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The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies

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ABSTRACT

Litterbags have been utilized in soil ecology for about 50 years. They are useful because they confine organic material and thus enable the study of decomposition dynamics (mass loss and/or nutrient loss through time, colonization by soil biota) *in situ*, i.e. under field conditions. Researchers can easily restrict or permit access to certain size classes of soil fauna to determine their contribution to litter mass loss by choosing adequate mesh size or applying specific biocides. In particular, the mesofauna has received much attention since it comprises two very abundant and diverse microarthropod groups, the Collembola (springtails) and Acari (mites). We comprehensively searched the literature from the mid-1960s to the end of 2005 for reports on litterbag experiments investigating the role of microarthropods in terrestrial decomposition. Thirty papers reporting 101 experiments satisfied our selection criteria and were included in the database. Our meta-analysis revealed that microarthropods have a moderate but significant effect on mass loss. We discuss in detail the interactions of the microarthropod effect with study characteristics such as experimental design (e.g. number of bags, duration of experiment), type of exposed organic matter, climatic zone and land use of the study site. No publication bias was detected; however, we noticed a significant decrease in the microarthropod effect with publication year, indicating that, in the first decades of litterbag use, soil zoologists may have studied "promising" sites with a higher *a priori* probability of positive microarthropod effects on litter mass loss.

A general weakness is that the treatments differ not only with respect to the presence or absence of microarthropods, but also with regard to mesh size (small to exclude microarthropods, wide to permit their access) or presence (to exclude microarthropods) and absence (to permit their access) of an insecticide. Consequently, the difference between the decomposition rates in the treatments is not a pure microarthropod effect but will be influenced by the additive effects of mesh size and insecticide. The relative contribution of the "true" microarthropod effect remains unknown without additional treatments controlling for the differential mesh size/insecticide effect. A meta-analysis including only those studies using different mesh size and for which the data were corrected by subtracting an estimated mesh size effect based on data from the literature yielded a significantly negative microarthropod effect on litter decomposition. These results cast doubt on the widely accepted hypothesis that microarthropods generally exert a positive effect on litter mass loss. We conclude that after 40 years of litterbag studies our knowledge on the role of microarthropods in litter mass loss remains limited and that the inclusion of a third treatment in future studies is a promising way to retain litterbags as a meaningful tool of soil biological studies.

Key words: Collembola, decay rates, exponential model, litter mass loss, mesofauna, oribatid mites.

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I. INTRODUCTION

Litterbags have belonged to the standard equipment and procedures of soil ecology for over 50 years (Bocock & Gilbert, 1957). They enable the study of the decomposition dynamics of organic materials (mass loss and/or nutrient loss through time, colonization by soil biota) *in situ*, i.e. under field conditions. Litterbags can be used to exclude faunal size classes selectively in order to separate the contributions of various taxa to organic matter decomposition. By choosing adequate mesh size, researchers can restrict or permit access of the three large groups of soil animals, as defined by their body width: microfauna (< 100 μm), mesofauna (0.1 – 2 mm) and macrofauna (> 2 mm) (Swift, Heal & Anderson, 1979). In particular, the mesofauna has received much attention as it contains two abundant and diverse arthropod groups, the Collembola (springtails) and Acari (mites), along with scarcer groups such as Protura, Diplura, Pseudoscorpiones, Symphyla and Pauropoda. Collembola and the most important mite group, the Oribatida, are ubiquitous members of the soil fauna and have colonized virtually all terrestrial habitats throughout the world (Coleman, Hendrix & Crossley, 2004). Under optimal conditions, such as forest soils rich in organic matter, collembola populations can reach densities of 100,000 per m^2 and oribatid mites 400,000 per m^2 (Petersen & Luxton, 1982). Although these arthropods belong to the mesofauna, they are typically known as microarthropods and we use this term below.

Litterbag studies are prolific for various reasons. Firstly, the large variety of litter (e.g. leaves, stems and roots of thousands of woody and herbaceous plant species, pure and mixed natural and artificial substrata), ecosystems (e.g. forests, grasslands, agricultural fields), climatic conditions (e.g. tropical, temperate, boreal), and direct and indirect anthropogenic impacts (e.g. tillage, fertilizer, pesticides, enhancement of atmospheric [CO_2]) offers opportunities for exploring microarthropod effects under a large number of combinations of factors.

Secondly, the litterbag technique is simple and inexpensive. Litterbag experiments can be set up without the necessity for excessive funding for costly technical equipment and only require a desiccation chamber and a balance scale. Replicate bags can easily be produced, and statistical requirements can be met with comparably little effort.

The simplicity of the litterbag approach does, however, raise various issues. In a review on the use of enclosed model ecosystems in soil ecological studies, Kampichler, Bruckner & Kandeler (2001) found that the overwhelming number of experimental field studies used litterbags instead of more advanced methods such as litter baskets or field mesocosms. As pointed out by the authors, this research strategy is understandable since litterbag studies yield more results per unit time than more complex experimental systems. Thus, publication of these results, when statistically significant, can help researchers meet publication benchmarks and further career opportunities. If the experiments are unsuccessful, the loss of expenditure is limited. Similar criticisms on research policy were also made by Carpenter (1996) and Kokko & Sutherland (1999) who questioned the bias of current ecological research towards short-term experiments under controlled conditions to increase the probability of obtaining "publishable" results.

Non-significant results generally have a lower chance of being published in high-ranking ecological journals (Csada,

James & Espie, 1996; Koricheva, 2003), and we suspect that litterbag experiments are especially prone to publication bias. First, scientists may tend to keep non-significant results in their file drawers, or submit them to less prestigious or regional and local journals (submission bias). Second, editors and referees prefer manuscripts with greater originality that tend to corroborate actual theoretical trends (Møller & Jennions, 2001) and may easily reject a manuscript reporting non-significant results obtained by the unspectacular litterbag method (reviewer and editorial bias). If these aspects of publication bias do apply, the conventional wisdom, that microarthropods have mainly positive effects on terrestrial decomposition in the field, may represent a distortion of reality.

Although a large number of litterbag studies have accumulated during the last decades, the most recent attempt to synthesize these results was almost a quarter of a century ago (Seastedt, 1984). This was basically a narrative account of a limited number of empirical studies ($n = 15$) with a modest attempt at quantitative synthesis, mostly by calculating the parameter k of the exponential decomposition model $M_t = M_0\ exp\ (kt)$ across experiments and treatments, where M_0 is the initial amount of litter, and M_t is the remaining mass in litterbags at time t. Seastedt (1984) concluded that microarthropods have a variable but generally significant positive effect on litter disappearance averaging approximately 20%. These findings still represent the accepted view of the role of microarthropods in terrestrial decomposition and are reproduced in the most recent text books on soil ecology (e.g. Coleman *et al.*, 2004).

Herein, we aim at synthesizing the results of litterbag studies during the last 40 years. First we briefly review the history of the litterbag approach. Then we present the methodological approach of our meta-analysis, describing the characteristics of the experimental protocols of the included studies (mesh sizes, duration of experiments, years of publication, etc.) and report on the substrata, ecosystems, etc. that they cover. Further, we test the hypothesis that litterbag studies are prone to publication bias and yield a biased image of the role of microarthropods on terrestrial decomposition. Based on the results of our meta-analysis and the test of publication bias, we draw conclusions on microarthropod effects and analyse their interactions with study characteristics. It is not our intention to discuss mechanisms by which microarthropod-microbial interactions contribute to decomposition (see review by Lussenhop, 1992). Finally, we present a summarizing critique of the litterbag method, pointing out methodological flaws that may affect the estimation of the role of microarthropods.

II. THE HISTORY OF THE LITTERBAG APPROACH

Bocock & Gilbert (1957) inaugurated the use of litterbags in soil biology. The technique of confining organic material and following its degradation had been used previously by botanists: Falconer, Wright & Beall (1933) is the first record of which we are aware. These early attempts used wire containers to separate litter from the surrounding soil or placed it between layers of glass wool (Gilbert & Bocock, 1962). The rapid development and availability of synthetic fibres after World War II allowed the construction of bag-shaped confinements. K. L. Bocock and O. J. Gilbert compared a range of products and chose nylon netting as it was inexpensive, durable, biologically inert and strong. Due to their high flexibility, nylon bags – typically measuring between 10 cm x 10 cm x 1 mm and 20 cm x 20 cm x 1 mm – and the enclosed leaves could be embedded easily in the litter layer on the forest floor (Gilbert & Bocock, 1962).

Bocock (1962) was the first to use nettings of graded mesh to assess the contributions of different animal size classes [several authors wrongly attributed this advance to Crossley & Hoglund (1962), who used bags of various mesh sizes to test only for effects of the bag microclimate and of larger predators on colonizing mites]. Bocock's (1962) approach was rapidly taken up by soil ecologists (e.g., Edwards & Heath, 1963).

Kurcheva (1960) reported on the first use of a chemical (naphhaline) to exclude animals from the decomposition process of fresh litter. When animals were present, about half of the litter disappeared in 140 days, when no animals were present only one-tenth of the litter vanished (Kurcheva, 1960). This method of establishing treatment samples which contain microarthropods (no insecticide applied) and treatment control samples (free of microarthropods, insecticide applied) was adopted in various litterbag studies (e.g. Witkamp & Crossley, 1966; Heneghan *et al.*, 1999). Nonetheless, litterbag studies using insecticides never attained the popularity of studies using graded mesh. One reason for this is that naphthalene is likely to be toxic to all arthropods, not just microarthropods, thus, under natural conditions, it is difficult to attribute results to the absence of microarthropods alone. This criticism was, however, overlooked by several authors (e.g. Seastedt & Crossley, 1980, 1983; Blair, Crossley & Callaham, 1992).

Further developments of litter and soil confinement techniques such as litter cages (Blair, Crossley & Callaham, 1991) and mesocosms based on undisturbed soil monoliths (Bruckner et al., 1995; Kampichler *et al.*, 1999) are structurally and biologically more complex than the relatively two-dimensional litterbag. They are not used as frequently in soil ecological experiments and are not considered further here.

III. A META-ANALYSIS OF LITTERBAG STUDIES

Since the days of Seastedt (1984) powerful research synthesis methods have been developed that are commonly referred to as meta-analysis (Rosenthal, 1991; Hunt, 1997; Gurevitch & Hedges, 2001). Meta-analysis combines measures of effects from primary studies into an estimate of the overall strength of the effect and uses this estimate for the determination of significance; a significant result means that there is statistical support to test the significance of the overall effect.

We use meta-analysis to assess the hypothesis that microarthropods accelerate the decomposition process of terrestrial litter in the field. In contrast to earlier approaches of research synthesis such as vote-counting (Hedges & Olkin, 1980) or combined probability methods (Rosenthal, 1978), meta-analysis yields an overall effect size that can be used for the interpretation of the strength of the statistical findings (Gurevitch & Hedges, 2001).

(1) Scope of the survey, data sources and selection criteria

We made an extensive survey of the literature published until the end of 2005. We expected the sources to be highly heterogeneous in terms of mesh size, litter material, geographic distribution and land use; thus, we restricted our survey to articles that met the following selection criteria:

(1) studies should be focused on the importance of microarthropods for decomposition in the field;
(2) studies should use (*a*) graded mesh sizes or (*b*) naphthalene or a similar agent to establish an experimental treatment (litter with microarthropods) and a control (litter without microarthropods);
(3) since we aimed to achieve a "common currency" to compare diverse experiments (i.e. fitting of an exponential decomposition model), studies should measure decomposition in terms of mass loss and not element losses over time (the number of papers on the latter was much smaller);
(4) studies should consist of at least two sampling dates to allow for the fitting of an exponential decomposition model.

We searched the *Biological Abstracts* (*Biosis Previews* since 2003), volumes 1957 to 2005 (1957-1968 printed volumes, 1969-2005 electronic database) using various combinations and truncations of the key words: litterbag, meshbag, Oribatida, Collembola, microarthropod, mesofauna, arthropod, decomposition and soil. Additionally, we searched the *Catalogue of Oribatid Literature* (compiled by the late Eduard Piffl, Vienna, and Heinrich Schatz, Innsbruck; unpublished Microsoft Word file; edition April, 2001) and all volumes of the *Proceedings of the International Colloquia on Soil Zoology*: Rothamsted 1958, Oosterbeek 1962, Braunschweig 1966, Dijon 1970, Praha 1973, Uppsala 1976, Syracuse 1979, Louvain-la-Neufe 1982, Moscow 1985, Bangalore 1988, Jyväskylä 1992, Dublin 1996 and České Budějovice 2000. Reference lists of relevant articles were screened for articles not included in the above-mentioned databases.

We did not examine diploma and PhD theses, because we are not aware of any international database that includes them: libraries and databases of some countries include these works, others do not. We decided to omit them entirely from the search, in order to avoid bias.

We sometimes encountered, but did not make all the necessary efforts to obtain original papers from China, Japan, and the former Soviet Union. These countries have regional or national publication organs that are virtually inaccessible from abroad, and the effort involved in interlibrary loan, translation, and interpretation was not justifiable. Consequently, our references are restricted to those available in western European libraries.

(2) Study parameters

In order to characterize the litterbag experiments described in the literature, we recorded the experimental protocol (duration of experiment, number of exposed bags per treatment, number of sampling dates, technique of microarthropod exclusion, mesh size, type of organic material), the climate, and the land use type of the study site for each experiment. If nettings of oblong mesh form were used, we calculated the side length of a size-equivalent square. The climate at the study sites was assessed by reference to the ten main global climate classes in Walter & Lieth (1960–1967).

(3) Meta-analysis methods

Despite the long history of the litterbag method, cross comparison of studies was hampered by the lack of a generally accepted standard of analytical protocol. The ways chosen to report the results were numerous and inconsistent, thus the results were occasionally rendered incomparable. More than 25 years ago, Wieder & Lang (1982) proposed the use of statistical decomposition models that would allow unification of analysis and easy quantitative comparisons; their recommendation has rarely been adopted by soil zoologists. While a few researchers reported parameter values of (different) decomposition models, the majority described decomposition in litterbags as a percentage of initial mass lost. They compared treatment and controls either graphically by plotting mass loss curves or by various descriptive and inferential statistical procedures (confidence intervals, ANOVA, etc.), sometimes taking into account only the remaining mass at the end of the experiment and sometimes including time as a factor.

We considered it necessary to reanalyse each of the studies in the database applying the exponential decomposition model $M_t = M_0\ exp\ (kt)$. The majority of papers did not report original data, but presented results as decomposition curves with remaining organic mass (or mass lost) on the ordinata and time on the abscissa. We scanned these diagrams to a computer and measured the data points of the curves with a screen ruler ("kruler" under Linux/KDE). To establish a uniform method of analysis, we used the mean remaining mass at the different sampling dates of each study for model fitting, even when the complete original data (i. e. the remaining mass in each litterbag) were reported. Thus, the only indicator of experimental effort in our analysis is the number of sampling dates, while the number of replicate litterbags at each sampling date was not taken into account. We determined the parameter k for treatment (k_T) and control (k_C). Soil zoologists assume that the difference between k_C in bags with fine mesh (or in bags with insecticide) and k_T in bags with coarse mesh (or in bags without insecticide) characterizes the contribution of microarthropods, k_M, to decomposition (but see Section VII). This means that $M_t = M_0\ exp\ ((k_C + k_M)t)$, where k_C includes the contribution of microflora and microfauna to

decomposition, as well as physical and chemical mass loss (for example, leaching), and where k_M represents the additional microarthropod effect. Conventional wisdom says that $|(k_C + k_M)| > |k_C|$ i.e. microarthropods accelerate mass loss. We tested the precision of our determination of k by selecting 10% of the database and repeating datapoint measurements without knowing the results of the first measurement run. Measurement errors fell within 2% and 3% of k and the standard error s of the fitted model, respectively, thus confirming the validity of the measurement procedure (data not shown).

In meta-analysis, effect size is a measure of the strength of the relationship between variables, taking into account not only whether an effect is significant but also its size. We chose Hedges' d as effect size (Hedges & Olkin, 1985), which calculates as

$$d = \mathcal{J}(k_T - k_C) / S \tag{1}$$

where S is the pooled standard error calculated as

$$S = \sqrt{\frac{(n_T - 1)s_T^2 + (n_C - 1)s_C^2}{n_T + n_C - 2}} \tag{2}$$

with n_T and n_C denoting sample sizes (i.e. number of sampling dates) of treatment and control, respectively, and s_T and s_C indicating their corresponding standard errors. $\mathcal{J}$ is a correction factor against small sample sizes which calculates as

$$\mathcal{J} = 1 - 3/[4(n_C + n_T - 2) - 1]. \tag{3}$$

We first calculated cumulative effect size, E_{cum}, and total heterogeneity, Q_T (Hedges & Olkin, 1985), according to

$$E_{cum} = \frac{\sum_{i=1}^{n} w_i E_i}{\sum_{i=1}^{n} w_i} \tag{4}$$

and

$$Q_T = \sum_{i=1}^{n} w_i E_i^2 - \frac{\left(\sum_{i=1}^{n} w_i E_i\right)^2}{\sum_{i=1}^{n} w_i} \tag{5}$$

where n is the number of studies, E_i is the effect size of the i^{th} study, and the weight (w_i) is the reciprocal of the variance of the i^{th} study. E_{cum} represents the overall magnitude of the microarthropod effect. It is considered to be significant when its confidence limits – obtained by bootstrapping with 999 iterations – for $p = 0.05$ do not include zero. When tested against a χ^2-distribution with $n - 1$ degrees of freedom, a significant Q_T indicates that the variance among effect sizes of the studies is greater than expected by sampling error and implies that other explanatory variables may affect the results. In this case we either compared effect sizes between different categories of study parameters (land use type, climatic zone, etc.) or calculated linear regressions between effect sizes and continuous study parameters (duration of bag exposure, etc.). As for the overall cumulative mean effect size, bootstrapping was also used to generate confidence intervals around cumulative effect sizes in the categorical models.

To test for publication bias, we used failsafe numbers (Rosenthal, 1979; Orwin, 1983), normal quantile plots (Wang & Bushman, 1998) and rank correlations between the standardized effect size, E^*, and sample size, n, across studies (Begg, 1994), . The standardised effect size of each study, E_i^*, is calculated as

$$E_i^* = \frac{(E_i - \bar{\bar{E}})}{\sqrt{v_i - \left(\sum 1/v_j\right)^{-1}}} \tag{6}$$

where E_i is the effect size of the i-th study, $\bar{\bar{E}}$ is the mean effect size, vi is the variance of the i-th study and the summation is over all studies.

Significant correlations between E^* and n indicate that larger effect sizes are more likely to be published than smaller effect sizes. A failsafe number is the number of non-significant, unpublished, or missing studies that need to be added to a meta-analysis to change its result from significance to nonsignificance (Rosenthal's N_R), or the number of additional studies needed to reduce an observed mean effect size to a desired minimal effect size (Orwin's N_O). Strange gaps or very nonlinear curves in the normal quantile plot are indications of a publication bias or of multiple populations in the data set.

All analyses mentioned (calculation of effect sizes of primary studies, cumulative effect size, total heterogeneity, categorical and continuous model meta-analysis), as well as calculation of the indicators of publication bias, were performed with MetaWin 2.0 (Rosenberg, Adams & Gurevitch, 2000).

IV. CHARACTERISTICS OF LITTERBAG STUDIES

Our literature survey embraced 58 publications which investigated the effects of microarthropods on terrestrial decomposition using litterbags. Of these, only 30 satisfied our criteria for inclusion in the meta-analysis. These papers report a total of 101 litterbag experiments (Table 1). Many papers exhibited methodological shortcomings, gave incomplete information or were not directly concerned with the quantification of decomposition. We omitted studies from our analysis based on the following reasons:

(1) In approximately 5% of all studies, litterbags were used in laboratory microcosms or in pots inside greenhouses, for example, Setälä, Marshall & Trofymow (1996) and Förster *et al.* (1996), and did not relate to the role of microarthropods under field conditions.
(2) Approximately 9% of all papers reported the use of meshes of unsuitable size to exclude microarthropods. For example, Reddy & Venkataiah (1989) and Yamashita & Takeda (1989) applied mesh sizes of 1.0

Table 1. Papers investigating the effects of microarthropods on terrestrial decomposition with litterbags, that were included in the meta-analysis. *n*(exp), number of experiments reported in paper; *n*(dates), number of sampling dates; *n*(bags), number of litterbags used; duration, time of litter exposure (days); excl. techn., exclusion technique of microarthropods (ins, exclusion by insecticide; mesh, exclusion by graded mesh); mesh size, mesh size used for microarthropod exclusion (μm); climate type, ten main climatic zones defined by Walter & Lieth (1960-67) (I, equatorial ever-wet zone or two periods of rain, frost-free, temperatures mostly above 20 °C, low seasonal temperature course; II, tropical and subtropical area of summer rain, cooler dry period; III, arid subtropical desert zone, occasional radiation frosts; IV, area of winter rain, not completely frost-free, but no distinct cold season; V, warm temperate ever-wet zone, with significant seasonal temperature course, but only occasional frosts; VI, temperate humid zone, with distinct, but not very long cold season; VII, temperate arid zone, with hot summers and cold winters; VIII, boreal zone with very long cold season, mean monthly temperature of the warmest month above 10 °C; IX, arctic area, at most with brief frost-free season, warmest month below 10 °C; X, mountain climate amidst the above-mentioned climatic zones, individually very different); land use, land use type of experimental site (broad-leaved forest, grassland, agriculture, other); litter type, material confined in litterbags (leaves, herbs, straw, roots, cellulose, other). NA, not applicable; ND, no data available.

References in chronological order of publication	n(exp)	n(dates)	n(bags)	Duration	Excl. techn.	Mesh size	Climate type	Land use	Litter type
Witkamp & Crossley (1966)	1	35	35	330	ins	NA	V	broad-leaved forest	leaves
Curry (1969)	2	6	24	284	mesh	500	VI	grassland	herbs
Williams & Wiegert (1971)	2	3	24	365	ins	NA	V	grassland	herbs
Wood (1971)	6	4	12	605	mesh	500	IV	broad-leafed forest, grassland	leaves
Anderson (1973)	5	11	44	335	mesh	1000	VI	broad-leaved forest	leaves
Santos & Whitford (1981)	2	5	25	30	ins	NA	VII	other	other
Santos *et al.* (1981)	1	2	ND	80	ins	NA	VII	other	other
Broadbent & Tomlin (1982)	6	5	40	70	mesh	700	VI	agriculture	herbs
Douce & Crossley (1982)	3	9	36	420	ins	ND	IX	grassland	herbs
Elkins & Whitford (1982)	1	4	24	365	ins	NA	VII	broad-leaved forest	leaves
Seastedt & Crossley (1983)	2	12	60	364	ins	NA	V	broad-leaved forest	leaves
Parker *et al.* (1984)	2	4	12	96	ins	NA	VII	grassland	leaves, roots
Jensen (1985)	1	5	150	130	mesh	500	VI	agriculture	straw
House & Stinner (1987)	3	4	12	110	mesh	1000	V	agriculture	herbs
Schell-Bringmann (1987)	4	4	20	180	mesh	1140	VI	other	herbs, other
Beck (1989)	1	23	46	1500	mesh	200	VI	broad-leaved forest	leaves
Hopkins *et al.* (1990)	2	5	15	180	mesh	1000	VI	grassland	cellulose
Potter *et al.* (1990)	1	5	25	700	mesh	1200	VI	grassland	other
Blair *et al.* (1992)	2	7	28	351	ins	NA	V	broad-leaved forest	other
Heisler (1994)	4	5	20	270	mesh	125	VI	agriculture	straw
MacKay *et al.* (1994)	1	3	45	150	ins	NA	VII	other	tree leaves
Wise & Schaefer (1994)	5	7	42	494	mesh	1000	VI	broad-leaved forest	leaves, herbs
Siedentop (1995)	4	2	14	166	mesh	1300	VII	agriculture	leaves, straw, cellulose
Judas et al. (1995)	6	13	39	340	mesh	1000	VI	broad-leaved forest	roots
Vreeken-Buijs & Brussaard (1996)	1	5	60	365	mesh	1500	VI	agriculture	straw
Heneghan *et al.* (1998)	3	8	48	250	ins	NA	I, II, V	broad-leaved forest	leaves
Tian *et al.* (1998)	7	5	20	194	mesh	500	I, II, V	broad-leaved forest, agriculture, other	leaves
Heneghan *et al.* (1999)	3	10	60	280	ins	NA	I	broad-leaved forest	leaves
Höfer *et al.* (2001)	8	6	60	365	mesh	250	I	broad-leaved forest	leaves
Smith & Bradford (2003)	12	2	10	60	mesh	2000	VI	grassland	herbs

and 0.5 mm. Since the lower body size limit of microarthropods is about 0.2 mm, we rejected these studies from our analysis. We included those studies that applied insecticides to kill microarthropods inside the litterbags when an appropriate mesh size (≈1 mm) was used to allow access of mesofauna, but exclude macrofauna. Experiments with larger mesh were included only when macro- or megafauna were reported absent from the study site by the authors.

(3) Approximately 5% of all studies reported loss of variables other than mass (for example, nutrients) or some other measure of decomposition (e.g. Seastedt & Crossley 1980; Scholle *et al.* 1993).

(4) Approximately 9% of all papers reported the collection of litterbags only at the end of the exposure period (e.g. Herlitzius, 1983a, 1983b; Tingle & Grant, 1995). We did not consider these since time series with two dates (initial mass at exposure, remaining mass at

collection) fail to permit the determination of the standard error of the fitted exponential decomposition model.

(5) In a considerable number of papers (20%), the reported experimental procedure was ambiguous or seemed dubious, and important details were not given (e.g. the number of replicate litterbags or plots per treatment). In some cases, results were not fully published. Although we tried to draw the missing information from parallel studies, or we contacted the authors for assistance, a number of otherwise adequate papers, however, could not be sufficiently reconstructed and were excluded from the analysis.

The following subsections characterize the studies included in our meta-analysis and identify knowledge gaps and methodological biases of litterbag exclusion experiments. Although this refers to only a subset of all litterbag studies performed, we believe we have provided a reliable and extensive overview of relevant studies appearing in peer-reviewed publications during the last half century.

(1) Temporal dynamics of litterbag studies

Despite the availability of alternative methods such as litter cages, mesocosm studies, and N- and C-isotope studies, litterbags are still frequently used. We observed an approximately linear increase in published experiments over time (Fig. 1A), which, however, marginally fails to reach significance (regression of number of experiments per pentad on publication year: $d.f. = 7$, $P = 0.06$, $R^2 = 0.38$). This relationship may be due to the highly fluctuating number of publications per pentad and to the fact that some early litterbag experiments were excluded from the analysis since they did not specifically focus on microarthropods but on the soil fauna in general (e.g. Bocock, 1962; Edwards & Heath, 1963).

(2) Characteristics of experimental protocol

Litterbag experiments are typically short term: 80% lasted one year or less (Fig. 1B). Only four experiments with durations of 2.5 and 4 years (Anderson 1973; Beck 1989, respectively) were regarded as long-term studies. Furthermore, a linear regression of study duration on publication year revealed that experiments became shorter in time with a slope of -9.112 ($P < 0.001$).

Litterbag experiments are performed with little effort: 40% of all experiments used less than 20 bags per treatment (Fig. 1C). The mean number of bags per study was constant over time as analysed by a linear regression of number of bags per publication year (slope $= -0.086$; $P = 0.70$).

The number of sampling dates is generally low: in more than half of the experiments, bags were recollected on five occasions or less (Fig. 1D). This renders the studies' results doubtful, since the estimation of the parameters of the function becomes less reliable when fewer data points are available to fit the function. Similar to experimental duration, the number of sampling dates also decreased over the years (slope $= -0.17$; $P < 0.001$). Thus, although litterbag experiments are low-technology and inexpensive, the effort invested by researchers becomes less over time.

Duration of experiments, number of sampling dates and number of replicate bags are only loosely correlated. In the longer-lasting experiments, researchers tend to collect bags at more sampling dates ($r = 0.63$; $P > 0.001$), however the number of bags used only correlates weakly with duration ($r = 0.46$; $P > 0.001$). The most extreme cases are Beck (1989), who used two bags per date (46 bags per treatment in a four year study with 23 sampling dates), and Jensen (1985), who exposed 30 replicate bags per date (150 bags in a four month experiment with five sampling dates).

In 77% of the experiments, microarthropods were kept out of the control bags by the use of fine mesh. In the remaining 23% of the experiments, naphthalene was applied to establish a microarthropod-free control, under the assumption that this insecticide repels arthropods and has no side effects on microbial decomposition (but see Section VII).

Fine mesh size used for microarthropod exclusion ranged typically between 20 and 100 μm. To include microarthropods and exclude larger soil biota, the most common mesh sizes were 0.5 and 1 mm (Fig. 1E), but meshes ranged from 25 to 2000 μm. This variability is surprisingly high. Unfortunately, the authors almost never explain the reasons for choosing their netting. We suspect that the choice of a specific mesh size is initially determined by the availability of appropriate netting material. Prior knowledge of the local soil mesofauna may also guide the choice. The convenient mesh size for a given site depends on whether the microarthropod community is predominantly composed of small (for example, astigmatic mites) or larger (within the size limits of mesofauna) species.

The mesh size increased linearly and significantly with time (regression of mesh on publication year, slope $= 17.9$; $P = 0.003$).

The type of organic matter most commonly used in litterbag studies is tree leaf and herbaceous litter (Fig. 1F). Other types of material (roots, woody material, straw, etc.) were seldom investigated, with no more than seven experiments for any individual material type.

(3) Climatic zones

Among the ten major climatic zones defined by Walter & Lieth (1960–1967), we observed a strong bias towards studies in the temperate humid zone with distinct warm and cold seasons. These amounted to 50% of all experiments (Fig. 1G). This fact might simply reflect the geographic location of the majority of research institutions in temperate Europe and North America. Second to the temperate areas were the studies performed in the wet tropics (17% of experiments), which can be explained in part by the high level of biological interest in this region. Studies in other climatic zones are limited; no studies are available from either the arid subtropical desert zone or the boreal zone with its very long cold season. An analysis of the temporal dynamics of this climatic bias reveals that the interest in tropical and subtropical studies is more recent, whereas the

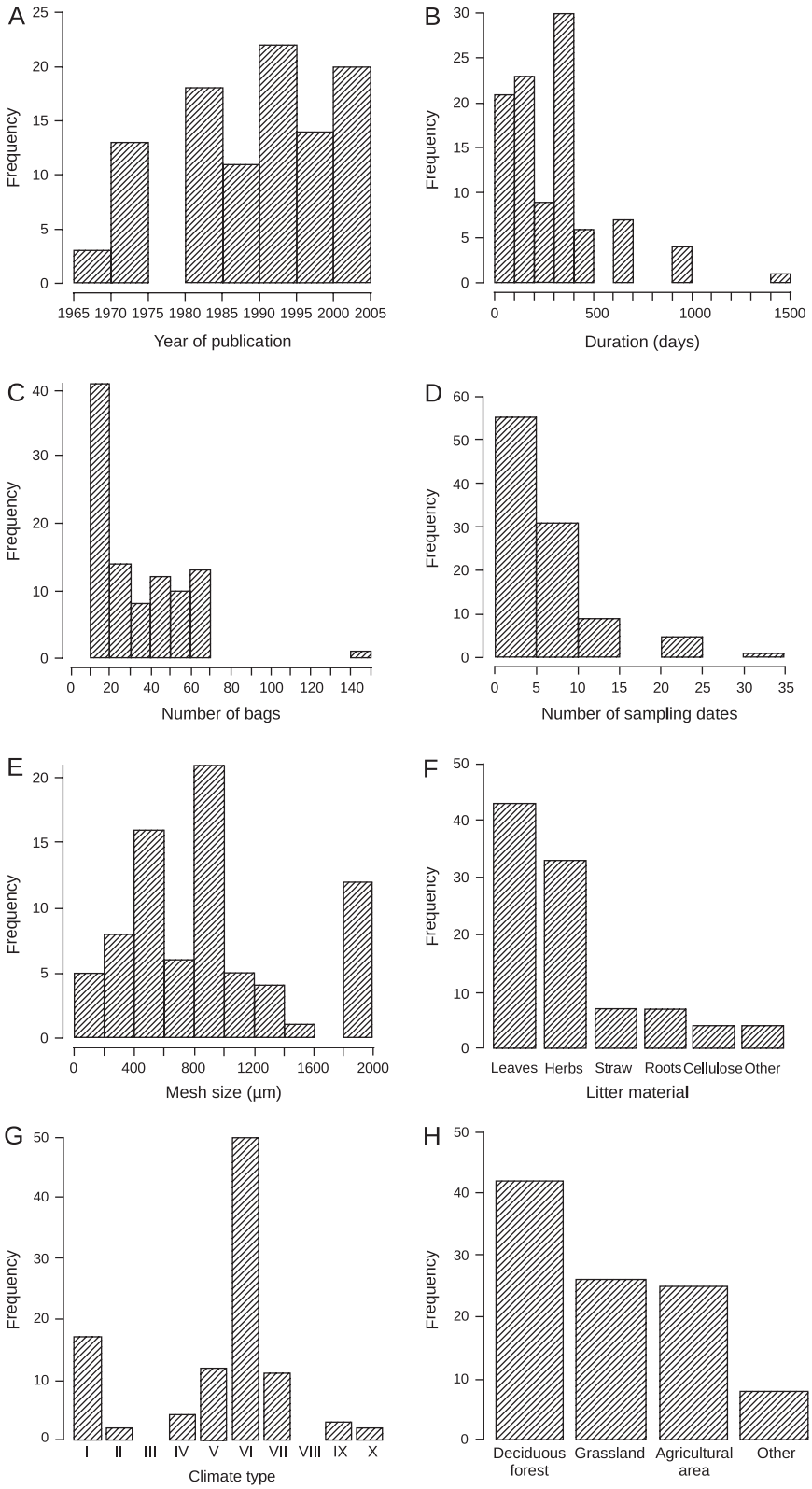

Fig. 1. Frequency distributions of characteristics of litterbag experiments. (A) Number of litterbag experiments published between 1965 and 2005; (B) duration of experiments; (C) number of litterbags per treatment; (D) number of sampling dates; (E) mesh size used for macrofauna exclusion; (F) litter materials exposed in litterbags; (G) frequencies of experiments in the ten main climatic zones defined by Walter & Lieth (1960–67) (see Table 1 for definition of zones); (H) frequency of litterbag experiments in various land use systems.

temperate humid zone – and, to a lesser extent, the warm temperate ever-wet zone and the temperate arid zone – were studied continuously throughout the history of litterbag experiments (Fig. 2).

(4) Land use systems

Deciduous forests (including managed, as well as pristine, forests) have received most attention by soil zoologists (Fig. 1H) accounting for >40% of all litterbag experiments (Table 1). Grasslands and agricultural areas are represented in 25% of experiments each. It is noteworthy that not a single study in coniferous forest has entered our database. This observation coincides with the lack of experiments in the boreal zone.

(5) Interactions among study parameters

Most characteristics of litterbag studies co-vary with each other. For example, the technique of exclusion determines to a large extent the study effort. In insecticide experiments, a significantly larger number of litterbags ($m = 36$) was used than in experiments with graded mesh size ($m = 21$, $U = 1014$, $P = 0.045$); also the number of sampling dates tended to be larger in insecticide experiments ($m_{\text{insecticide}} = 8$, $m_{\text{graded mesh}} = 5$, $U = 1106.5$, $P = 0.087$). By contrast, there was no difference in study duration between studies applying different microarthropod exclusion techniques ($m_{\text{insecticide}} = 310$ d, $m_{\text{graded mesh}} = 270$ d, $U = 845$, $P = 0.701$). While in graded mesh experiments all types of land use and organic materials are represented, in 12 of the 21 insecticide studies, tree leaves were used and exposed in deciduous forest. Most of the insecticide experiments were performed in climate zones V (warm temperate ever-wet) and VII (temperate arid), while the majority of graded mesh experiments took place in zones I (ever-wet tropics) and VI (temperate humid).

Associated with decreasing experimental effort and increasing mesh size from the 1960s to present, mesh size was negatively correlated with parameters characterizing experimental effort in graded mesh experiments (experimental duration: $r = -0.41$, $P > 0.001$; number of litterbags: $r = -0.46$, $P < 0.001$; number of sampling dates $r = -0.24$, $P = 0.037$).

The choice of organic material exposed was greatly influenced by the type of land use in the study area. In deciduous forests, 32 of 42 experiments used tree leaves, while in grasslands litterbags contained herbaceous litter in19 of 26 experiments. Also, climatic zone and type of organic material are not consistently represented in the dataset: the only material used under almost all climatic conditions was tree leaves, while the only climatic zone in which a broad range of materials was used was the temperate humid zone.

Studies within deciduous forests were distributed among six of the ten climatic zones; experiments in grasslands showed a distinct bias towards the temperate zone (65% of all grassland experiments) whereas no litterbag studies were concerned with tropical and subtropical grasslands.

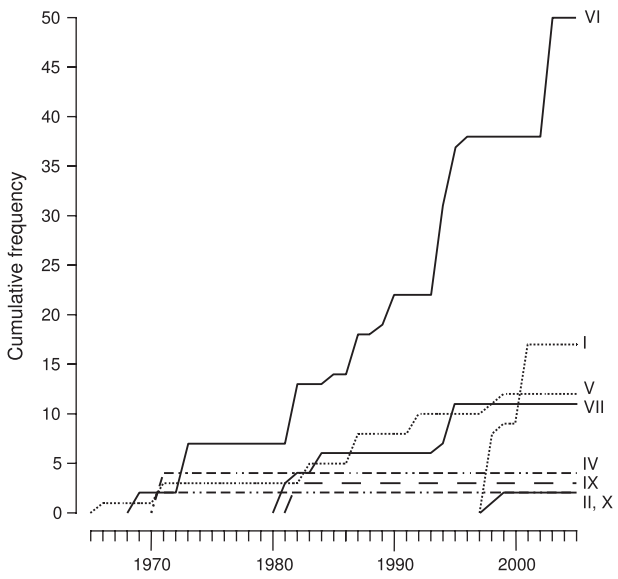

Fig. 2. Temporal dynamics of publications of litterbag studies in the ten main climatic zones defined by Walter & Lieth (1960–67) (see Table 1 definition of zones).

V. PUBLICATION BIAS IN LITTERBAG STUDIES

Rank correlations between E^* and n did not indicate publication bias (Kendall's $\tau = 0.018$, $P = 0.787$; Spearman's $r = 0.049$, $P = 0.628$). Failsafe numbers (Rosenthal's $N_R = 9721.8$; Orwin's $N_O = 351.1$) and the normal quantile plot (not shown) also yielded no hints of a publication bias. At first sight this seems surprising, contradicting our earlier reasoning. This may be a result of the large proportion of studies that not only reported on microarthropod effects, but included a third treatment with coarse netting which allowed access of macrofauna to the exposed litter. This treatment rendered fauna effects significant in almost all studies. It is likely that a considerable number of studies reporting nonsignificant or even negative effects of microarthropods would not have been published without the accompanying "successful" macrofauna treatment. Thus, we consider the results of the meta-analysis a real and unbiased estimate of the impact of microarthropods on terrestrial decomposition.

VI. THE EFFECT OF MICROARTHROPODS ON LITTER DECOMPOSITION

The cumulative effect size, E_{cum}, across all experiments amounted to 1.48 ($P < 0.05$). In other words, microarthropods exercise a moderate but significant effect on mass loss (Fig. 3). Total heterogeneity is very high ($Q_T = 163$, $P < 0.001$), indicating that the variance among effect sizes is greater than expected by sampling error. The set of effect sizes is not homogeneous and other explanatory

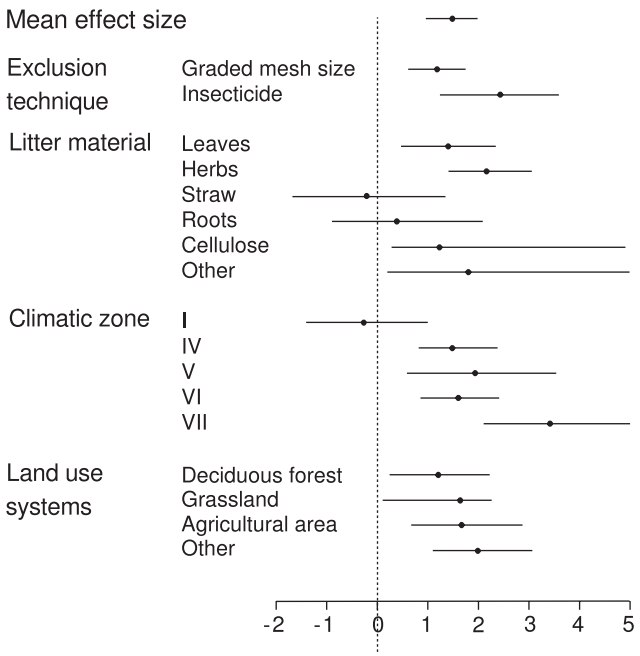

Fig. 3. Effect sizes and bootstrapped 95% confidence intervals for various categories of litterbag studies. See Table 1 for definition of climatic zones. Climatic zones II, IX and X were excluded from analysis due to low replication number (see Fig. 2).

variables must be investigated. This is not surprising since the litterbag studies stem from a huge variety of climatic zones and land use types and differ in various parameters of the experimental protocol (see Section IV). In this section, we analyse more closely the relationships among effect sizes and parameters of experimental protocol, climate and land use types.

(1) Temporal dynamics of the cumulative effect size

We regressed effect sizes on publication year and obtained a highly significant slope of -0.089 ($P < 0.001$) (Fig. 4). In other words, the effect of microarthropods on terrestrial decomposition has been decreasing during the last 40 years. We interpret this paradoxical result in two ways. First, soil zoologists may have initially studied "promising" sites with a higher *a priori* probability of positive mesofauna effects on litter mass loss, guided by earlier experiments or field studies. Second, the eagerness of soil zoologists to corroborate the ecological importance of soil fauna may have caused a submission bias during the 1960s, 1970s and 1980s, as non-supporting results were hidden in the grey literature (unpublished theses or project reports) or not published at all. Negative mesofauna effects tend to appear in the dataset from the mid-1990s onward (Fig. 4). Thus, in the most recent work, soil zoologists tended to be less biased, either in the choice of their study sites or in the submission of results or both. This simple analysis demonstrates that we are still far from obtaining a reliable

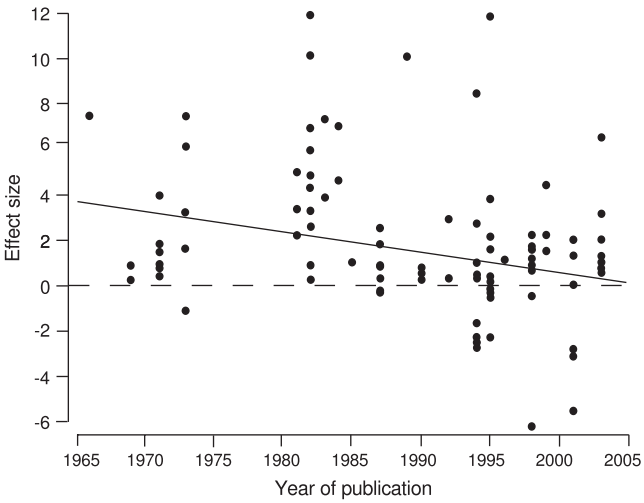

Fig. 4. Linear regression of effect size on publication year of litterbag experiments.

estimation of the real mean effect of microarthropods on decomposition across substrates, land use systems and climatic zones.

(2) Dependence of the effect size on the experimental protocol

Effect size did not depend on the number of litterbags used (slope = 0.0055; $P = 0.58$). The outcome of any particular study, however, tended to be related to experimental duration: a linear regression is close to statistical significance ($P = 0.055$) with a slope of 0.0018 (Fig. 5). The residuals are not distributed randomly around the regression line; there is a considerable lack of studies with negative effect sizes (that is, microarthropods retard litter mass loss)

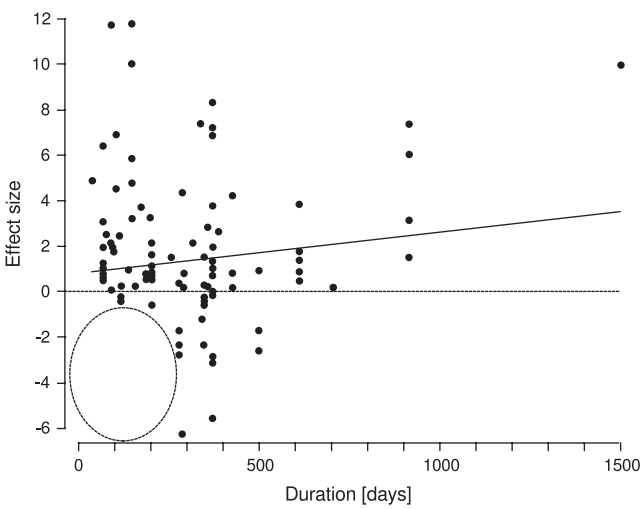

Fig. 5. Linear regression of effect size on experimental duration of litterbag experiments. The ellipsis highlights the lack of studies with negative effect sizes in short term studies (< 250 days).

in short-term studies (< 250 days). On the one hand, this might indicate a publication bias – short term studies with "negative" results tend not to be published. On the other hand, the observed gap may be due to the fact that the studies come from multiple statistical populations (see Section VI.4).

There was a discernable difference between the mean effect sizes of the graded mesh and the insecticide technique (Fig. 3). Although their confidence intervals overlapped, the effect of insecticide experiments tended to be double the mean graded mesh effect (2.45 *versus* 1.19). This might indicate that naphthalene not only affects microarthropods, but microflora and microfauna as well.

Mesh size had a weak (slope = 0.0008) statistically insignificant influence ($P = 0.09$) on effect size. Thus, the high variability of mesh sizes used by the various authors did not systematically affect the role of microarthropods in litter mass loss.

Microarthropods exerted a significant effect on mass loss in the decomposition of tree leaves, herbaceous litter, cellulose and the category "other materials", with herbaceous litter showing the highest effect sizes (Fig. 3). The confidence intervals of straw and roots, on the contrary, include zero and indicate no effect of microarthropods on mass loss. This contradicts common wisdom which assumes that microarthropods exert their major influence/importance in the decomposition of recalcitrant litters by causing it to become more accessible to microbial attack [for example, Dunger (1983), Coleman *et al.* (2004)]. The opposite seems to be true. Highest single effect sizes, for example, were found for herbaceous litter ($d = 11.87$; Broadbent & Tomlin, 1982) and cellulose ($d = 11.8$; Siedentop, 1995), while straw ($d = -2.78$; Heisler, 1994) and recalcitrant tree leaves (beech: $d = -2.60$; Wise & Schaefer, 1994) even attained negative effect sizes, that is, microarthropods retarded mass loss considerably.

(3) Dependence of the effect size on climate and land use type

The mean effect size in the wet tropics was close to zero (−0.26) and significantly lower than the mean effect size in the temperate arid zone (3.44) (Fig. 3). The mean effect sizes of all other climatic zones in the dataset were significantly different from zero. They varied narrowly between 1.49 and 1.95 with exception of the arid temperate zone with hot summers and cold winters whose mean effect size was close to 3.5.

Mean effect sizes of all land use types were significantly different from zero with almost identical effects in agricultural fields and grassland systems (Fig. 3).

(4) Dependence of the effect size on interactions among study parameters

Due to the various interactions among study parameters (see Section IV.5), the interpretation of our results is not simple and straightforward. For example, the remarkable temporal dynamics of cumulative effect size (Fig. 4) can be explained by the shift of research attention given to the various climatic zones (Fig. 2) and the organic material exposed in litterbags. Early studies of herbaceous litter with high effect sizes (for example, Anderson, 1973; Broadbent & Tomlin, 1982), together with the late initiation of studies in the wet tropics (Heneghan *et al.*, 1998, 1999; Höfer *et al.*, 2001) showing distinctly lower effect sizes than experiments from other climatic zones (Fig. 3), contribute to the negative slope of the regression of effect size on publication year.

In a plot of effect size *versus* experimental duration, a gap at low values becomes apparent (Fig. 5) which is caused by the interaction of study parameters rather than publication bias. Microarthropods had a pronounced impact on the mass loss of easily decomposable material such as herbaceous litter. Naturally, since experimental duration is closely related to decomposition rate, the median duration of studies using quickly degraded herbaceous litter ($m = 110$) was significantly lower than that of more recalcitrant tree leaves ($m = 365$, $U = 232$, $P < 0.001$). Accordingly, a considerable proportion of data points to the left of Fig. 5 represents short-term experiments with herb litter and positive microarthropod effects.

The interaction between organic material and climate – those study parameters that showed the most pronounced differences among classes (Fig. 3) – could not be analysed due to the non-balanced distribution of exposed litter types among climate zones. The low effect sizes in the tropics most probably were not an artefact of biased litter choice; tree leaves (main litter material used in studies in the tropics) showed contrasting, although not statistically different, microarthropod effects between the ever-wet tropics [$E_{cum,tropics} = -0.30$, 95% confidence interval = (−1.70, 0.95)] and the humid temperate zone [$E_{cum,temperate} = 2.52$, 95% confidence interval = (0.10, 5.17)].

VII. A CRITIQUE OF LITTERBAGS

(1) Microarthropod effect or hidden treatment effect?

Since the first reports of litterbag data, caveats on the adequacy of the approach for quantifying decomposition have been published, for example with reference to different decomposition rates (Bocock & Gilbert, 1957) and divergent microclimatic conditions in bagged *versus* unconfined litter (Witkamp & Olson, 1963), or on the loss of fragmented but not decomposed litter which affects the estimation of decay rates (Parker *et al.*, 1984). While these studies argued for representative decomposition in the litterbag interiors, a number of reports indicated differences due to mesh size. For example, St. John (1980) found different abundances of vegetative fungal structures in fine and coarse mesh litterbags, while Lousier & Parkinson (1976) noted different amounts of moisture. Bocock (1962) had previously pointed out that conditions in all nettings must be identical in order to compare treatments legitimately with and without soil fauna; his message, however, has largely been ignored during the long history of graded mesh litterbag studies.

Although there is evidence from some studies that naphthalene affects microbial activity (Seastedt & Crossley, 1983; Blair, Crossley & Rider, 1989) this has never been taken seriously by researchers applying this technique (apart from occasional warnings about the validity of the results).

That different mesh sizes (fine *versus* coarse) or different chemical treatments (insecticide application *versus* none) affect decomposition differently regardless of microarthropod presence has almost never been taken into account when interpreting litterbag results. In fact, the difference between the decomposition rate in the controls, k_C, and the microarthropod treatment, k_T, is not a purely microarthropod effect, k_M, as presented in Section III.3, but is the additive effect of the differential mesh size effect, k_{mesh} (or the differential insecticide effect, $k_{insecticide}$, respectively), and the "true" microarthropod effect, k_{TM}. Thus, we consider the formula

$$k_T = k_C + k_{mesh} + k_{TM} \quad (7)$$

for graded mesh studies, and

$$k_T = k_C + k_{insecticide} + k_{TM} \quad (8)$$

for insecticide studies. However, without an additional control for the mesh or the insecticide effect, the relative contributions of mesh or insecticide treatment and microarthropods remain completely unknown.

We are aware of only two studies which tested for the effect of different mesh size on mass loss (Siedentop, 1995; Bradford *et al.*, 2002), both performed without the presence of microarthropods. They report differential mesh size effects between −4.6% (coarse mesh size slightly retards decomposition) and 69.2% (coarse mesh size drastically enhances decomposition), with an average of approximately 25% ($\bar{x} = 26.5$, *S.E.* = 9.9; *n* of experiments reported = 8). Explanations for this could be (1) that coarser mesh bags are more exposed to leaching and, thus, to mass loss (Anderson, 1973) especially in the early phases of a litterbag study, (2) that finer mesh slows initial microbial litter colonization (Wise & Schaefer, 1994), and (3) that different microclimatic conditions affect the contribution of microflora and microfauna to decomposition. Siedentop (1995) found a moisture increase in bags with fine mesh of up to 25% in the field and 48% in the laboratory, a result similar to those reported by Curry (1969) and Lousier & Parkinson (1976). It is possible that the better aeration of litter confined in coarse netting promotes microbial decomposition unless exposed to very dry conditions. The mean effect sizes were significantly larger than zero in all climatic zones with the exception of the wet tropics (Fig. 3): whereas in other climatic zones a coarse net permits better aeration and loss of excess humidity thus accelerating decomposition, the extremely wet conditions in the equatorial tropics inhibit this beneficial effect.

In summary, a considerable proportion of increased mass loss in the presence of microarthropods may be due to the differential mesh size effect, resulting in overestimation of the microarthropod effect. This is a major flaw of the method and the results of 40 years of litterbag studies must be rigorously scrutinized. Similarly, in studies applying the insecticide approach the mean effect size (Figure 3) was larger than that in graded mesh studies, suggesting that naphthalene has considerable additional effects on microflora, leading to overestimation of the role of microarthropods.

(2) The effect of microarthropods on litter decomposition revisited

Since the "apparent" microarthropod contribution to decomposition, k_M, is the sum of the mesh size effect, k_{mesh}, and the true microarthropod effect, k_{TM}, we subtracted k_{mesh} from the treatment effect, k_T, and ran the meta-analysis again including graded mesh studies only. For a study reporting $|k_C| = 0.1$ and $|k_T| = 0.2$, for example, we subtracted $|k_{mesh}| = 0.025$, corresponding to 25% of $|k_C|$ as based on the mean mesh size effect derived from Siedentop (1995) and Bradford *et al.* (2002), from $|k_T|$, yielding $|k_{T\text{-}mesh}| = 0.175$. While the difference $|k_C| - |k_T| = k_M = 0.1$ gives the apparent microarthropod effect, $|k_C| - |k_{T\text{-}mesh}| = k_{TM} = 0.075$ is an estimate of the true microarthropod effect.

Taking into account the pure mesh size effect in this way has a dramatic consequence for the meta-analysis: the cumulative effect size, E_{cum}, across all graded mesh experiments decreases from 1.19 ($P < 0.05$) (Fig. 3) to −0.81 ($P < 0.05$) indicating that microarthropods no longer exert a positive effect on litter decomposition rate but actually have a negative effect, provided that the estimation of k_{mesh} by Siedentop (1995) and Bradford *et al.* (2002) holds for all studies. A mesh effect of only 7% would be sufficient to render the cumulative effect size non significant; a mesh effect of 20% or higher turns the significantly positive microarthropod effect into a significantly negative one. However, we do not seek to replace one piece of conventional wisdom ("microarthropods affect decomposition positively") with another ("microarthropods have a negative effect") based on only two studies of mesh size effect, since we expect there to be interactions between the mesh size effect and study parameters such as type of organic matter exposed, land use type or climatic zone. Consequently, there is a clear need for more data on the influence of mesh size *per se*. We are deeply concerned by the fact that during 40 years of litterbag studies the relative contributions of the mesh size effect and the completely unknown insecticide effect to litter weight loss have been almost completely ignored. In consequence, we cannot supply even a tentative estimation of the real role of microarthropods in terrestrial decomposition.

VIII. CONCLUSIONS

(1) Litterbag studies enjoy great popularity in soil biological research with the number of published experiments continually increasing. A large proportion of these papers, however, suffer from considerable shortcomings, for example, incomplete information on experimental design, incomplete presentation of results, and a mixture of analytical

protocols that render much of the data almost incomparable. We propose, therefore, the adoption of a generally accepted standard of experimental and analytical protocol (number of sampling dates and number of replicate bags to be used, which results should be reported and how they should be presented, how decomposition models should be fitted and their statistical parameters reported) in order to facilitate comparative studies and future research synthesis (A. Bruckner and C. Kampichler, in preparation).

(2) We identified major biases in the data with regard to land use type and climatic zone of the experimental areas, and the type of organic matter exposed. These may have resulted in a biased estimation of the role of microarthropods in litter breakdown. We suggest that future studies complement the existing database by concentrating on tropical and subtropical regions, the boreal zone, arctic regions and with mountain climates instead of adding to the mass of data from temperate climates. Organic matter other than tree leaves and herbaceous litter (for example, roots and twigs) is heavily underrepresented in existing studies, a criticism raised previously by Seastedt (1984).

(3) Tests of publication bias failed to reach statistical significance. We did, however, find an interesting inverse relationship between effect size and publication year, indicating that earlier soil zoologists may have chosen their study sites according to expectations of the importance of microarthropods. We do not wish to argue for random selection of study areas. However, if we are interested in revealing the true role of microarthropods, we must not delimit the range of study sites to the ''promising'' ones.

(4) According to the 101 experiments from 30 papers that entered our database, microarthropods have a modest but significant positive effect on mass loss in litterbags. Effect size varied between different litter materials, land use types and climatic zones, with the highest contribution to mass loss observed for herbaceous litter and in the arid temperate zone.

(5) In only one (Siedentop 1995) of these papers was there an attempt to control for the effect of mesh size. Data obtained by Siedentop (1995) and Bradford *et al.* (2002) indicate a considerable positive effect (25%) of coarse mesh size on litter mass loss. When the mesh size effect is taken into account, a meta-analysis yields a contrasting result: microarthropods have no effect or even a negative effect on mass loss in litterbags. Even a mesh size effect as low as 7% would be enough to nullify the significant microarthropod effect. Thus, the hypothesis that microarthropods have a positive effect on litter mass loss, seems doubtful and cannot be corroborated by the data.

(6) Even after 40 years of litterbag studies we still need more information on the effects of mesh size and insecticide treatment and how these effects depend on litter material, climatic conditions and land use type. Thus we suggest including three treatments in future experiments: fine mesh/without animals, coarse net/without animals, and coarse net/with animals for of the graded mesh approach; insecticide/without animals, no insecticide/without animals and no insecticide/with animals for of the insecticide approach. The inclusion of a third treatment may render litterbag studies more complicated, imply additional costs and even require parallel laboratory experiments; it is, however, a feasible method to retain litterbags as meaningful aids to the study of soil biology.

IX. ACKNOWLEDGEMENTS

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