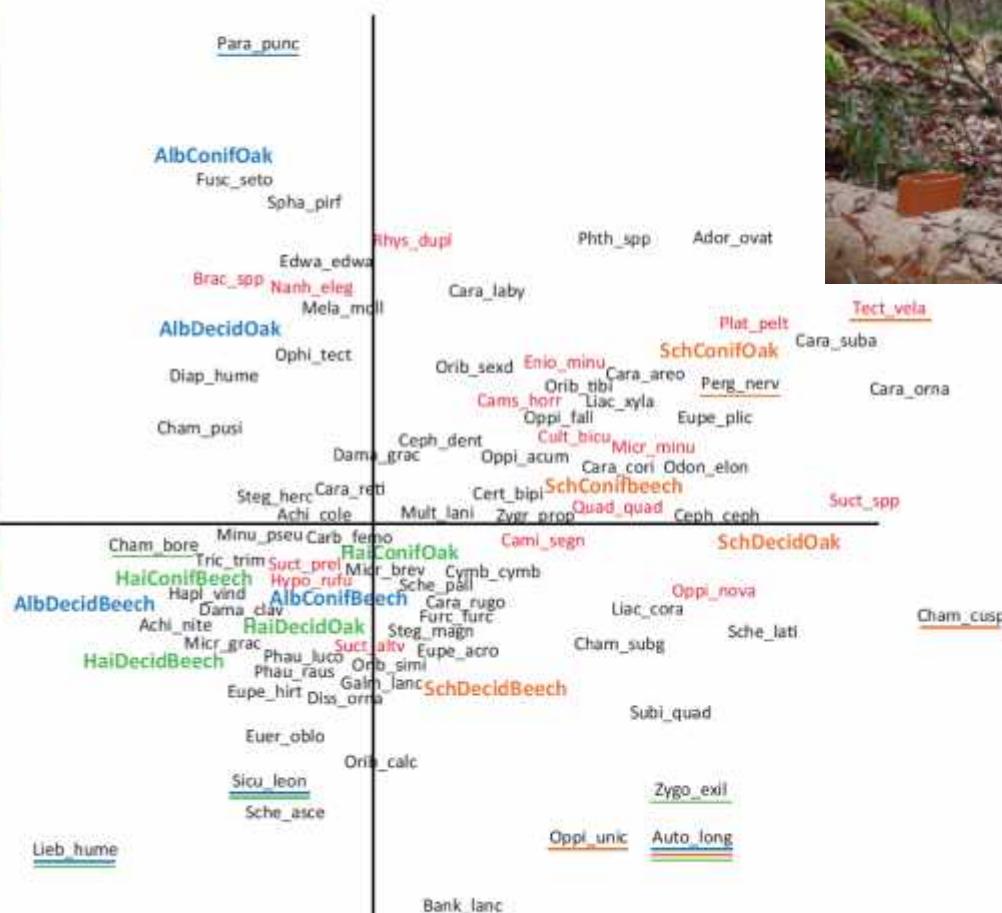
### Oribatid mites in earthworm middens



**Fig. 1.** PCA plot of species of (a) Gamasina and Uropodina (underlined), (b) Collembola, (c) Oribatida and (d) species and genera of Nematoda in middens (midden) and non-midden soil (soil). Eigenvalues of axis 1 and 2 are 0.37 and 0.21 (a), 0.24 and 0.16 (b), 0.26 and 0.18 (c) 0.29 and 0.17 (d), respectively. Full species, genera and family names are given in the Appendix



## Oribatid mites in dead wood



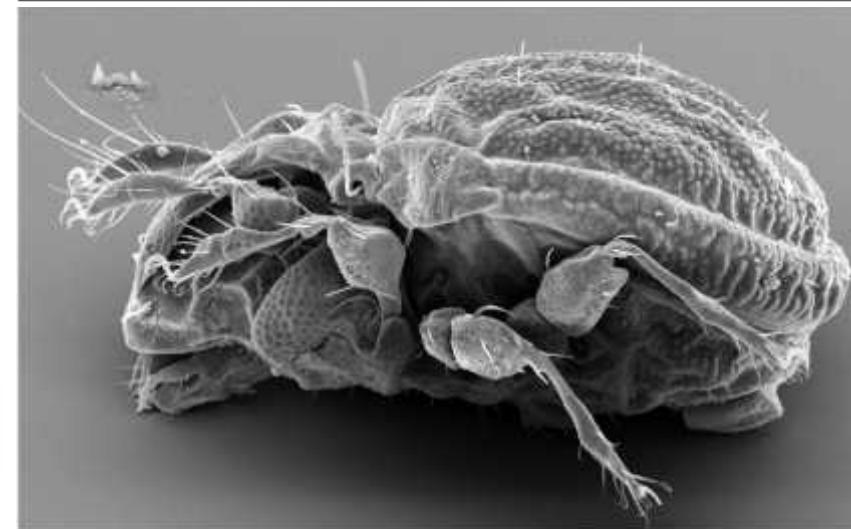
**Fig. 1.** Principal components analysis (PCA) of oribatid mites on different log types exposed in deciduous and coniferous forests in three regions in Germany. Parthenogenetic species are marked red; the five most abundant species of each region are underlined with the color of the respective region. Length of gradient 3.9; eigenvalues of 0.20 and 0.11 for the first and second axis, respectively. Alb = Schwäbische Alb; Hai = Hainich-Dün; Sch = Schorfheide-Chorin; Decid = deciduous forest; Conif = coniferous forest; Beech = beech log; Oak = oak log. For full names of species see Table 1.

## Oribatid mites in ant nests



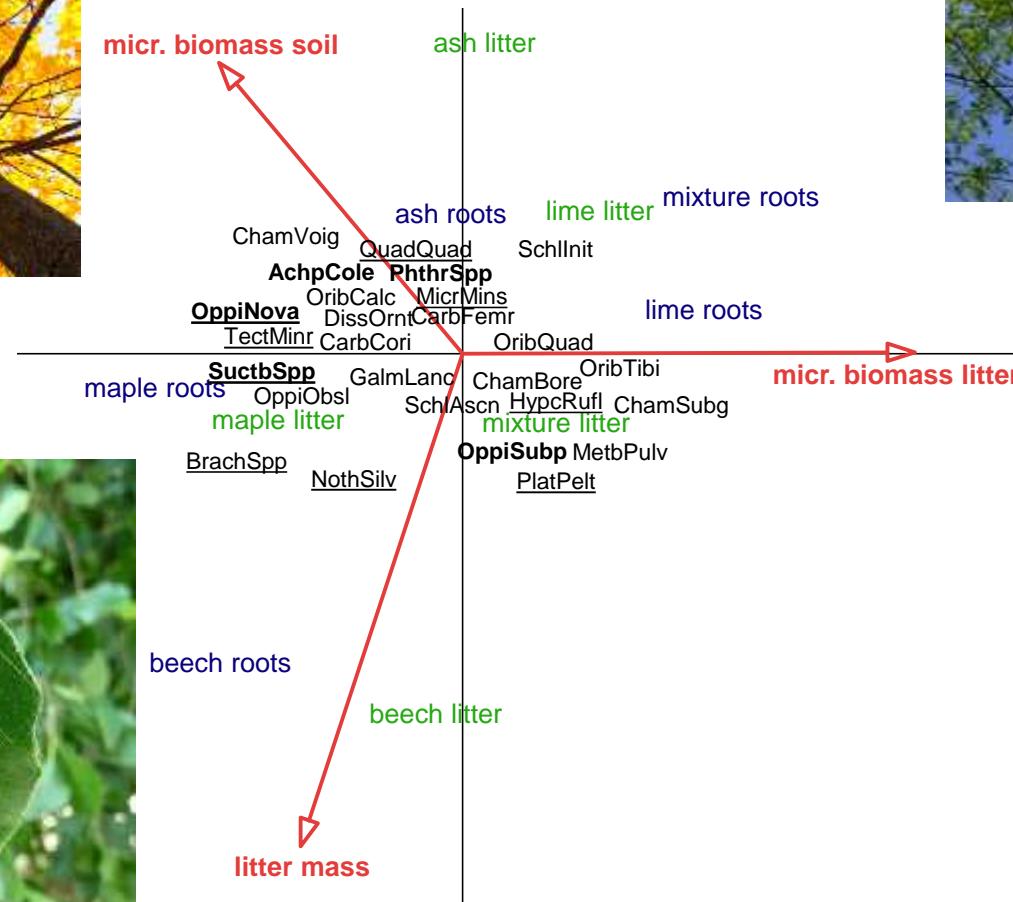
**Fig. 2.** Study area and samples at the island of Ruissalo, Turku, Finland. a) *Formica polyctena* nest mound, b) sample of the material collected from nest mound, c) oak forest where the study was conducted, d) sample of the material collected from soil.

Nest preference	Nest	Soil
Dermatidae		
<i>Epidamaceus bituberculatus</i> (Kulczynski, 1902) <sup>†</sup>	519 (9)	0
Cephaelidae		
<i>Cepheus cepheiformis</i> (Nicolet, 1855)	19 (4)	0
Eremaeidae		
<i>Eremaeus sibiricus</i> Nicolet, 1855 <sup>†</sup>	145 (7)	31 (4)
Astegistidae		
<i>Furciferula furcillata</i> (Nordensk öhl., 1901) <sup>†</sup>	202 (8)	1 (1)
Liaceridae		
<i>Liarus concinus</i> (C. L. Koch, 1841) <sup>†,‡</sup>	389 (10)	81 (10)
Carabodidae		
<i>Carabodes ornatus</i> Storkan, 1925 <sup>†</sup>	61 (8)	23 (5)
<i>Carabodes labyrinthicus</i> (Michael, 1879) <sup>†</sup>	56 (10)	25 (7)
<i>Carabodes areolatus</i> Berlese, 1916	44 (5)	4 (3)
Oppiidae		
<i>Opiella (Moritzoppia) unicarinata</i> (Paoli, 1908) <sup>†</sup>	203 (6)	5 (4)
Raruzella spp.	88 (6)	3 (2)
Licheremaeidae		
<i>Licheremaeus lichenophorus</i> (Michael, 1882) <sup>†</sup>	506 (6)	2 (1)
Galumnaidae		
<i>Pergalumna nervosa</i> (Berlese, 1914) <sup>‡,§</sup>	646 (8)	11 (2)
<i>Galumna elatina</i> (C. L. Koch, 1841)	298 (9)	3 (1)
Achipteridae		
<i>Paracalyptra puncata</i> (Nicolet, 1855) <sup>†,‡</sup>	17 (6)	3 (2)
Scheloribatidae		
<i>Scheloribates taipes</i> (C. L. Koch, 1844) <sup>†</sup>	142 (5)	14 (2)





Oribatid mites in beech, ash,  
lime, maple and mixed litter  
under different tree species





ELSEVIER

Applied Soil Ecology 9 (1998) 17–23

---

---

Applied  
Soil Ecology

---

---

in contrast to....

## Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acari: Oribatida) in litterbags

Randi A. Hansen\*, David C. Coleman

*Institute of Ecology, University of Georgia, Athens, GA 30601, USA*

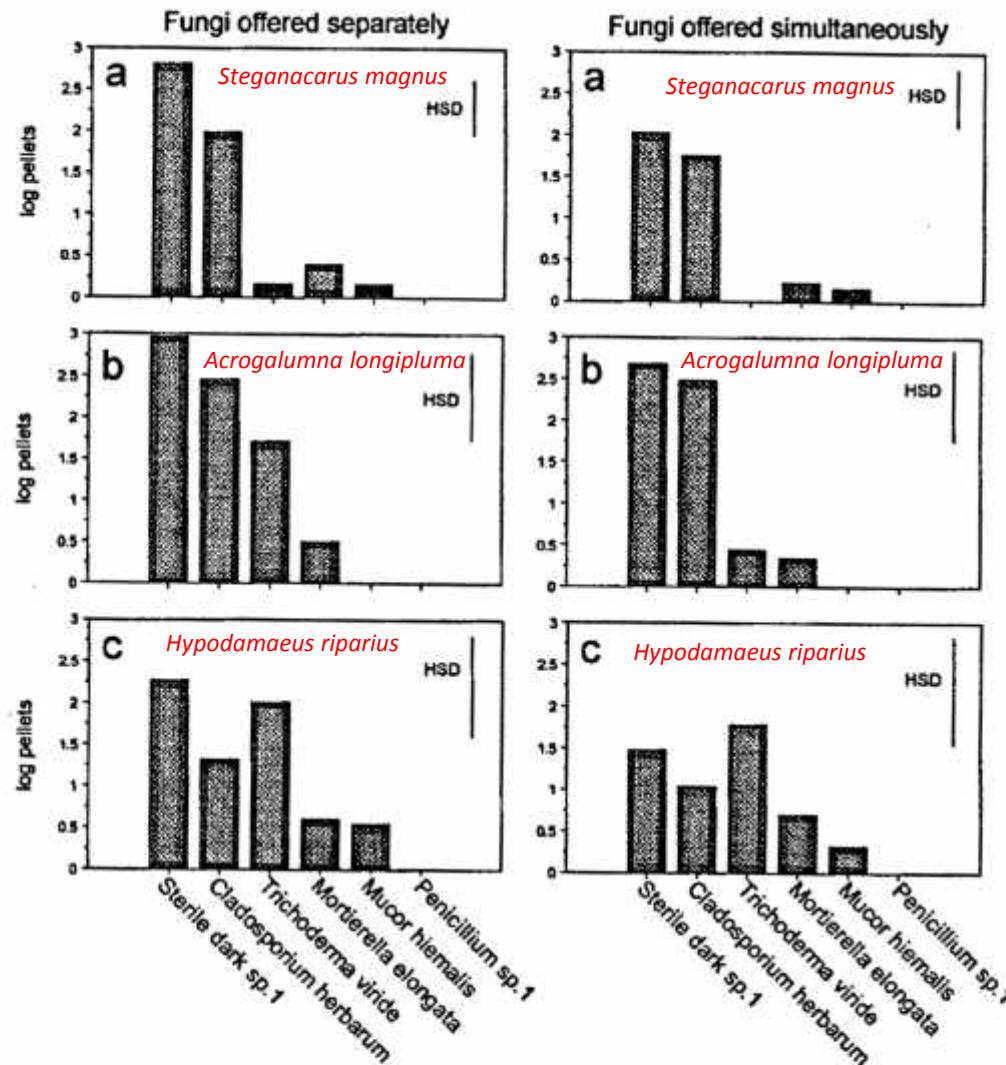
Received 26 July 1996; accepted 4 July 1997

---

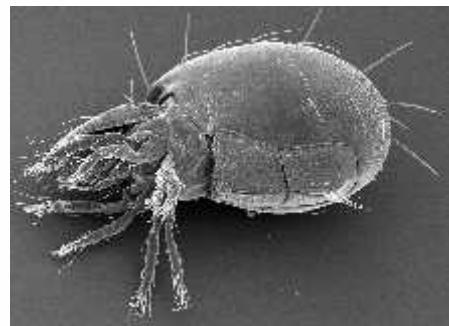
### Abstract

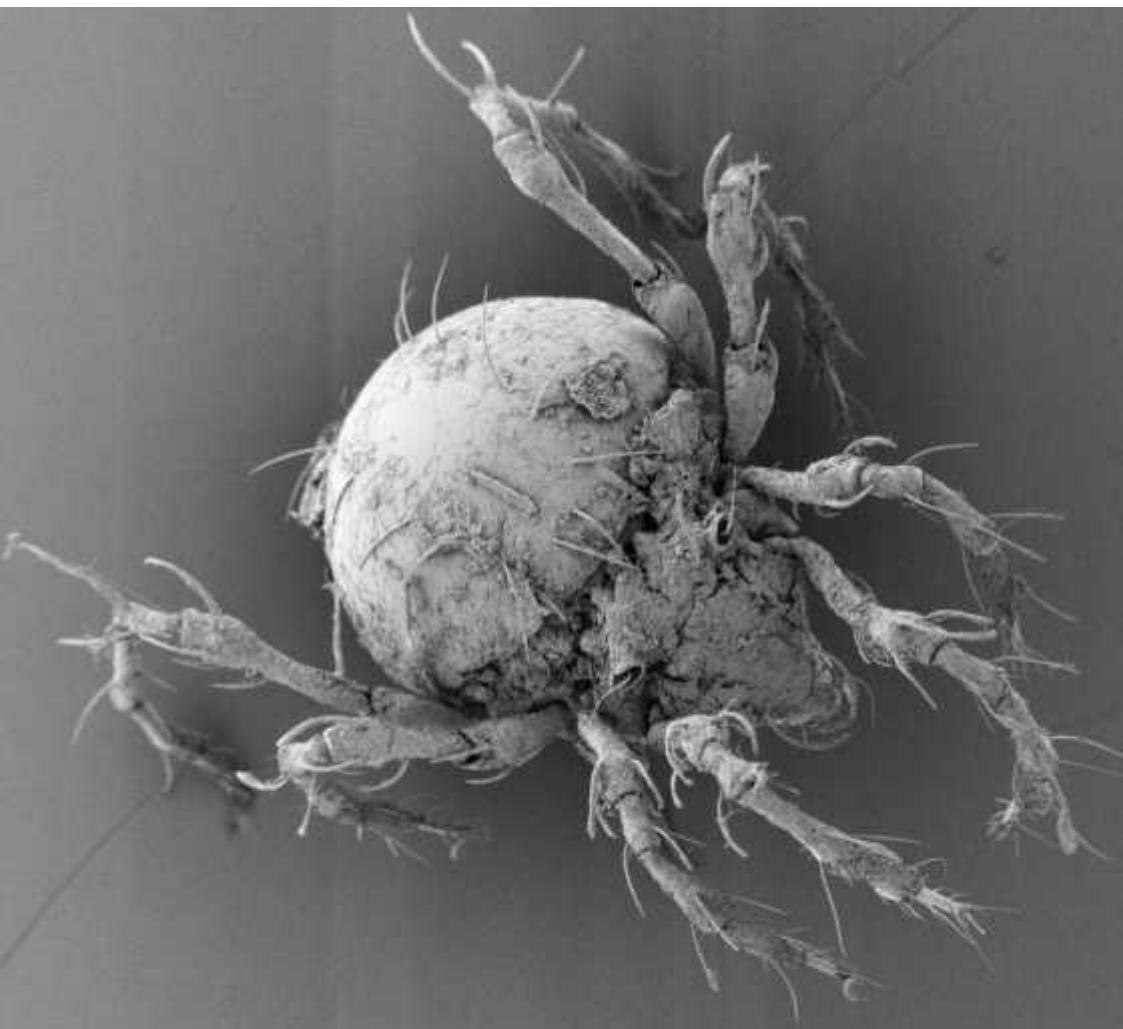
To investigate the relationship between litter complexity and composition and the diversity and composition of the oribatid mite fauna inhabiting it, an experiment was carried out at a single forested site in the mountains of North Carolina, USA. Natural litterfall was excluded from a series of 1 m<sup>2</sup> plots and replaced with treatment litters that varied in composition and complexity. Plots of pure birch, maple and oak litter comprised the simple litter treatments. Two complex litters were made of a mixture of these three litter species and a mixture of seven litter species. Treatment litters were applied to the plots in the autumn of 1993 and again in 1994. The oribatid mites extracted from litterbags of the treatment litters from both years are reported on here. Mixed litters had a significantly greater variety of microhabitats, as defined by substrate type and fungal growth form, than did the simple litters. Likewise, the oribatid mite species richness in litterbags of mixed litter was significantly higher than that in the simple litters. The fauna within replicates of each litter-type were more similar to each other than to those of other treatments. A third of the mite species tested showed a differential response among the simple litter-types. These results indicate a link between heterogeneity and diversity of mites active in a particular horizon of litter and some influence of litter-type upon species composition. Such patterns in habitat use by adult mites are strong, though not conclusive evidence of the ultimate role of heterogeneity in maintaining the diversity of oribatid mites. © 1998 Elsevier

What about distinct  
trophic niches?



**Fig. 1.** Number of faecal pellets from 20 oribatid mites of the species *Steganacarus magnus* (a), *Acrogalumna longipluma* (b) and *Hypodamaeus riparius* (c) from Göttinger Wald deposited close to microfungi during 5 days of incubation. Fungi were offered separately (left column) or simultaneously (right column). Log-transformed data; HSD, Tukey's honestly significant difference at  $p < 0.05$





Despite preferences for certain fungal species most oribatid mites are best considered “choosy generalists”.

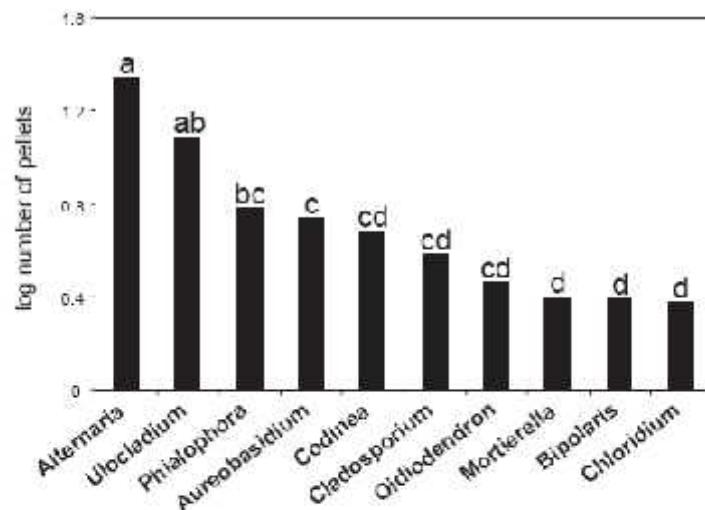


Available online at www.sciencedirect.com  
DOI:10.1016/j.pedobi.2010.07.001

**Pedo  
biologia**  
[www.sciencedirect.com/science/journal/00314130](http://www.sciencedirect.com/science/journal/00314130)

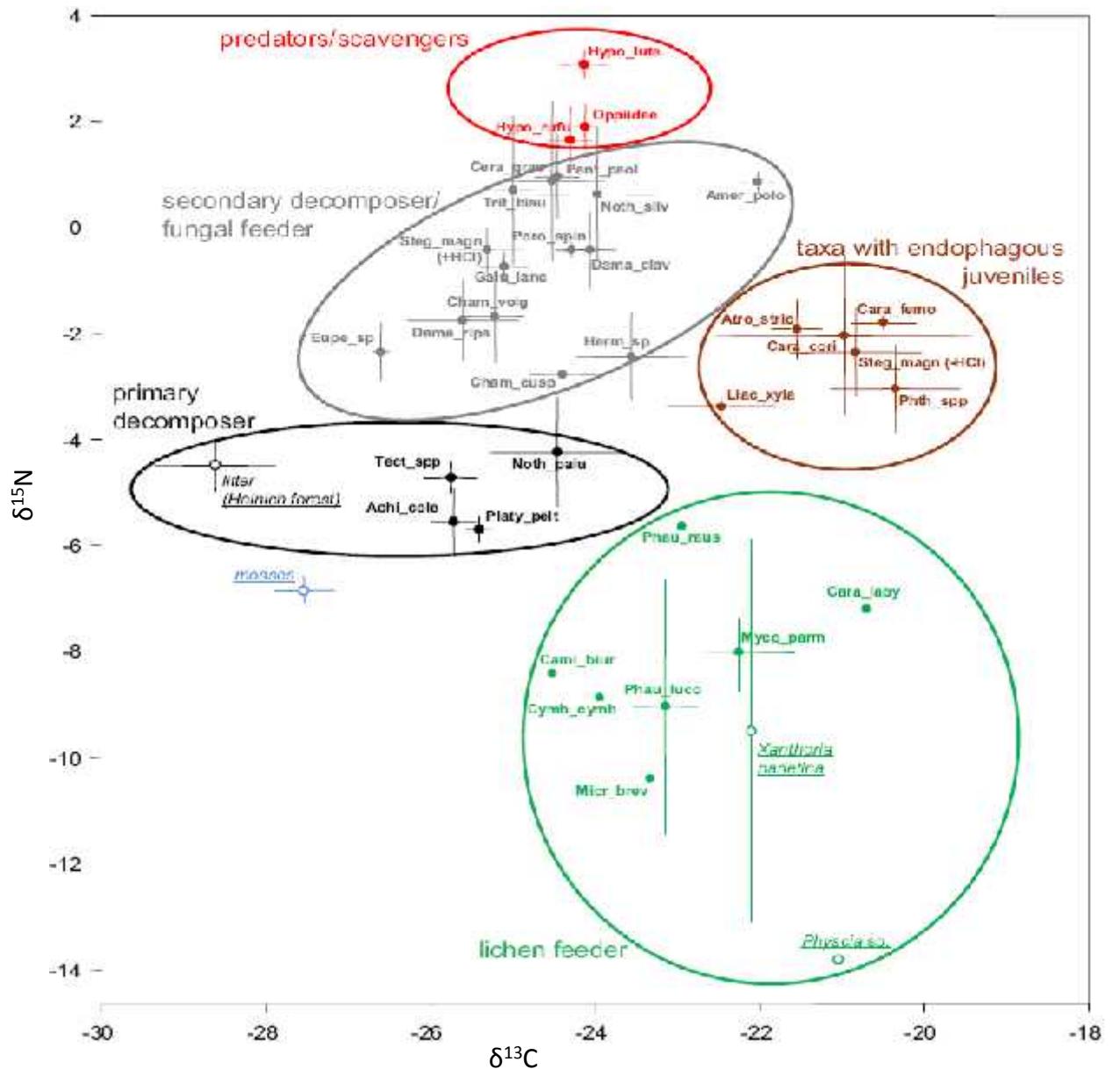
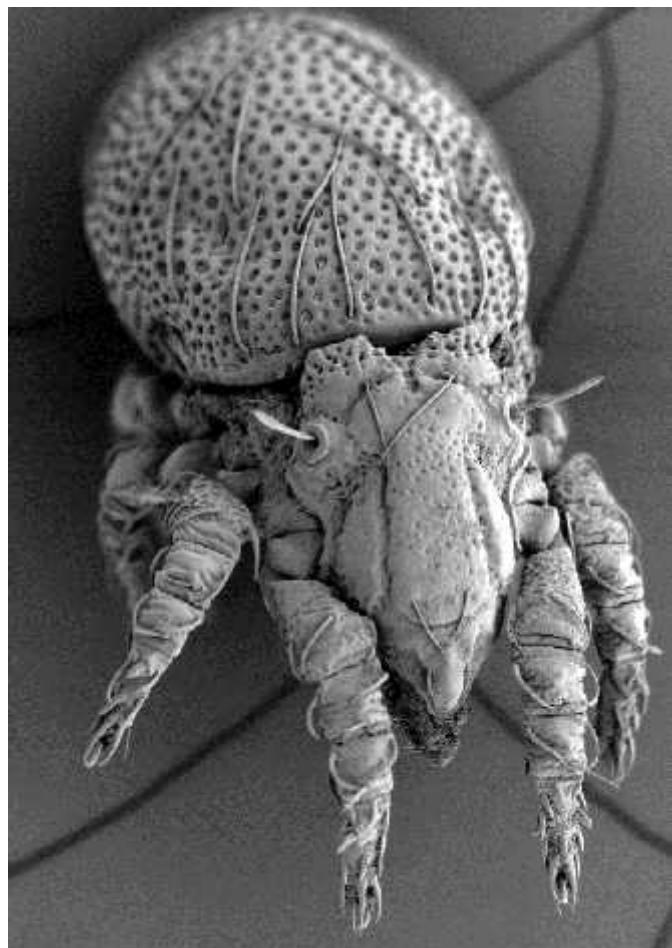
Feeding preferences among dark pigmented fungal taxa ("Dematiaceae") indicate limited trophic niche differentiation of oribatid mites (Oribatida, Acari)

Katja Schneider<sup>a</sup>, Mark Maraun<sup>b</sup>



**Figure 1.** Total Number of faecal pellets from all individuals of the 10 investigated oribatid mite species deposited close to each investigated fungus (*Alternaria alternata*, *Bipolaris spicifera*, *Chloridium* sp., *Cladosporium* sp., *Codinea* sp., *Oidiiodendron* sp., *Phialophora verrucosa*, *Ulocladium* sp., *Mortierella ramanniana* and *Aureobasidium pullulans*) during 10 days of incubation. Fungi were offered simultaneously. Log-transformed data; bars with different letters are significantly different.

# Stable Isotopes ( $^{15}\text{N}$ ; $^{13}\text{C}$ ) specialists or generalists?



Maraun et al. (2011) Soil Biology & Biochemistry

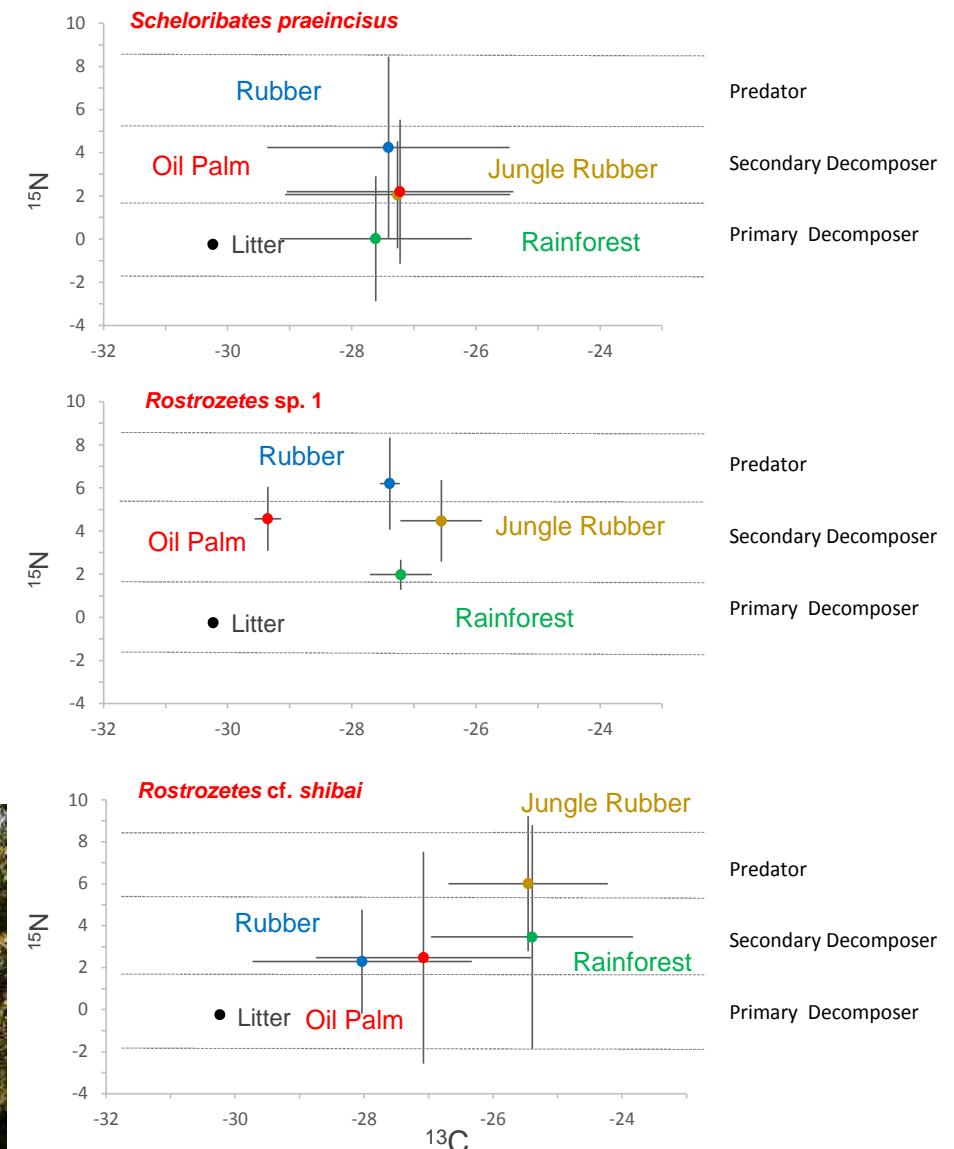


# Trophic plasticity in oribatid mites (Sumatra, Indonesia)

Specialisation or opportunism?

trophic stability or trophic plasticity?

(measurements on individual level....)



Krause et al. (2019) submitted

# Trophic stability of soil oribatid mites in the face of environmental change

Huijie Gan<sup>a,\*</sup>, Donald R. Zak<sup>a,b</sup>, Mark D. Hunter<sup>a</sup>

<sup>a</sup>University of Michigan, Department of Ecology and Evolutionary Biology, 830 N University, Ann Arbor, MI 48109, United States

<sup>b</sup>University of Michigan, School of Natural Resources and Environment, 440 Church Street, Ann Arbor, MI 48109, United States

---

## ARTICLE INFO

*Article history:*

Received 27 June 2013

Received in revised form

13 September 2013

Accepted 18 September 2013

Available online xxx

---

*Keywords:*

<sup>15</sup>N Stable isotope

N deposition

Oribatid mites

Stability

---

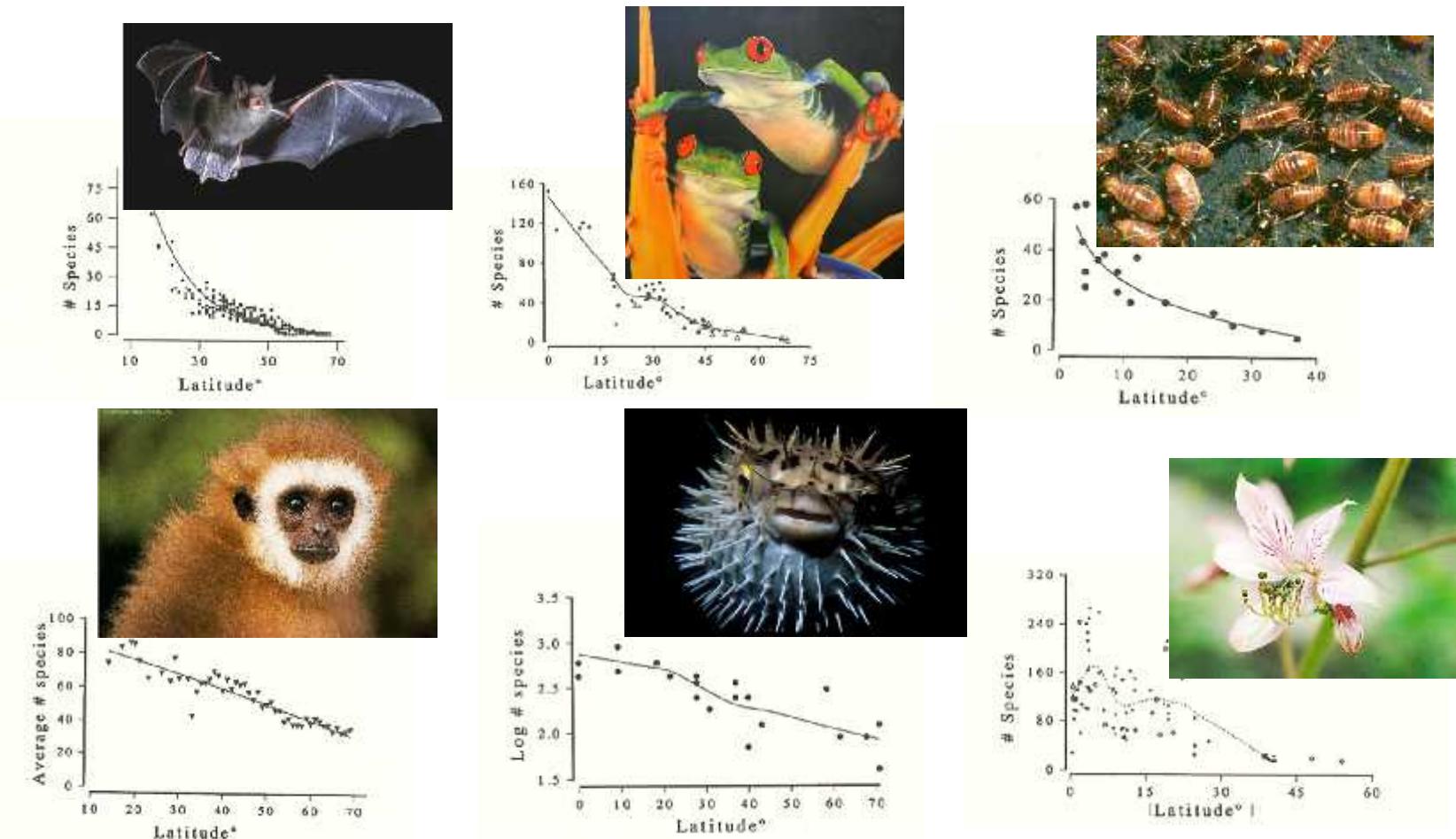
## ABSTRACT

A key issue in ecology is the degree to which trophic structure within communities responds to environmental change. Organisms with generalist diets are more flexible in their feeding habits than are specialists, and may be affected less in a changing environment. Soil fauna fulfill crucial ecosystem functions in terrestrial ecosystems and many are thought to have generalized diets. They may therefore be buffered from negative effects of environmental change. Here, we used <sup>15</sup>N isotope analysis to study trophic differentiation among 91 species of oribatid mites and their responses to chronic atmospheric N deposition. Combining our own measurements with published data, we established that the trophic positions of mite species were remarkably stable within and among forests, as well as between ambient and experimental N deposition. Trophic stability indicates a higher than expected level of feeding specialization, which may foster diversity, but limit the ability to switch food resources in a changing environment.

in contrast to...

## (2) The latitudinal biodiversity gradient (the second enigma?)

many more species of bats, amphibians, termites, mammals, fish, plants towards the tropics  
(hardly ever studied for below ground animals...)



## The latitudinal biodiversity gradient in oribatid mites

11,000 described species;  
~100,000 may exist.....may be not.....

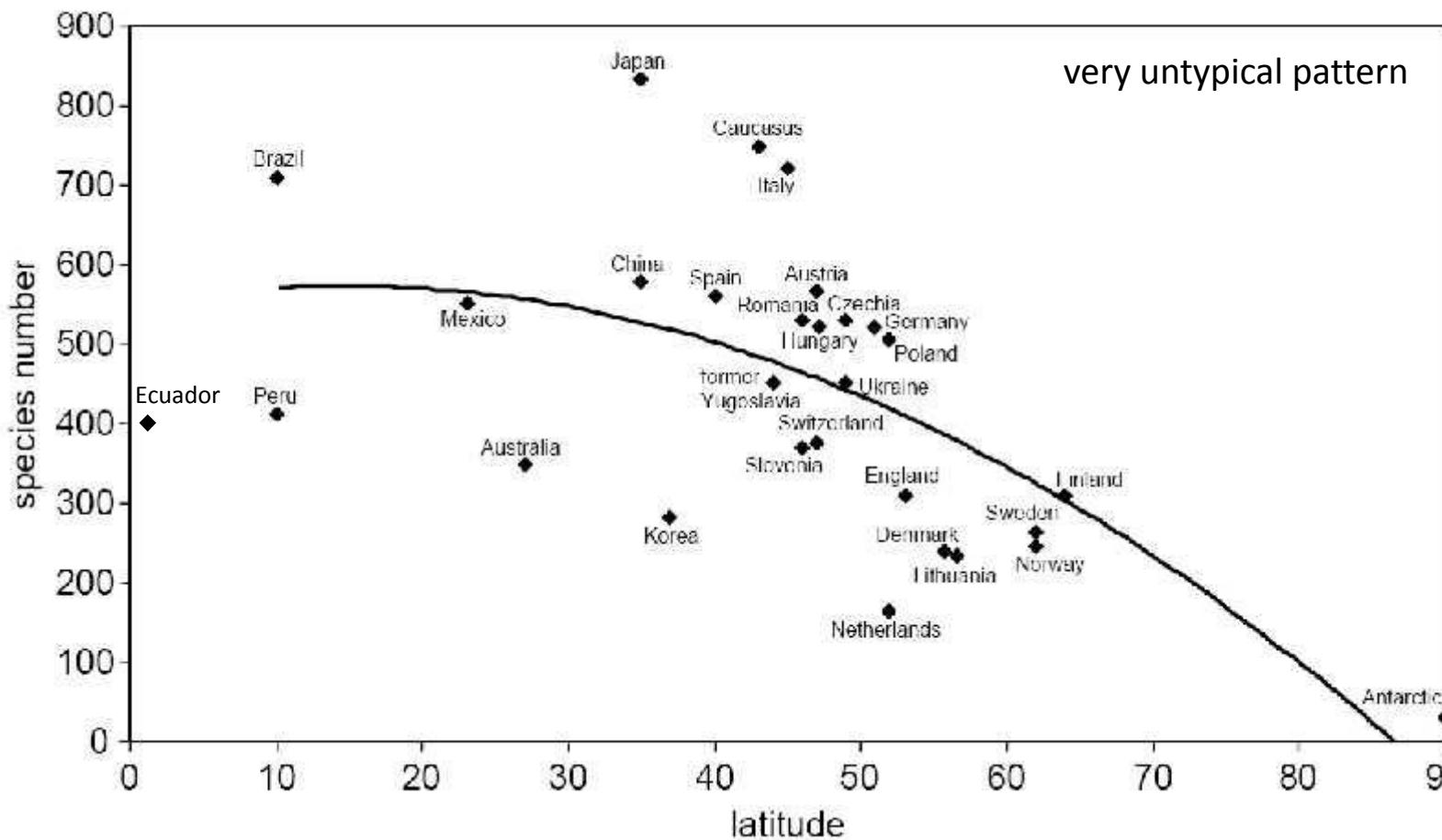
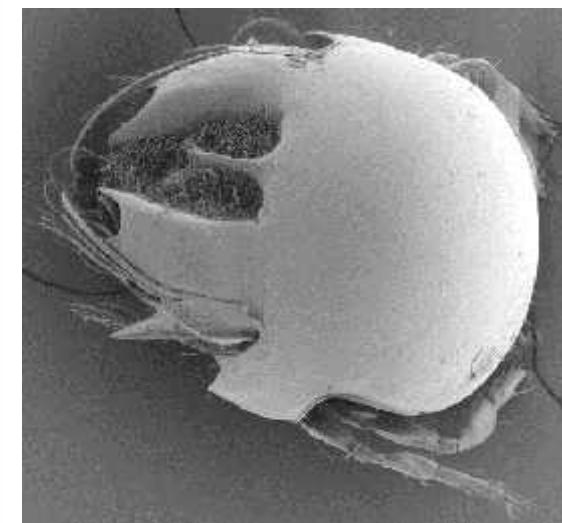


Fig. 1. The species latitude curve for oribatid mites of the world. The data were fitted to a second degree polynomial regression ( $y = 0.1x^2 + 3.3x + 551$ ;  $R^2 = 0.41$ ). Note that the algebraic sign (north or south) of the latitude of the countries is ignored.



## Oribatida vs. Coleoptera

### Oribatid mites

Few species: ~11,000

Long evolutionary time: ~550 my



### Beetles

Many species: ~1 Million

Short time: ~150 my

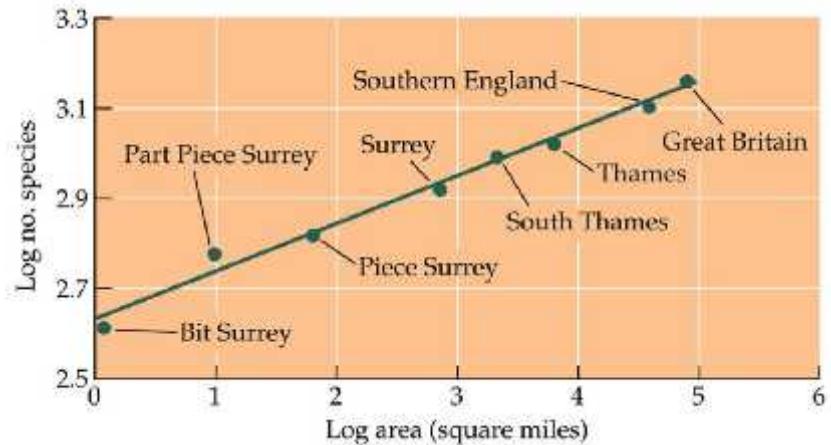
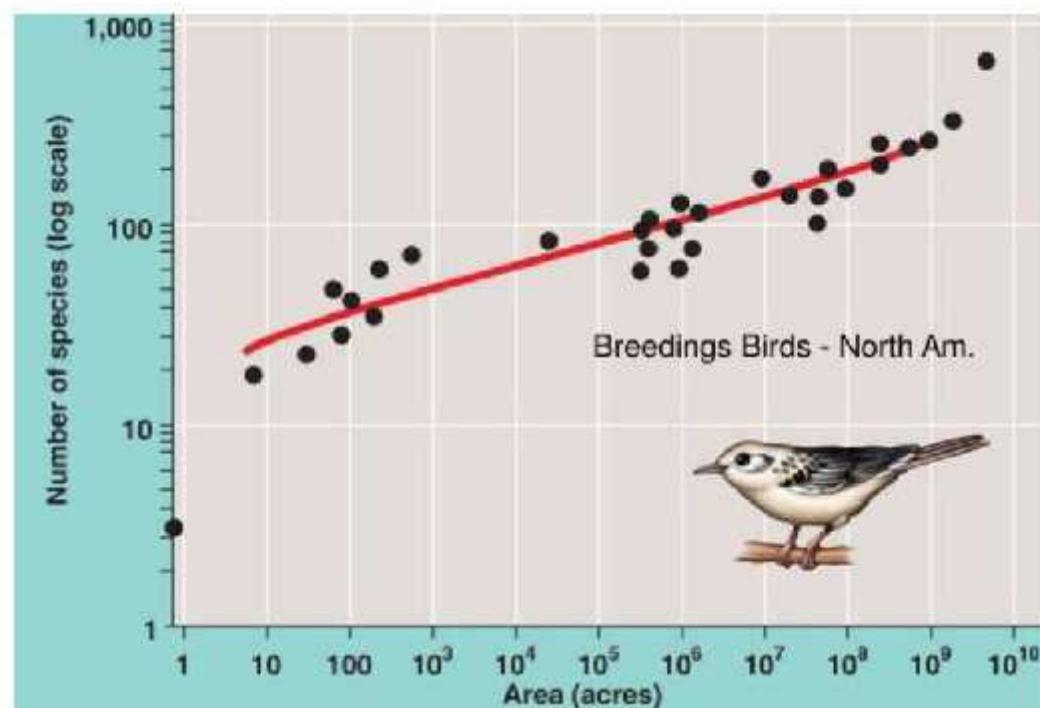
(after Grimaldi & Engel, 2004)



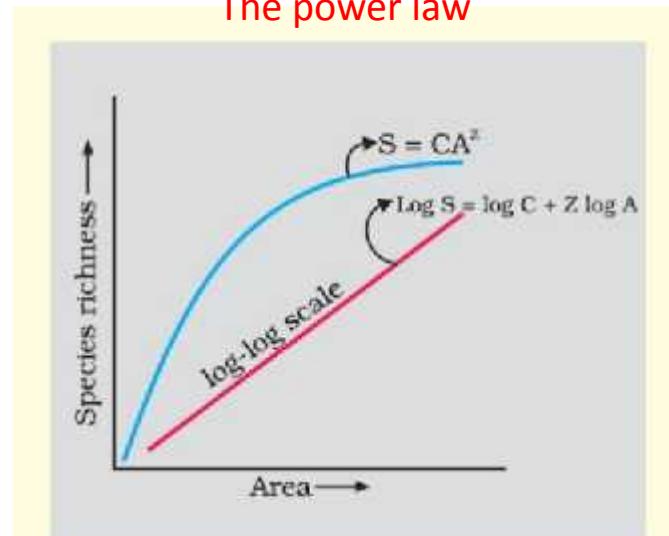
‘Time’ is not an important factor for the diversity of oribatid mites

Why are there so few tropical soil animal species ? This enigma remains as well

### (3) Species area relationships (another enigma?)



The power law



**Figure 15.2** Showing species area relationship.  
Note that on log scale the relationship becomes linear

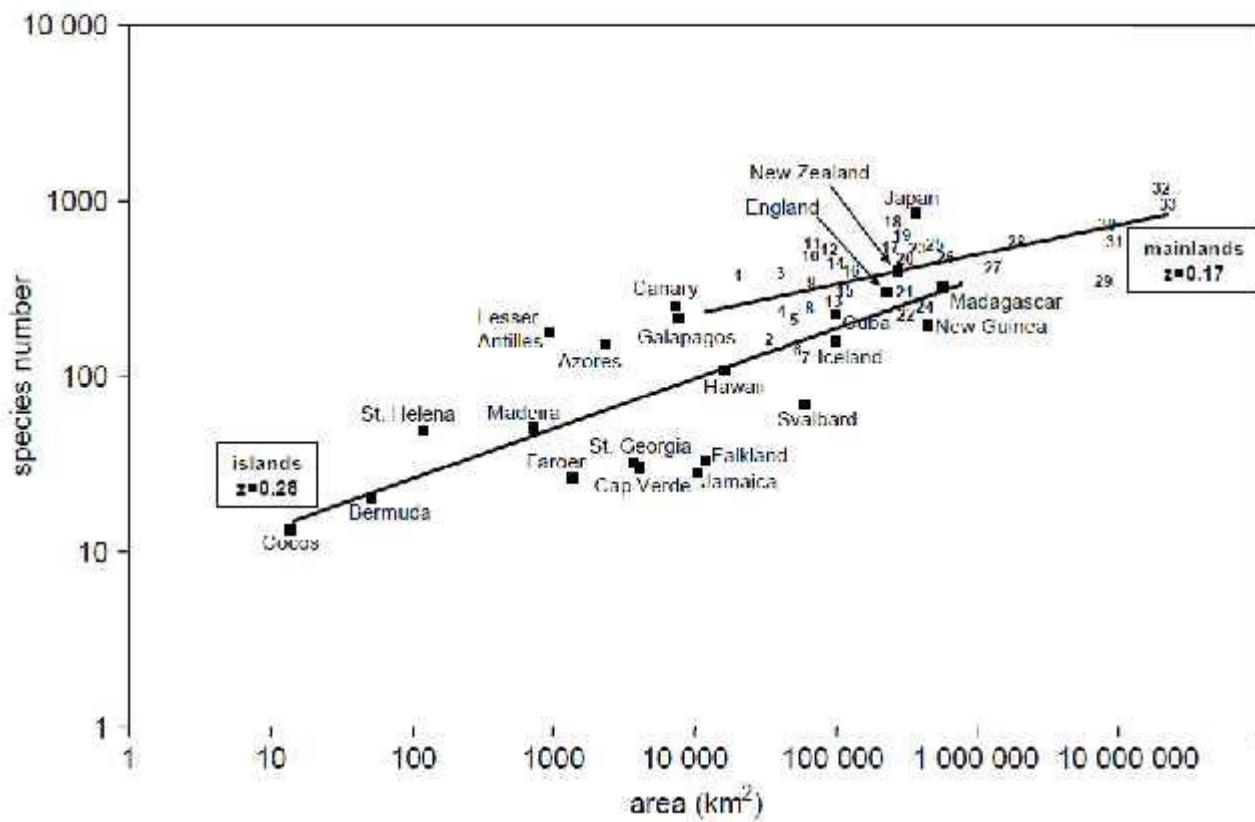
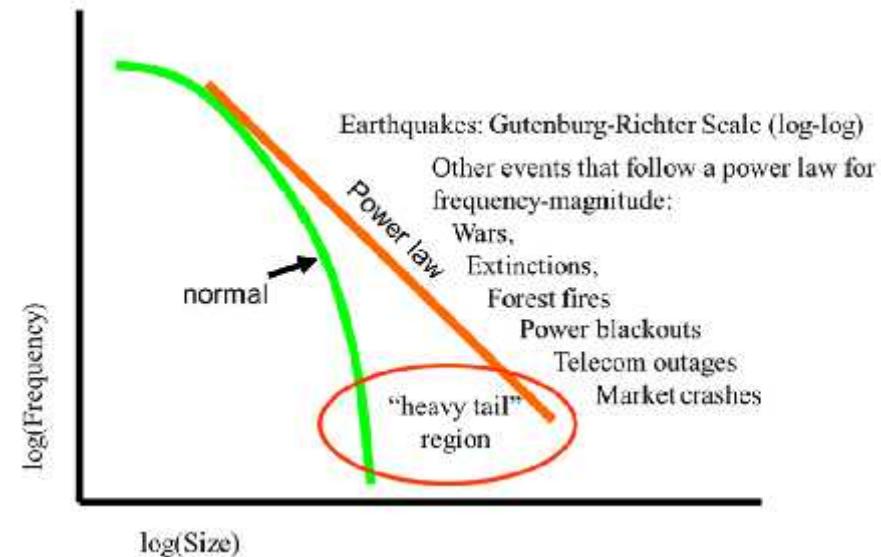
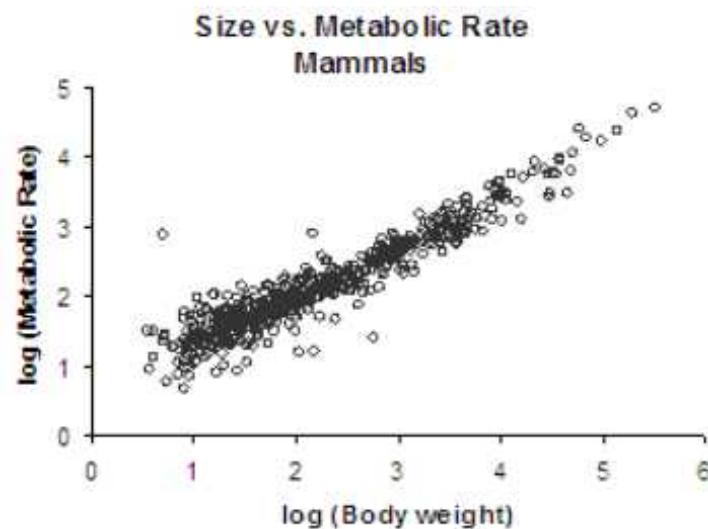


Fig. 2. Species-area relationship of oribatid mites for islands and countries of the world. Names of the islands are given in the figure, names of the mainland countries (or geographical regions) are indicated by numbers (1 Slovenia, 2 Netherlands, 3 Switzerland, 4 Denmark, 5 Costa Rica, 6 Florida, 7 Croatia, 8 Lithuania, 9 Panama, 10 Czechia, 11 Austria, 12 Hungary, 13 Korea, 14 former Yugoslavia, 15 Bulgaria, 16 former Czechoslovakia, 17 Romania, 18 Caucasus region, 19 Italy, 20 Poland, 21 Finland, 22 Norway, 23 Germany, 24 Sweden, 25 Spain, 26 Ukraine, 27 Peru, 28 Mexico, 29 Australia, 30 Brazil, 31 China, 32 Canada/USA, 33 former Soviet Union).





### The power law:

Number of words in English language....  
 Income in Italy  
 Commonness of names  
 Popularity of web sites  
 Citations of scientific papers  
 Number of species in biological taxa  
 Size of moon craters....

Size doesn't matter (no scale)

„Thick/heavy tail“: extreme values are unlikely - but not astronomically unlikely

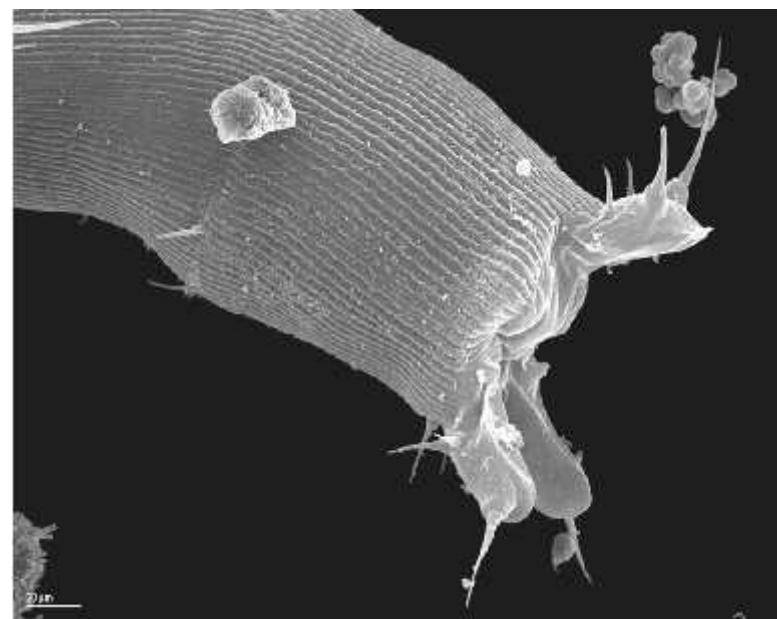
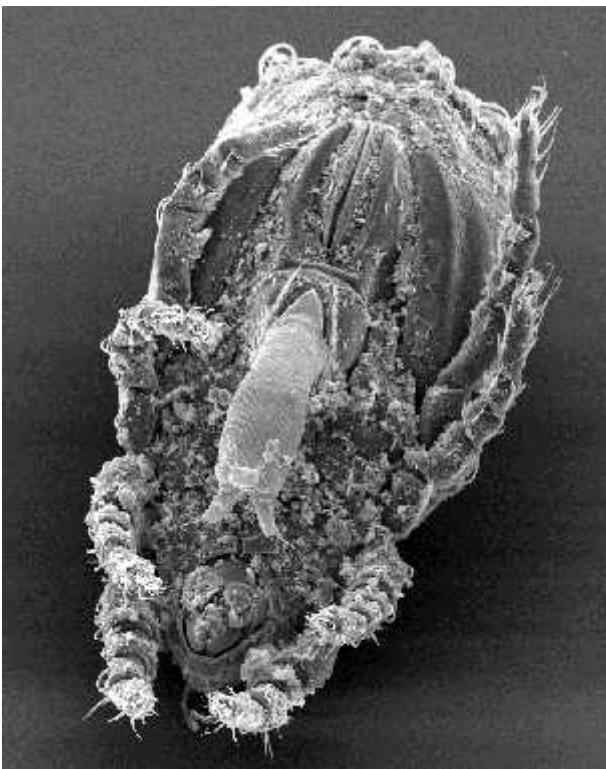
**The enigma of the log-log relationship .....remains**

## (4) Parthenogenesis & Sex: The last enigma

„too many“ parthenogens in oribatid mites...

(Norton et al. 1993, Norton 1994)

10 % of all oribatid mite species are parthenogenetic;  
but sometimes 90 % of all individuals



Norton, R. A., J. B. Kethley, D. E. Johnston, and B. M. O'Connor. 1993. Phylogenetic perspectives on genetic systems and reproductive modes of mites. Pp. 8-99 in: Evolution and Diversity of Sex Ratio in Insects and Mites (D. L. Wrensch and M. A. Ebbert, eds). Chapman & Hall Publ., NY.

1

Phylogenetic Perspectives on Genetic Systems and Reproductive Modes of Mites

Roy A. Norton, John B. Kethley,  
Donald E. Johnston, and Barry M. O'Connor

From: *Mites. Ecological and Evolutionary Analyses of Life-History Patterns* (M. Houck, ed.). 1994.  
Chapman & Hall, New York. 357 pp.

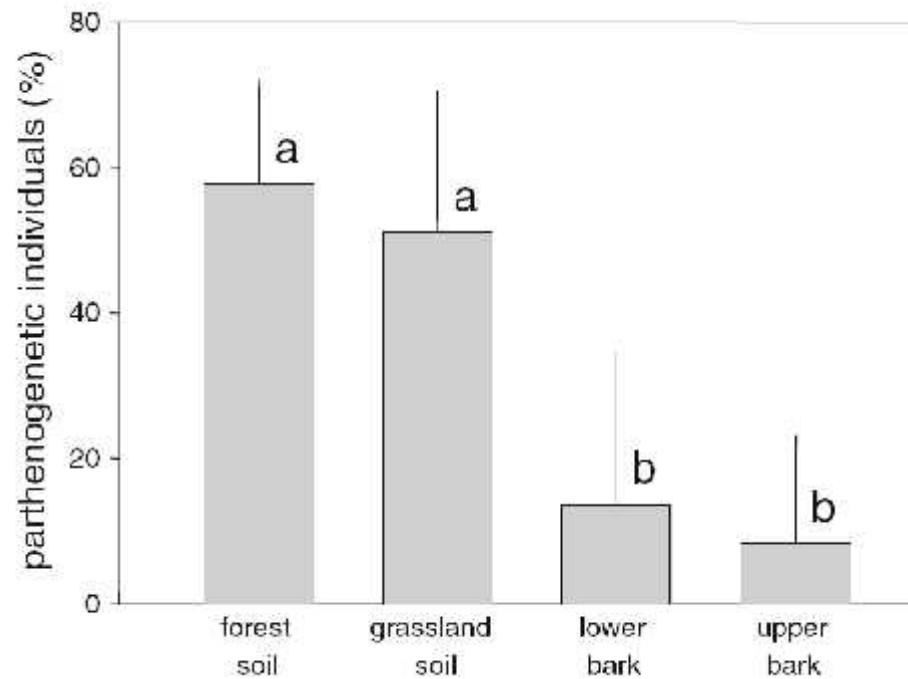
5

Evolutionary Aspects of Oribatid Mite Life Histories and Consequences for the Origin of the Astigmata

Roy A. Norton

## Microhabitats: much sex on bark (80-90 %) many parthenogens only in temperate/boreal soils !

**Fig. 6** Relative abundance of parthenogenetic individuals of oribatid mites of the forest soil, grassland soil, upper bark and lower bark. Data were arc-sin-square-root transformed prior to the analysis. Bars sharing the same letter are not significantly different (Tukey's HSD test;  $P > 0.05$ )



# Microhabitats: *Fomitopsis* (99 % sexuals)



**Table 1**

List of all oribatid mite species (and their abbreviations used in Fig. 3) found in *Fomitopsis pinicola* at the four altitudes (350, 580, 820 and 1160 m). Taxa for which stable isotopes measurements were carried out are marked in bold.

Species name	Abbreviation	Altitude
<i>Autogneta longilamellata</i> (Michael, 1885)	Auto long	350, 580, 820
<i>Banksinoma lanceolata</i> (Michael, 1885)	Bank lanc	820
<i>Belbidae</i> (=Damaeidae)	Belbidae	350, 820
<i>Caleremaeus monilipes</i> (Michael, 1882)	Cale moni	350, 820
<b><i>Carabodes areolatus</i> Berlese, 1916</b>	<b>Cara areo</b>	<b>350, 580, 820, 1160</b>
<i>Carabodes labyrinthicus</i> (Michael, 1879)	Cara laby	350, 820
<i>Carabodes reticulatus</i> Berlese, 1913	Cara reti	350, 580, 820, 1160
<i>Carabodes rugosior</i> Berlese, 1916	Cara rugo	350, 580, 820, 1160
<i>Cepheus cepheiiformis</i> (Nicolet, 1855)	Ceph ceph	350, 580
<i>Cepheus dentatus</i> (Michael, 1888)	Ceph dent	350, 580, 820
<i>Cepheus latus</i> (C.L. Koch, 1835)	Ceph latu	580, 820
<i>Chamobates borealis</i> (Trägårdh, 1902)	Cham bore	350
<i>Chamobates cuspidatus</i> (Michael, 1884)	Cham cusp	350, 580
<i>Chamobates spinosus</i> Sellnick, 1928	Cham spin	350
<i>Chamobates voigtii</i> (Oudemans, 1902)	Cham voig	350, 580, 820
<b><i>Dolicheremaeus dorni</i> (Balogh, 1937)</b>	<b>Doli dorn</b>	<b>350, 580</b>
<b><i>Hafenrefferia glivipes</i> (C.L. Koch, 1839)</b>	<b>Hafe gliv</b>	<b>350</b>
<i>Hermannella punctulata</i> Berlese, 1908	Herm punc	820
juvenile Damaeidae	juve Dama	350
juvenile Oribatida	juve Orib	350, 580, 820, 1160
<i>Liacarus coracinus</i> (C.L. Koch, 1841)	Liac cora	350, 580
<i>Liebstadia humerata</i> Sellnick, 1928	Lieb hume	580
<i>Liebstadia longior</i> (Berlese, 1908)	Lieb long	350, 580, 1160
<b><i>Mesotritia nuda</i> (Berlese, 1887)</b>	<b>Meso nuda</b>	<b>350</b>
<i>Minunthazetes pseudofusiger</i> (Schweizer, 1922)	Minu pseu	580
<b><i>Neoliiodidae</i></b>	<b>Neoliiodidae</b>	<b>350, 820</b>
<i>Oppiella nova</i> (Oudemans, 1902)	Oppi nova	350, 1160
<b><i>Oribatella quadricornuta</i> Michael, 1880</b>	<b>Orib quad</b>	<b>580, 820</b>
<i>Oribatella sexdentata</i> Berlese, 1916	Orib sexd	350, 580
<i>Phthiracaridae</i>	Phthiracaridae	350, 820
<i>Ramusella clavipectinata</i> (Michael, 1885)	Ramu clav	350, 580, 820

## More sex at low densities ! (counterintuitive)

High densities = many resources?

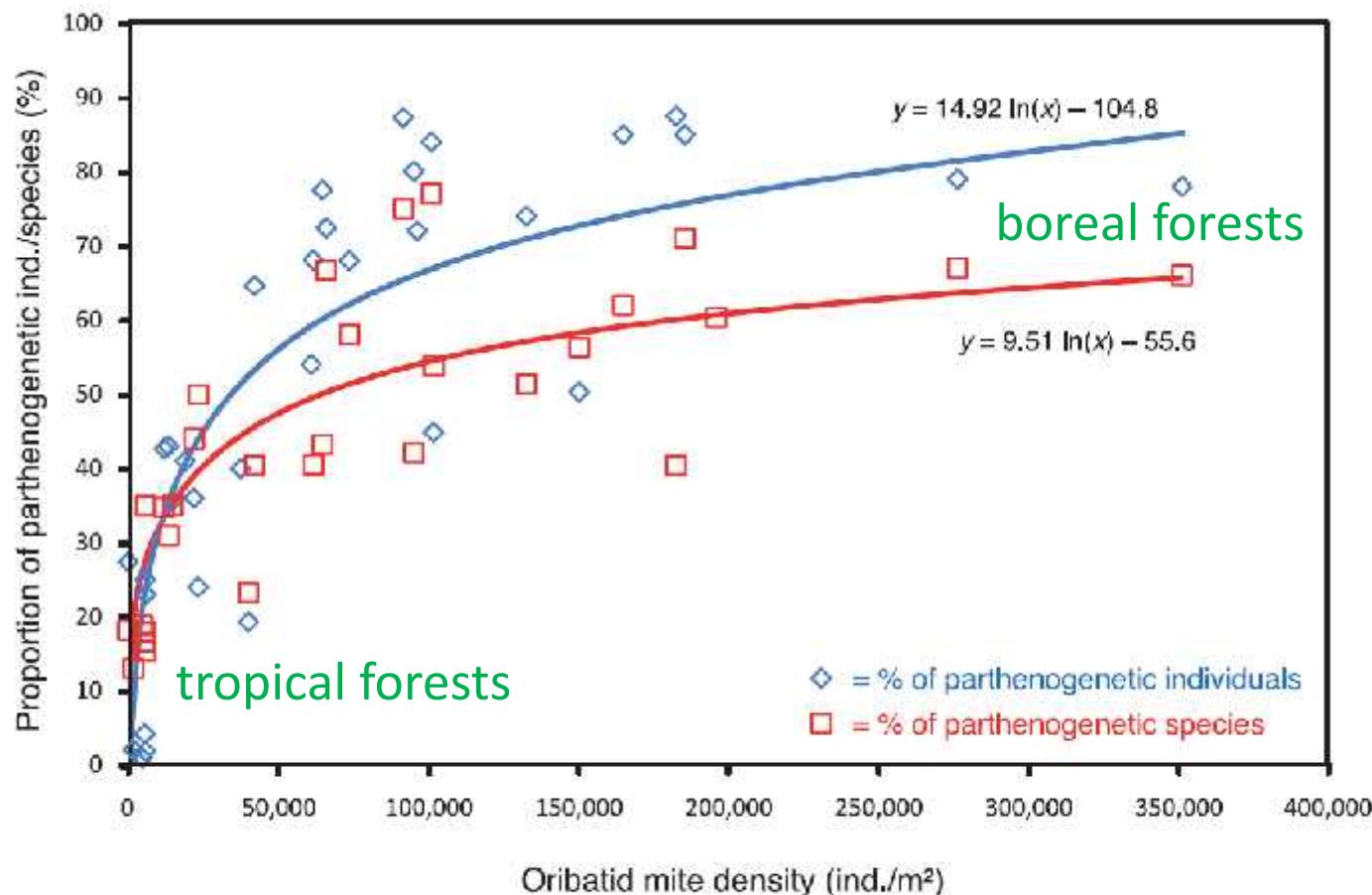
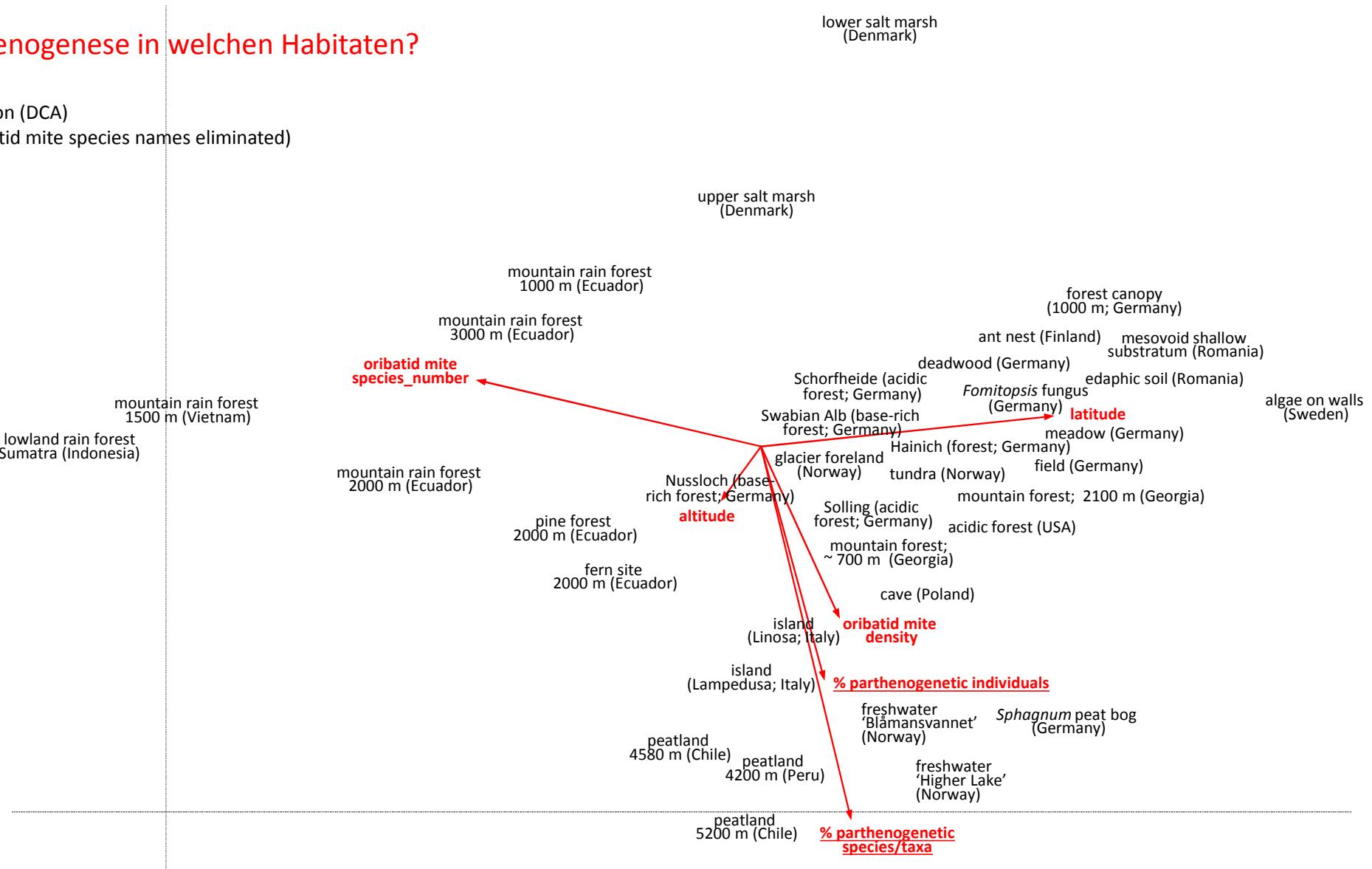


Fig. 2. Relationship between the proportion of parthenogenetic individuals/proportion of parthenogenetic species and oribatid mite density on a global scale. For details, see text.

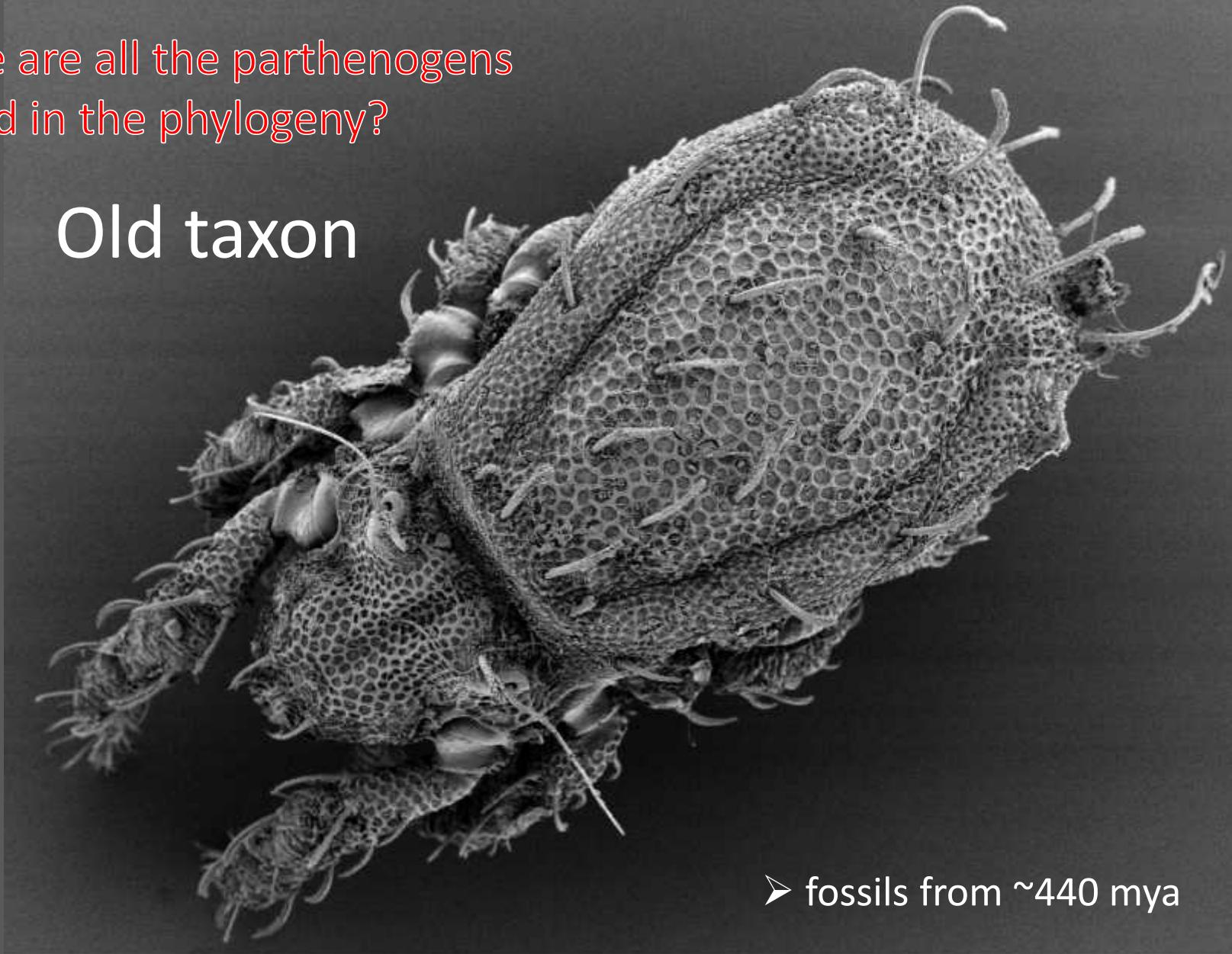
## Parthenogenese in welchen Habitaten?

Ordination (DCA)  
(all oribatid mite species names eliminated)



Where are all the parthenogens  
located in the phylogeny?

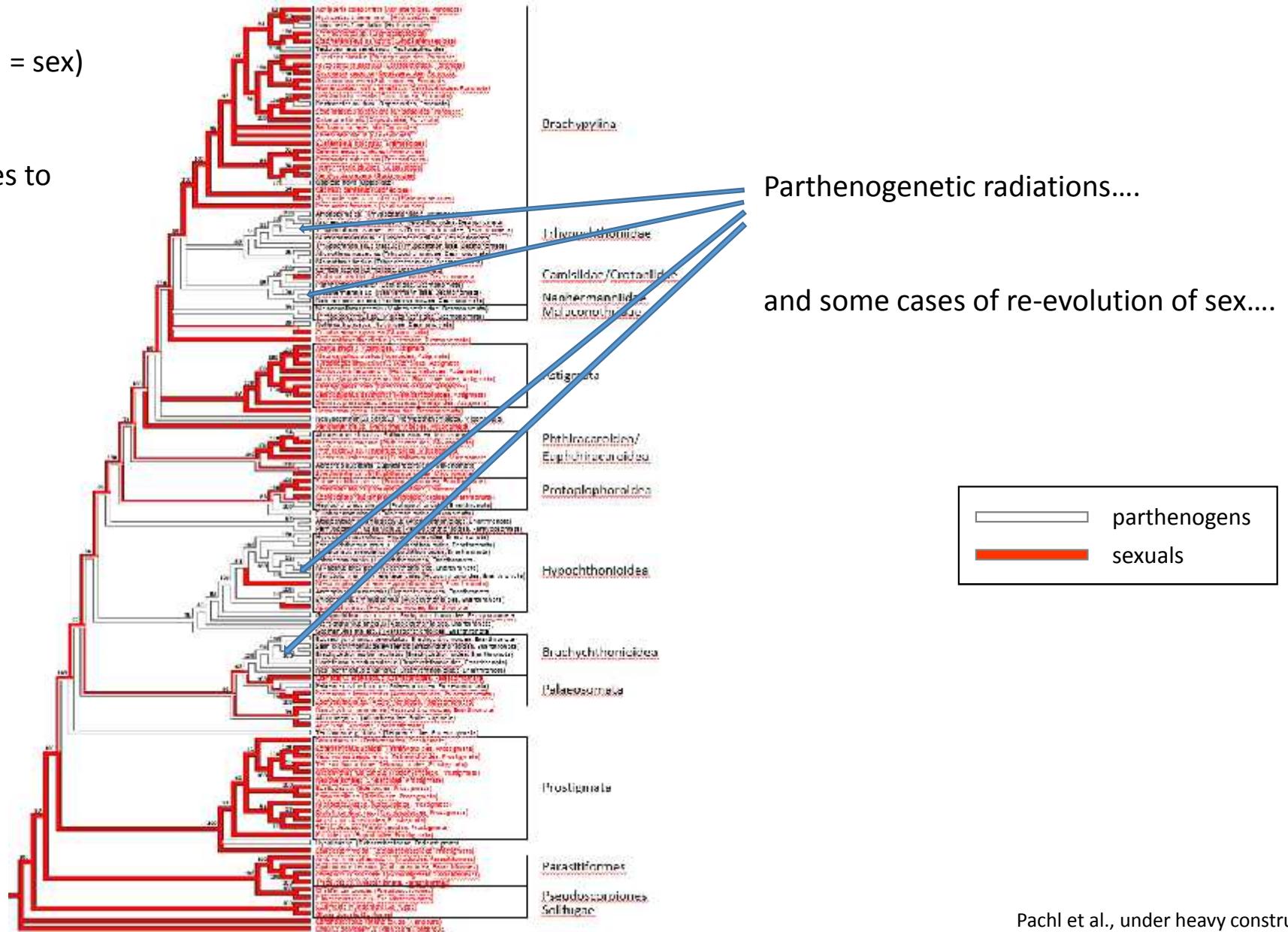
Old taxon



➤ fossils from ~440 mya

The „backbone“ (red = sex)  
....tends to be sexual

....with many switches to  
parthenogenesis



## Is soil ecology really ecology?

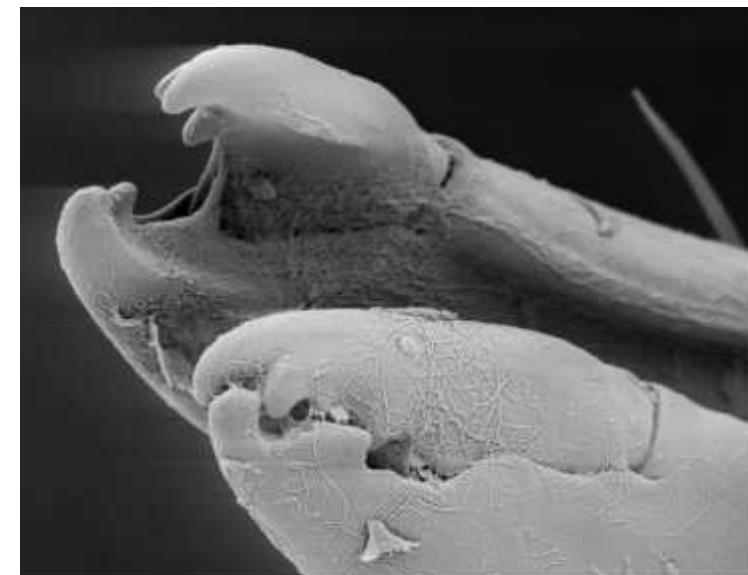


Against all odds:

- (1) Too many soil living species
- (2) Too few species in the tropics
- (3) Trophic generalists, with a  $^{15}\text{N}/^{13}\text{C}$  niche (Choosy generalists?)
- (4) Too many parthenogens
- (5) Parthenogenetic radiations
- (6) Non-adaptive radiations ?
- (7) Re-evolution of sex (frequently); against Dollo's law
- (8) Parthenogens in the „wrong“ habitats (old, stable systems)



Many strange patterns; more data/experiments needed....





Danke für's  
Zuhören !

many resources  
= parthenogenesis  
(Scheu & Drossel 2007)

does that solve the enigma?

