

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 m² 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 Science B.V.

Keywords: Oribatid mite; Habitat heterogeneity; Species diversity; Leaf litter

1. Introduction

The maintenance of species diversity is a complex phenomenon whose determinants may act on a broad

range of spatial scales, from the interactions of individuals on local habitat patches to landscape and regional dynamics. Understanding the relationship between the diversity of local assemblages and their local habitat is the first step in knitting together the network of factors controlling the level of diversity at any given site. The oribatid mites that inhabit the soil and litter, consuming microflora and decaying plant material, are the most diverse and often the most

*Corresponding author. Present address: Department of Biological Sciences, University of South Carolina, Columbia, SC 29208, USA; Tel.: (803) 777 3706; fax: +1 (803) 777 4002; e-mail: hansen@sc.edu

abundant of the microarthropods. At the site studied here, a core of 5 cm diameter can contain the adults of over 50 species of oribatid mites.

The question of the maintenance of this diversity has been cast in terms of classical equilibrium theory in which the dual observations of high diversity and apparently high similarity in feeding habits and habitat use among species are difficult to reconcile (Anderson, 1975; Usher et al., 1978; Wallwork, 1983). It has been concluded that there is ample opportunity for partitioning in the heterogeneous environment of the soil, but that the differences among species required for their co-existence are subtle and difficult to detect in the cryptic soil habitat. Non-equilibrium theory offers alternative models in which spatial and temporal heterogeneity mediates competitive interactions preventing competitive exclusion from reducing diversity. Without competition driving species differentiation, resources remain largely unpartitioned and very similar species can co-exist. In either paradigm, heterogeneity is a determinant of species diversity. In the first, diversity is deterministically linked to species composition. In the second, diversity may be largely independent of species composition.

This experiment was designed to examine the response of an oribatid assemblage to alterations in the heterogeneity and composition of the litter habitat. We report here on the assemblage response measured from the mites colonization of litterbags from within plots of treatment litters. Such sampling does not measure the level of co-existence a habitat maintains. Rather, it compares the active mite fauna within a stratum of the treatment habitats. Two questions will be addressed. First, do more complex habitats house more diverse mite faunas than simple habitats? Such a pattern in habitat use might culminate in differences in the level of co-existence each habitat supports. Second, is there some characteristic assemblage of oribatid species active in a particular litter-type? Such differences in species responses to habitat types should be in evidence if models of resource partitioning in the litter habitat are applicable.

2. Materials and methods

This experiment was carried out at Coweeta Hydrological Laboratory, an experiment station in the

Nantahala mountains of North Carolina, USA. The site is a mesic, mixed hardwood forest whose dominant tree species are *Quercus rubra* (scarlet oak), *Acer saccharinum* (sugar maple) and *Betula alleghaniensis* (yellow birch). Of secondary importance are *Fraxinus pennsylvanica*, *Acer pensylvanicum*, and *Castanea dentata*. A substantial herb layer is present from April to October.

Forty-two 1 m² plots were established in a grid across the site. Hardware cloth (1 cm mesh size) covered each plot to exclude natural litterfall. In November 1993 and 1994, each plot received 400 g of litter, the average litterfall for the site. Treatment litters were of six different types. Simple litter-types were yellow birch, scarlet oak or sugar maple. There were two mixed litter treatments. One consisted of equal parts of these three litter species. Another consisted of equal parts of these three species, the leaves of the three other tree species abundant on the site and mixed herb litter. At each application of treatment litter, litterbags containing 8 g of treatment litter were placed in the plots.

The simple treatment litters were chosen to span a range of chemistry, decomposition rate and architecture. Since each of the simple litters decompose at different rates, the mixed litters contain, at any given time, a greater variety of stages of decay. To the extent that leaf chemistry and stage of decomposition determines the microfloral growth, the mixed litters should contain a greater variety of microflora. Since the litter-types differ in size and architecture, the mixed litters are also more structurally complex than the simple litters.

The six treatments were arranged in a randomized block design. Six plots of each of the simple litter-types and 12 plots of each of the two mixed litters were distributed equally between two spatial blocks. Each of the three simple litters was represented by only half the number of plots as the mixed litters because the contrast of the greatest interest was among the levels of litter complexity.

Litterbags were collected at the intervals over the year following their placement. From the first year's litterbags, microarthropods were extracted from litterbags that had been in the field for 302, and 353 days. In the second year, microarthropods were extracted from the bags after 129, 164, 251 and 306 days in the field. Extractions were carried out within 24 h of

Table 1
Microhabitat categories used in analysis of litter heterogeneity

Substrate types	Fungal morphologies
1. Intact leaf	1. Diffuse hyaline hyphae
2. Partially skeletonized leaf	2. Dense hyphal mat
3. Skeletonized leaf	3. Discrete fungal colonies
4. Petiole	4. Pigmented hyphae
5. Root	5. Rhizomes
6. Mycorrhizal root	6. Fungal fruiting bodies
7. Humus	
8. Fecal pellets	

collection using modified Tullgren extractors (Crossley and Blair, 1991).

Conditions in the treatment litters were characterized in several ways. The moisture and mass loss were recorded from litterbags. The microhabitat heterogeneity of the treatment litters was measured with a technique similar to that of Anderson (1978). The microhabitats were identified according to the classes of substrate-type and fungal morphology (Table 1). Each combination of substrate and fungal growth form was regarded as a novel microhabitat. Four cores (5 cm diameter) were taken from the plots in each treatment. The number of different microhabitats encountered along a 5 cm transect was counted at four depths of 0.25, 0.5, 0.75 and 1.0 cm.

The general linear models procedure in SAS (SAS, 1989) was used for all analyses. Characterization of the treatment litters included analyses of moisture and mass loss. Mass loss of treatment litters was compared at each date using Tukey's studentized range test with a significance level of 0.05. Analyses of oribatid mites included abundance, richness and Fisher's alpha diversity index. Oribatid mite abundances were log-transformed to improve normality and homogeneity of variance. Fisher's Alpha is a parameter of the log

series distribution (Fisher et al., 1943). It is useful as a measure of richness that is insensitive to sample size and its adoption as the standard diversity index has been advocated by several authors (Magurran, 1988; Rosenzweig, 1995). The distribution of individual species among the simple litter-types was analyzed, using log-transformed abundances, for the 25 species that made up 90% of the total abundance in those litterbags. Percent similarity, a measure of the shared abundance of each species between two samples proportional to the total abundance in the samples (Bray and Curtis, 1957), was calculated for all pairs of bags within each date. Mean similarity within and among treatments was calculated for each date, and those values averaged across the four collection dates.

3. Results

3.1. Characterization of the treatment litters

The mix of the three simple litters falls within the range of decomposition rates spanned by the simple litters (Table 2). The mix of seven litters decayed more rapidly than other litters in both years. The birch litter was wetter than the other types at each of the six dates, significantly so on three occasions ($p < 0.02$).

Microhabitat variety increased with depth in each litter-type. The two mixed litters contained a significantly higher variety of microhabitats than the simple litters at all depths ($p < 0.001$). The mixture of seven litters contained more microhabitats than the mixture of three at depths of 0.25 and 0.5 cm ($p < 0.02$) (Fig. 1).

3.2. Oribatid mite diversity and species composition

In total, 7168 adult oribatid mites in 105 species were collected from the bags (see Table 3). In the first

Table 2
Percent mass remaining of treatment litters on four collection dates. Tukey's groupings (Alpha=.05, df=36, 37, 37, 37 for dates, respectively)

Treatment	Aug. 1994 % remaining	Oct. 1994 % remaining	July 1995 % remaining	Sept. 1995 % remaining
Birch	71.1 ^A	68.5 ^A	71.4 ^A	68.9 ^A
Oak	68.5 ^A	63.5 ^{A B}	71.9 ^A	57.8 ^A
3-Mix	62.4 ^A	63.4 ^{A B}	70.9 ^A	67.8 ^A
Maple	62.1 ^B	61.6 ^{A B}	70.2 ^B	60.0 ^A
7-Mix	60.2 ^B	59.0 ^{A B}	64.2 ^B	60.5 ^A

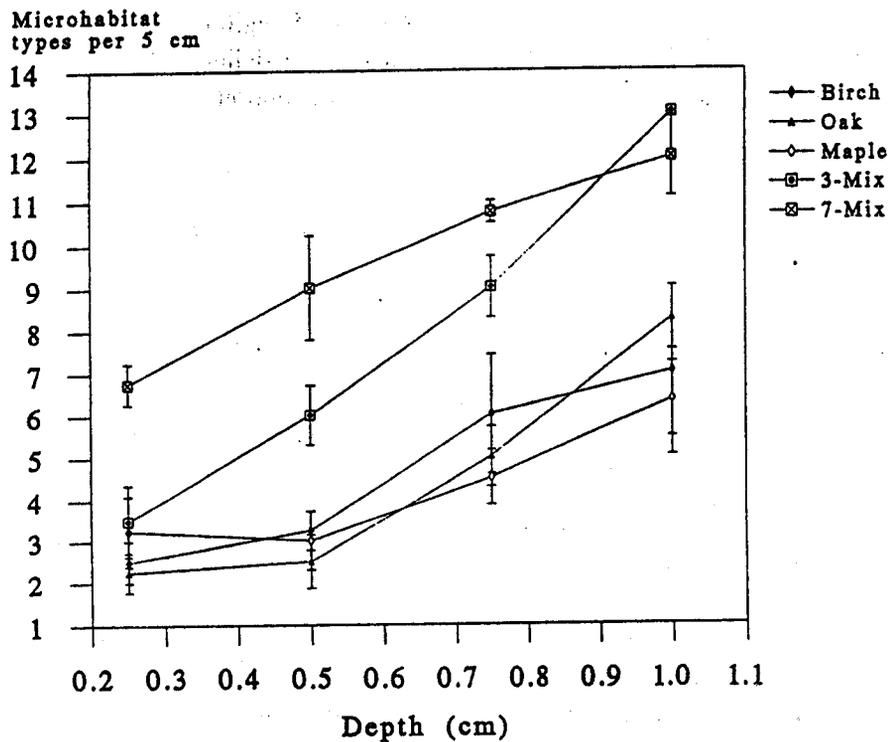


Fig. 1. Microhabitat variety among treatment litters at four depths. In four cores from each treatment-type, the number of different microhabitats encountered along a 5 cm transect was recorded at four depths. Microhabitat categories are described in Table 1.

Table 3

Abundance and diversity of adult oribatid mites in litterbags on four collection dates in late summer and early fall of 1993 and 1994

	Oak	Birch	Maple	3-Mix	7-Mix	Contrast simple vs. mixed litter
Aug. 1994: 302 days						
Abundance	39	25	46	40	46	$F_{1,37}=1.01, p<.320$
Richness	11.7	8.8	13.5	15	15.7	$F_{1,37}=6.37, p<.016^*$
Fisher's Alpha	6.7	6.1	7.0	9.9	9.7	$F_{1,29}=1.92, p<.177$
Oct. 1994: 353 days						
Abundance	29	20	59	31	46	$F_{1,37}=3.64, p<.064$
Richness	11.2	8.8	16.7	14.3	16.0	$F_{1,37}=10.63, p<.002^{**}$
Fisher's Alpha	7.4	8.2	8.9	10.6	10.6	$F_{1,28}=5.73, p<.023^*$
July 1995: 251 days						
Abundance	38	24	39	36	41	$F_{1,36}=1.34, p<.254$
Richness	9.7	8.7	12.8	14.8	15.8	$F_{1,36}=6.8, p<.013^*$
Fisher's Alpha	5.6	7.3	7.4	12.2	9.9	$F_{1,31}=5.1, p<.031^*$
Sept. 1995: 306 days						
Abundance	38	35	39	42	47	$F_{1,36}=2.45, p<.126$
Richness	12.2	8.5	12.2	13.4	15.3	$F_{1,36}=9.17, p<.004^{**}$
Fisher's Alpha	7.2	4.4	5.7	7.1	9.1	$F_{1,29}=11.47, p<.002^{**}$

two collections of 1994 litter, made in early March and early April, adult oribatid abundance and richness were very low, with means of 2.5 individuals in 1.5 species in March and 7.9 individuals in 4 species per

bag in April. Neither abundance nor richness differed significantly among treatments in these months. The remaining four sets of litterbags, those collected in August and October 1994 and in July and September

1995, contained substantial numbers of individuals. There was no difference in overall abundance or richness among these months.

In each of the four sets of litterbags, the two mixed litter treatments contained more species than did simple litters. Birch litter contained significantly fewer individuals than the other litters in three of the four sets ($p < 0.004$). Due to this variation in sample size, Fisher's Alpha may be the appropriate measure for the comparison of diversities. Alpha was higher in the mixed litter on all four collection dates. There were no differences in the diversity among the simple litter-types, or between the mix of three litters and the mix of seven.

Using percent similarity as the measure, the species composition within replicates of each litter-type were more similar to each other than to samples from other treatments except in the case of maple and 3-mix litter which were not distinct (Table 4).

In order to detect species preferences for individual litter-types, we restricted analysis to the simple litter treatments and compared the abundance of the 25 species most abundant in those bags. Nine showed significant differences. Three species, *Cepheus sp nr. corae* (Jacot), an *Oribatella* species and *Ferolocella tessellata* (Berlese) were most abundant in oak litter. Two more, *Platynothrus peltifer* (Koch) and *Dyobelba sp nr. tectopediosa* (Jacot), had higher abundance in oak than in birch litter. A species of *Polypterozetes* was less abundant in oak litter. Maple litter contained more *Nanhermannia dorsalis* (Banks) than the other two litters. *Rhysotritia ardua* (Koch) was more abundant in maple than in birch litter. *Eupelops silvestris* (Jacot) had its highest abundance in birch litter with low abundance in oak. Given the number of comparisons, 1.25 significant responses would be expected by chance.

4. Discussion

While the litters span a range of quality and decomposition rate, the simple and mixed litters do not differ consistently in any measured characteristic other than microhabitat heterogeneity. The behavior of the birch litter is an exception to this. One consequence of reducing the variety of components that make up a habitat is a loss of structure. Pure birch litter forms a closely packed mat which, combined with a high wettability, results in a litter layer that is water-logged for much of the time. This is the likely cause of the low abundances in the birch bags.

That microhabitat variety is higher in deeper strata and where a greater variety of litter-types occurs is an intuitive result. The descent through the litter layer reflects the progress of decomposition and the proliferation of microhabitats with depth reflects the concomitant progress of microbial and animal activity. As one would predict, the litters with greater initial variety in lability of substrates increase in their microhabitat variety more rapidly as the decomposition trajectories of the component litters diverge.

Myriad studies have shown that oribatid mite numbers and richness increase as decomposition proceeds. Abundance and richness increase with depth in the litter (Pande and Berthet, 1975), and, in litterbags, with days in the field (Seastedt et al., 1983). Anderson (1975) found greater oribatid abundance and richness in more rapidly decomposing litter-types. In this study, oribatid numbers and richness were correlated with decomposition rate within the simple litters. Likewise, the more rapidly decomposing of the two mixtures hosts the richer and more abundant fauna. Decomposition rate is potentially a confounding factor in the overall comparison of simple vs. mixed litters, since birch litter decomposes significantly more slowly than

Table 4

Percent similarity for the oribatid assemblages within and among treatment-types. Mean percent similarity was calculated for the replicate comparisons within each collection date and the mean of those four values is reported here.

	Oak	Birch	Maple	3-Mix	7-Mix
Oak	0.301				
Birch	0.193	0.263			
Maple	0.230	0.246	0.284		
3-Mix	0.271	0.259	0.297	0.314	
7-Mix	0.218	0.222	0.258	0.267	0.291

the other litters, while the mix of seven decomposes more rapidly (Table 2). To compare heterogeneity while holding the stage of decomposition constant, the appropriate comparisons are maple vs. the mix of seven litters and oak and maple vs. mix of three litters. If litterbags from the four dates are pooled together, richness is higher in mixed litter in both these contrasts (maple vs. 7-mix: $F_{1,161}=4.02$, $p<0.04$, oak and maple vs. 3-mix: $F_{1,161}=7.08$, $p<0.009$). Likewise, Fisher's Alpha remains higher in the mixed litter (maple vs. 7-mix: $F_{1,132}=7.78$, $p<0.006$, oak and maple vs. 3-mix: $F_{1,132}=14.83$, $p<0.0002$).

These results demonstrate that there is indeed a link between the heterogeneity of the litter habitat and the diversity of the oribatid mites to be found there. They confirm those of Anderson (1978) who compared the oribatid richness among sites that differed in the nature and complexity of their litter and soil profiles. In this experiment, all litterbags sampled the same pool of mite species and experienced the same environment. Therefore, the responses observed here are particularly strong evidence for the role of litter heterogeneity as factors potentially correlated with heterogeneity, which may vary among sites, such as productivity, total amount of habitat and environmental conditions, can be ruled out as contributors to the phenomenon.

The overall faunal similarity among litterbags is low. This is to be expected since each bag is a very small sample of the assemblage, including only 5–10% of the 168 species that have been collected on the site. Even with this daunting potential for variation in species composition, a consistent pattern of greater similarity within a litter-type than among litter-types does emerge. In addition, each litter-type is next most similar to the litter mix with which it has the most litter constituents in common. Faunas of birch and oak litter most closely resemble those of the litter mixture containing one-third birch and one-third oak leaves. The maple fauna is indistinguishable from that of this mixture. The fauna in the mixture of seven litters is most similar to that of the mixture of three, with which it shares 43% of its litter constituents. These trends in species composition suggest that species do differentiate among litter-types, though few species showed a marked affiliation with only one litter-type.

Walter (1985) found no evidence of oribatid mite specificity among three coniferous litter species. In

contrast to the litterbags in Walter's study, these sampled a captive assemblage exposed to only one litter habitat. As such, the mite response in this study is not a straightforward reflection of habitat selection and so the results are not directly comparable. In this experiment, detectability of species responses to litter-types may have been enhanced if litter simplification has exerted selection on the species pool in the plot available to colonize the litterbags. Alternately, the observed degree of specificity might be an underestimate since the sample includes captive species which, if given the choice among several litter-types might have selected another.

While both patterns are consistent, neither the higher mite diversity in mixed litter, nor the higher coherence of species composition within litter-types are dramatic. Litterbag sampling is just an indicator of the dynamics of the entire assemblage, reflecting as it does, only the activity of a minority of the species at only one life stage. Each species' habitat use is complex, based on a multiplicity of objectives. Feeding, dispersal, oviposition and optimizing environmental conditions are all objectives that vary with life stage. How the responses detected here manifest when integrated over whole life cycles and populations and over the entire assemblage remains to be seen. Given the consistency of the results over time it may be that these small but detectable differences in oribatid mites active in homogenous and heterogeneous habitats could aggregate into an effect on species co-existence of a greater magnitude. The captive assemblages in these plots have been exposed to treatment habitats over several generations. A sampling of the complete habitat used by the assemblage, from litter to humus should reveal the ultimate impact of the responses seen here upon species co-existence.

Acknowledgements

Thanks to Dr. Roy A. Norton who provided oribatid mite species identifications. This work was funded, in part, by an NSF doctoral fellowship to the author.

References

- Anderson, J.M., 1975. Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. *J. Anim. Ecol.* 44, 475–495.

- Anderson, J.M., 1978. Inter- and intra-habitat relationships between woodland *Cryptostigmata* species diversity and the diversity of soil and litter microhabitats. *Oecologia* 32, 341-348.
- Bray, J.R., Curtis, J.T., 1957. An ordination of upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27, 325-349.
- Crossley Jr., D.A., Blair, J., 1991. A high efficiency, 'low technology' tullgren-type extractor for soil microarthropods. *Agric. Ecosys. Env.* 34, 187-192.
- Fisher, R.A., Corbet, A.S., Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12, 42-58.
- Magurran, A.E., 1988. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, NJ, 179 pp.
- Pande, Y.D., Berthet, P., 1975. Observations on the vertical distribution of soil Oribatei in a woodland soil. *Trans. R. Ent. Soc. (Lond.)* 127(3), 259-275.
- Rosenzweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge University Press, New York, 436 pp.
- SAS., 1989. *SAS/STAT User's Guide*. Version 6. SAS Institute, Cary, NC, USA.
- Seastedt, T.R., Crossley Jr., D.A., Meentemeyer, V., Waide, J.B., 1983. A two-year study of leaf litter decomposition as related to macroclimatic factors and microarthropod abundance in the southern Appalachians. *Holarc. Ecol.* 6, 11-16.
- Usher, M.B., Davis P.R., Harris J.R.W., Longstaff, B.C., 1978. A profusion of species? Approaches towards understanding the dynamics of the populations of the microarthropods in decomposer communities. In: Anderson, Turner and Taylor (Eds.), *Population Dynamics*. The 20th Symposium of the British Ecological Society, Blackwell Scientific Publications, London, pp. 359-384.
- Wallwork, J.A., 1983. Oribatids in forest ecosystems. *Ann. Rev. Entomol.* 28, 109-130.
- Walter, D.E., 1985. The effects of litter-type and elevation on colonization of mixed coniferous litterbags by oribatid mites. *Pedobiologia* 28, 383-387.