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Millipedes as Model Detritivores

by

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A b s t r a c t : This paper asks to what extent millipedes can be considered model macrodetritivores — consumers of dead organic matter that exceed 10 mm in length and range between 2 mm and 20 mm in width. Evidence is examined from evolutionary and ecological perspectives. The persistent fossil record of the Diplopoda since perhaps the Late Ordovician strongly supports their representation of the macrodetritivore guild. Moderate or variable support for the concept comes from comparisons of 1) published biomass values of macrodetritivores in tropical and temperate ecosystems and 2) food selection patterns and life history strategies within the guild. Comparisons of habitat selection and climate-related seasonal activity provide more modest support. Application of the concept is limited in arid regions, where millipede diversity is low relative to that of other macrodetritivores.

1. Introduction:

Millipedes are important members of the soil and litter fauna in temperate and tropical parts of the world, where they and other invertebrates aid in the breakdown of plant organic matter. Their general role in this process has been recognized since the early decades of this century (BLOWER 1955); more recent studies have emphasized the interactions of these animals with microorganisms directly responsible for decomposition (ANDERSON et al. 1985, ANDERSON 1987).

This paper focuses on whether millipedes can be viewed as functional representatives, or "models," of that portion of the decomposer fauna they approximate in feeding behavior and body size, two descriptors of what I will call the "macrodetritivore guild." The question, of course, has no simple answer — in part because of obvious biological differences among the higher taxa involved, but also because the collective ecological effects of these organisms vary with location and assemblage composition (EDWARDS 1974). Despite that, I contend that any attempt to scrutinize the Diplopoda in a comparative ecological context adds to our grasp of their relative ecological roles. Hence this review.

2. Definitions:

Various expressions describe dead organic matter and the relatively omnivorous animals that consume it. "Litter" commonly applies to the uppermost layer of decaying organic matter in terrestrial ecosystems. "Detritus" is a more general term that describes freshly dead or partly decomposed organic material (RICKLEFS 1990). "Detritivores" are animals that feed on detritus (BEGON et al. 1986); many authors call them "saprovores" or "saprotrophs." The prefix, "sapro," refers to decay, while the suffix, "troph," implies no particular method of food utilization. "Vore," on the other hand, refers to food ingestion by animals (SWIFT et al. 1979). Some authors, e.g. LA-MOTTE (1989), separate these animals into "saprophages" and "geophages," depending on whether they eat mainly surface material or soil. In this paper I refer to millipedes and animals with broadly similar ecological roles as "detritivores."

Invertebrate faunas associated with soil have been variously classified by length and/or width (WALLWORK 1970, SWIFT et al. 1979, ANDERSON 1987) into "micro," "meso" and "macro" categories. Groups of these organisms whose adult lengths exceed 10 mm and whose widths range between 2 mm and 20 mm are termed "macrofauna;" those that typically consume dead organic matter I call "macrodetritivores." Moreover, I consider them to be a "guild" (see HAWKINS & MACMAHON 1989) because they use the same class of environmental resources in the same general way.

The guild includes some apterygote insects such as thysanurans, also some termites, most land molluscs, amphipods, isopods, earthworms and millipedes, and detritivorous orthopteroid insects such as cockroaches and crickets. Larvae of dipterans (e.g. tipulids) and larvae as well as adults of many coleopterans such as scarabaeids and tenebrionids also frequently fit this category. So, it can be argued, do some species of ants.

3. Macrodetritivore Evolution:

Millipedes were among the first groups of terrestrial macrodetritivores (Tab. 1). Fossil burrows may have been excavated by millipedes in Late Ordovician soils (RETALLACK & FEAKES 1987). Fossil remains of *Archidesmus*, a myriapod-like arthropod from the Late Silurian and Early Devonian, have been reported by BERGSTROM (1978), whose partial description of yet another possible myriapod from the Early and Middle Cambrian suggests a marine ancestry for the group (GUPTA 1979).

By the Carboniferous, millipede-like archidiplopods, which may have been amphibious (HOFFMAN 1969), as well as "typical" diplopods (BERGSTROM 1978) were probably significant components of soil and litter invertebrate communities (ROLFE 1985). SOLEM (1985) suggests that Carboniferous forest litter may have been continually moist due to the shade and humidity produced by deciduous leaves of arborescent plants, and that such conditions may have promoted the appearance of certain groups of land snails. Also favored should have been millipedes, some of which had by then evolved body forms similar to those of modern species (KRAUS 1974). This morphological diversity surely reflected the various ways these animals moved through litter and soil, and should have enabled them, along with mites (ROLFE 1985) and other Carboniferous detritivores (Tab. 1), to play an important role in terrestrial decomposition.

One can only speculate as to how the ancient millipedes coped with existing and newly evolving detritivores. Perhaps some groups met extinction after reaching a certain "detritivore saturation level" at a given location, and/or as more modern taxa (Tab. 1) appeared on the scene. Clearly millipedes remained common animals, because today they are represented by up to 80,000 species (HOFFMAN 1979).

4. Millipedes in the Modern World: a Biomass Perspective:

Globally, among macrodetritivores in mesic woodlands and regions characterized by calcareous soils, millipedes now rank somewhat behind earthworms and termites — but probably ahead of other groups — in terms of their contribution to litter breakdown (EDWARDS 1974). This view is illustrated in Tables 2 and 3, which give a sampling of standing crop macrodetritivore biomass (a convenient if not particularly useful measure of ecological importance) from sites in Europe, North America, Southeast Asia and tropical Africa. Because of the scarcity of data relating especially to the biomass of detritivorous Coleoptera and Diptera larvae, the tables are far from complete. However, certain tentative conclusions may be drawn from them, even though the values they show often range greatly in a given habitat.

One conclusion is that millipedes can have greater biomass in temperate ecosystems than in the tropics. Relatively low values in some tropical areas, e.g. Sarawak montane forest (COLLINS

Table 1: Fossil or inferred evidence of sequential appearance and radiation of invertebrate higher taxa dominated by or including terrestrial species of macrodetritivores.

Eras/periods	Evidence	Taxa	Source
Paleozoic			
Late Ordovician	Burrows	Possible Diplopoda	RETALLACK & FEAKES (1987)
Late Silurian/early Devonian	Fossil	*Archidesmus* (Myriapoda)	BERGSTRÖM (1978)
Early Devonian	Fossil	Machiloidea = Archaeognatha	LABANDIERA et al (1988)
Carboniferous	Assumed	Ancestral Coleoptera	LAWRENCE & NEWTON (1982)
Carboniferous	Fossil	Typical Diplopoda	BERGSTRÖM (1978)
Carboniferous	Fossil	Pulmonate Gastropoda	SOLEM (1985)
Upper Carboniferous	Fossil	Blattaria	DURDEN (1969)
Upper Carboniferous	Fossil	Ensiferan Orthoptera	BOUDREAUX (1979)
Permian	Fossil	Coleoptera	CROWSON (1960)
Permian	Fossil	Diptera	OLDROYD (1964)
Mesozoic			
Jurassic	Fossil	Dermaptera	BOUDREAUX (1979)
Jurassic	Fossil	Scarabaeoid Coleoptera	CROWSON (1960)
Jurassic	Fossil	Tipulid-like Diptera	OLDROYD (1964)
Jurassic-Cretaceous	Fossil	Main radiation of Coleoptera	LAWRENCE & NEWTON (1982)
Cretaceous	Assumed	Ancestrial talitrid Amphipoda	FRIEND & RICHARDSON (1986)
Cretaceous	Fossil	Main radiation of Diptera	OLDROYD (1964)
Cretaceous	Assumed	Oligochaeta	EDWARDS & LOFTY (1977)
Cenozoic			
Eocene	Fossil	Talitrid Amphipoda	SCHRAM (1986)
Eocene	Fossil	Isoptera	BOUDREAUX (1979)
Mid-Tertiary	Fossil	Oniscoid Isopoda	SCHRAM (1986)

1980), fail to support the generalization of SWIFT et al. (1979: 115) that macroarthropod biomass is highest in the tropics because "tropical saprotrophic animals (have) larger individual body size(s)" than do their temperate counterparts. Tropical millipedes can in fact be very large, but to my knowledge a causal relationship has not been demonstrated between body size and population or guild biomass in these organisms.

A second conclusion is that millipede biomass may be relatively high in recently disturbed sites. This is especially evident in a southeastern U.S.A. pine plantation (CORNABY 1973), and is also inferred from studies in a cultivated region of Senegal by GILLON & GILLON (1979) (Tab. 3). The pattern is supported by the observation by IATROU & STAMOU (1989) that degraded environments "may favor the presence of Diplopods." However, each type of disturbance appears to have its unique effects; thus, LAVELLE & PASHANASI (1989) found that the originally high biomass of millipedes in a Peruvian Amazonian forest was dramatically reduced by cropping.

A third conclusion drawn from Tables 2 and 3 is that earthworm and termite biomass in the tropics can be comparatively immense — yet in temperate ecosystems earthworm biomass can be even

Table 2: Comparative habitat-specific biomass in non-diplopod terrestrial macrodetritivores. * No distinction is made between live and dry mass values as these are not always evident in literature cited. Also, all values are assumed or stated to be means. ** Values given for EDWARDS (1974) were derived from references given in that source.

Taxa	Habitat/Location	Biomass $[mg/m^2]$ *	Source **
Pulmonata			
Total species	Mixed oak forest/USA	150	CORNABY (1973)
Total species	Plantation pine forest/USA	250	CORNABY (1973)
Oligochaeta			
Earthworms	Old grassland/Netherlands	250000	HOOGERKAMP et al. (1983)
Earthworms	Mesic forests/temperate	8400-84000	SATCHELL (1983)
Earthworms	Mesic forests/tropical	3700	SATCHELL (1983)
Earthworms	Savanna/Ivory Coast	30000	LAMOTTE (1989)
Earthworms	Ridge, Mt.Mulu/Sarawak	728-3117	COLLINS (1980)
Isopoda			
Total species	Grassland-woodland/UK	2.1	EDWARDS (1974)
Total species	Woodland/Denmark	<500	EDWARDS (1974)
Total species	Xero-agroecosystem/Egypt	4-55	GHABBOUR (1983)
Total species	Ridge, Mt.Mulu/Sarawak	25-68	COLLINS (1980)
Isoptera			
Total species	Ridge, Mt.Mulu/Sarawak	89-1769	COLLINS (1980)
Total species	Savanna/Ivory Coast	585	LAMOTTE (1985)
Total species	African savannas	1000-50000	WOOD & SANDS (1978)
Diptera (Larvae)			
Total species	Ridge, Mt.Mulu/Sarawak	13-38	COLLINS (1980)
Total species	Woodland/Denmark	5000-7000	EDWARDS (1974)

greater than it is in the tropics. Where the biomass of one or both groups is relatively high, that of other species such as millipedes is much lower, suggesting a more regulating than energy moving role for the latter in certain decomposer food webs. In general, however, the proportion of millipede biomass in soil and litter in both temperate and tropical ecosystems can be considerable, as was suggested in SWIFT et al. (1979).

5. Resource Use by Macrodetritivores:

The term "resource," as used in this paper, refers specifically to food and habitat. At times, of course, food (e.g. leaf litter) constitutes most or all of the habitat of a detritivore.

5.1. Food Selection:

A wide range of preferred foods, the palatability of which may be altered by microbial action (SAKWA 1974), has been described for tropical and temperate zone millipedes (e.g. LEWIS 1971, STRIGANOVA & PRISHUTOVA 1990). In the tropics, fungi appear to be the primary decomposer organisms (BECK 1971, cited by LEVINGS & WINDSOR 1982), and many other groups of detrital consumers have evolved to feed on them. Thus, according to BECK diplopods in Amazonia are exclusively fungivorous. Also, TAYLOR (1982) has demonstrated fungal preferences in a

Table 3: Comparative habitat-specific biomass in diplopods. * No distinction is made between live and dry mass values as these are not always evident in literature cited. Also, all values are assumed or stated to be means. ** Values listed were derived from references in EDWARDS (1974).

Taxa	Habitat/location	Biomass [mg/m^2] *	Source
Cylindroiulus punctatus	Limestone woods/UK	2–92	BLOWER (1979)
C. punctatus	Limestone slope/Thuringia	183–1756	DUNGER & STEINMETZGER (1981)
Glomeris marginata	Limestone woods/UK	12–1112	BLOWER (1979)
Ophyiulus pilosus	Limestone woods/GB	214–2271	· BLOWER (1979)
Narceus annularis	Wooded slope/USA	2860	SHAW (1968)
Orthoporus ornatus	Desert shrubland/USA	>24	CRAWFORD (1976)
Three species	Alpine habitats/Austria	1742	MEYER (1985)
Total species	Mixed forests/France	250–>1000	GEOFFROY (1979)
Total species	Limestone slope/Thuringia	185–2792	DUNGER & STEINMETZGER (1981)
Total species	Mixed oak forest/USA	35	CORNABY (1973)
Total species	Plantation pine forest/USA	3170	CORNABY (1973)
Total species	Woodland/Denmark	<500–5000	EDWARDS (1974) **
Total species	Savanna/Ivory Coast	316	LAMOTTE (1989)
Total species	Cultivated zone/Senegal	5000	GILLON & GILLON (1979)
Total species	Amazonian forest/Peru	6200±4000	LAVELLE & PASHANASI (1989)
Total species	Ridge, Mt.Mulu/Sarawak	10–276	COLLINS (1980)

North American spirostreptid millipede with tropical congeners, which suggests that preferential feeding on specific fungi may be common among tropical macrodetritivores. In addition, such behavior has been shown experimentally for other members of the temperate region decomposer community (VISSER 1985).

Millipedes have long been known to distinguish between natural food items (e.g. LYFORD 1943, VAN DER DRIFT 1965), as have other macrodetritivores. This occurs for example in litter-feeding isopods (WARBURG 1987) (but apparently not in terrestrial amphipods (FRIEND & RICHARDSON 1986)), in earthworms (SATCHELL 1983) and in litter-inhabiting tenebrionid beetles (ROGERS et al. 1978, CRAWFORD 1991). Preferences can be conditioned by the secondary compounds and fungi associated with specific food items (KURIHARA & KIKKAWA 1986).

5.2. Habitat Selection:

Animals select and use habitats in scale-related ways. Thus, MORRIS (1987) defines a macrohabitat as a unit of a habitat type in which an average individual performs all of its biological functions during a typical activity cycle. A microhabitat, by contrast, is defined by the physical/chemical variables that influence that individual's allocation of time and energy within the macrohabitat (MORRIS 1987). Both scales are important to macrodetritivores.

Among the diplopods, many species are broadly distributed over a variety of habitat types (e.g. FAIRHURST & ARMITAGE 1979). An extreme example is *Ommatoiulus moreleti* (LUCAS), an Old World millipede introduced into South Australia where it now occurs in large numbers in grassland and dry sclerophyllous woodland (BAKER 1978). In its capacity to colonize new habitats it resembles ubiquitous species of woodlice, cockroaches and earthworms.

BLOWER (1955) lists three types of millipede microhabitats in woodlands. In effect they are 1) soil surface and aerial parts of vegetation, 2) litter and soil, and 3) space under bark and in rotten wood. Differential use of two or more of these may be associated, for example, with seasonal life history (BANERJEE 1967) or daily thermoregulation (WOOTEN et al. 1975).

Factors felt to determine microhabitat preference in millipedes predictably include temperature and moisture. Temperature determination applies during winter in the case of *Enantiulus nanus* (LATZEL), which occupies xerothermous areas in the basaltic hills of Brandenburg (VOIGTLÄNDER 1987). Temperature also controls the vertical distribution, in winter, of *Cylindroiulus latestriatus* (CURTIS) and three species of isopods in an English dune grassland (DAVIS et al. 1977); relative humidity has the same effect in summer. Again, temperature is strongly associated with microhabitat selection by *Orthoporus ornatus* (GIRARD) millipedes in desert shrubland (WOOTEN et al. 1975). According to an ordination analysis by STAMOU et al. (1984), temperature also controls the distribution of julid millipedes — and scolopendrid centipedes — on Mount Olympus. However, the distribution there of earthworms, snails and slugs seems to be controlled by soil type.

The role of moisture, which can strongly influence the habitat selection of terrestrial isopods (WARBURG et al. 1984, WARBURG 1987), is relatively subtle in millipedes. Both groups display generally low resistance to desiccation (CLOUDSLEY-THOMPSON 1962, EDNEY 1977). Nevertheless, capacity to retard water loss appears to play no part in determining the microhabitat preferences of seven coexisting species in an Illinois woodland (O'NEILL 1969). Because the most tolerant of these species are also the most numerous, O'NEILL considered them best suited for dispersal during unfavorable periods. One of them, *Narceus americanus* (BEAUVOIS), follows moisture gradients that presumably bring it into contact with optimal feeding and substrate conditions (O'NEILL 1967a).

Transpiration rates of five millipede species occupying different habitat types — and therefore different microhabitats — in the Austrian Tyrol vary a great deal and may facilitate ecological isolation within a specific habitat (MEYER & EISENBEIS 1985). (The same relationship may hold for the seven species studied by O'NEILL (1969) in Illinois, since each occupies a different microhabitat in the same general area — O'NEILL 1967 b). Microhabitat occupation may also be associated with life history stategy in millipedes. Thus DUNGER & STEINMETZGER (1981) found that in a limestone area in Thuringia, semelparous species dominate moist places while iteroparous species dominate drier and warmer ones.

Habitat separation among species in the same general guild implies past and/or present competition. However, whether terrestrial macrodetritivores actually do compete for scarce resources in natural situations remains largely untested or appears to be negative (WISE 1981). For millipedes, inferences from field observations (e.g. MILLER 1974, DAVIS et al. 1977, MEYER 1985) are about all we have to go on.

6. Macrodetritivore Life History:

Member species of a "guild," i.e. species that use the same class of environmental resources in a similar way, do not necessarily have similar life histories. However, in the guild of large-bodied invertebrates that eat terrestrial detritus, one might expect somewhat consistent patterns of response to seasonal changes that affect their detrital foods and sheltered habitats (see discussion in HAWKINS & MACMAHON 1989). Here I explore whether broadly similar seasonal activities and life history "strategies" characterize millipedes and other groups of macrodetritivores.

6.1. Seasonal Activity and Climate:

As indicated above, macrodetritivores in mesic environments are relatively susceptible to desiccation. This being so, it is not surprising that daily activity in many of these animals is regulated by

habitat moisture (e.g. CLOUDSLEY-THOMPSON 1962). However, the regulation by moisture of their long-term or seasonal activity is less obvious. For example, in a 14-month pitfall trap study of native forest invertebrates in New Zealand, MOEED & MEEDS (1985) found that catches of millipedes, ground wetas (stenopelmatid orthopterans), isopods and amphipods tended to be positively correlated with mean monthly temperature, but not with mean monthly rainfall. The opposite was true for gastropods and earthworms, while results were somewhat mixed for cave wetas (rhaphidophorid orthopterans) and uncorrelated for cockroaches.

Yet in tropical Panama, Berlese extraction of litter macroarthropods resulted in a wet season increase for most groups, including millipedes; only psocopterans and thysanurans increased in the dry season, while the seasonal fluctuations of amphipods and isopods were not linked to either condition (LEVINGS & WINDSOR 1985). A pattern of strong millipede activity on the surface during tropical wet seasons has also been observed in tropical Africa (e.g. TOYE 1967, LEWIS 1971, GILLON & GILLON 1979). Perhaps enhanced fungal growth during tropical wet periods is positively associated with diplopod foraging (see earlier discussion).

The seasonal relationship of millipede activity and rainfall is more tenuous in other regions. Of three spirostreptid species studied in deserts on different continents by CRAWFORD et al. (1987), two become surface-active with the onset of seasonal rains, while one, in a winter-rainfall desert, hibernates in winter and forages during the long dry summer. Based on the observations of many authors in temperate regions, I conclude that as long as the microclimates of millipedes exceed a certain level of moisture, these and many other macrodetritivores are limited in activity only by extreme temperatures and their own life history constraints.

Therefore, while there is good reason to invoke moisture as a major influence on the seasonal organization of diplopod life history — particularly in the warm tropics where fungi may contribute significantly to millipede nutrition — the regulatory influence of temperature may be relatively more important for millipedes in temperate regions. While this general relationship may also apply to other groups of macrodetritivores, their specific long-term responses to climatic events can vary independently, both regionally and within assemblages.

6.2. Life History Strategies:

Terrestrial macrodetritivores are said to be "donor-controlled," and therefore do not exert feedback on their food resources (PIMM 1982). Isopods at least also appear not to be food limited (WARBURG et al. 1984), although this remains to be rigorously tested, and many of them occupy relatively benign habitats. Organisms living this way and common to such places are typically termed "K-selected" and considered more biotically interactive than "r-selected organisms living in temporary habitats such as dung and animal carcasses (SOUTHWOOD 1987). Millipedes in mesic environments typify the former group, calliphorid fly larvae typify the latter.

Habitats with high durational stability nevertheless present a spectrum of spatial and temporal conditions that selectively influence the life histories of organisms that use them. The spatial distribution of food and oviposition sites, for example, is associated with the reproductive strategies of millipedes. Thus, in temperate forests, iteroparous species — those distributing their reproductive effort over time and space — favor aggregated requisites such as dead wood. Alternatively, semelparous species — those laying one egg clutch at one place in a lifetime — prefer evenly dispersed requisites such as leaf litter (BLOWER 1970, READ 1988). Iteroparity is probably far more common than semelparity in terrestrial isopods (WARBURG 1987).

Since iteroparity allows females to lay eggs in different environments (READ 1988), it should be especially common in relatively mobile species of macrodetritivores occurring in heterogeneous habitats. Iteroparity is, in fact, predicted for most insects (FRITZ et al. 1982). And while the rapidly colonizing *Ommatoiulus moreleti* in Australia is said by BAKER (1978) be semelparous and to have a flexible lifespan, a cursory review of the literature (e.g. COTTON & MILLER 1974,

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SPAULL 1976, references in MEYER 1985) suggests that iteroparity is more common in millipedes generally. If so, as a group they share this trait with the majority of terrestrial arthropods, which, after all, also occupy habitats in which resources are not distributed uniformly.

7. Application of the "Model" Concept in Extreme Environments:

Species of millipedes inhabiting high latitudes and altitudes appear to have adjusted to cold seasons by taking refuge in thermally tolerable microhabitats (RANTALA 1985), by undergoing dormancy (implied in many studies), and/or by having abbreviated seasonal activity accompanied by relatively long life spans (MEYER 1990). Otherwise, because they are often abundant (e.g. MEIDELL 1979, MEYER 1985) and, like most macrodetritivores in mesic biomes, because they resist desiccation relatively poorly (PERTTUNEN 1953, EDNEY 1977, MEYER & EISENBEIS 1985), their ecological roles should conform to those of millipedes in more temperate climates.

By contrast, fewer millipede species occur in arid regions (CRAWFORD 1979), although their population densities there can be high (CRAWFORD et al. 1987). As with certain other desert macrodetritivores (EDNEY 1977, NICOLSON in press), they show impressive resistance to desiccation even though they typically rely on subterranean or crevice-located moisture. Those studied ecologically reach large size and experience highly variable habitats. If *Archspirostreptus tumuliporus judaicus* (ATTEMS) in Israel (BERKOVITZ & WARBURG 1985) is representative of unstudied desert spirostreptids, these should attain reproductive maturity several years before the ends of their long lives, and therefore should be iteroparous.

In fairly monotonous North American desert shrublands, *Orthoporus ornatus* has extensive and continuously distributed populations, and consumes a proportion of primary production in the range of that eaten by macrodetritivores in temperate forest ecosytems (CRAWFORD 1976). However, in more varied landscapes its distribution is highly discontinuous, which is typical of other desert species inhabiting similar terrain (CRAWFORD et al. 1987). Despite these observations, one seldom encounters millipedes in deserts. Other groups of desert macrodetritivores, particularly tenebrionid beetles, are far more evident in most arid regions, and in certain deserts arthropods such as polyphagid cockroaches, *Hemilepistus* isopods or termites are the dominant large detritivores (CRAWFORD 1991).

8. Conclusions:

My interpretation of the extent to which millipedes can be considered "model" macrodetritivores is summarized in Table 4. Recognizing that generalizations from incomplete data about highly complex comparisons are to be viewed with caution, I nevertheless feel that several broad, if tentative conclusions can be drawn.

I believe that the strongest argument for the issue in question comes from the apparently consistent presence — over very long evolutionary time — of millipedes in decomposer food webs. That they now represent a substantial fraction of the macrodetritivore biomass in many temperate and tropical ecosystems is further support for the argument. The capacity of millipedes and other macrodetritivores to select certain foods over others also provides support, as do similarities in life history strategies within the guild.

The representation of millipedes appears less valid when some aspects of their population biology are considered — at both regional and habitat scales. In both situations their standing crop biomass can vary tremendously — sometimes within the same species and often relative to the biomass of other macrodetritivores. Regionally, too, the responses of millipedes to seasonal changes in moisture and temperature seem not to typify the responses of other major groups. In addition, the diversity of millipedes relative to other guild members in arid regions bears little resemblance to what is seen in non-arid regions.

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Table 4: Summary: millipedes as model detritivores. * Symbols: +++ = well supported, ++ = moderately supported, + = modestly supported, −− = not supported.

Perspective	Validity of the "model" concept *)	Comments
Impact over evolutionary time	+ + +	Probably consistently strong
Impact (biomass measure) in ecological time	++/+	Varies with habitat, region
Food selection	++	Conditioned by fungi, plant chemistry
Habitat selection	+	Roles of moisture, temperature vary
Climate-related seasonal activity	+	Roles of moisture, temperature vary
Life history strategies	++	Broadly similar in many macrodetritivores
Extreme environments	+/−−	More similar in cold than arid regions

In the final analysis, it is difficult to view millipedes — or for that matter any group of animals — as models of a complex guild. Still, macrodetritivores are important ecological agents in a vital ecological process, and in that sense all groups contributing to the process exhibit model properties worth exploring.

9. Acknowledgements:

10. Literature:

ANDERSON, J.M., S.A. HUISH, P. INESON, M.A. LEONARD & P.R. SPLATT,P.R. (1985): Interactions of invertebrates, micro-organisms and tree roots in nitrogen and mineral element fluxes in deciduous woodland soils. − In: FITTER, A.H., D. ATKINSON, D.J. READ & M.B. USHER (eds.), Ecological interactions in soil-plants, microbes and animals, 451 pp., Blackwell Scientific Publications, Oxford: 377 - 392.

ANDERSON, J.M. (1987): Interactions between invertebrates and microorganisms: noise or necessity for soil processes? − In: FLETCHER, M., T.R.G. GRAY & J.G. JONES (eds.), Ecology of microbial communities, 440 pp., Cambridge University Press, Cambridge: 125 - 145.

BAKER, G.H. (1978): The distribution and dispersal of the introduced millipede, *Ommatoiulus moreleti* (Diplopoda: Iulidae), in Australia. − J. Zool. Lond. **185:** 1 - 11.

BANERJEE, B. (1967): Seasonal changes in the distribution of the millipede *Cylindroiulus punctatus* (LEACH) in decaying logs and soil. − J. Anim. Ecol. **36:** 171 - 177.

BEGON, M., J.L. HARPER & C.R. TOWNSEND (1986): Ecology: individuals, populations and communities. − Sinauer Associates, Inc., Sunderland, Massachusetts, 876 pp.

BERGSTRÖM, J. (1978): Morphology of fossil arthropods as a guide to phylogenetic relationships. − In: GUPTA, A.D. (ed.), Arthropod phylogeny, 762 pp., Van Nostrand Reinhold, New York: 3 - 56.

BERKOVITZ, K. & M.R. WARBURG (1985): Developmental patterns in two populations of the millipede *Archispirostreptus syriacus* (de Saussure) in Israel (Diplopoda). − Bijdr. Dierkende **55:** 37 - 46.

BLOWER, J.G. (1955): Millipedes and centipedes as soil animals. − In: KEVAN, D.K. McE. (ed.), Soil zoology, 512 pp., Butterworths Scientific Publ., London: 138 - 151.

− (1970): The millipedes of a Cheshire wood. − J. Zool. Lond. **160:** 455 - 496.

− (1979): The millipede faunas of two British limestone woods. − In: CAMATINI, M. (ed.), Myriapod biology, 456 pp, Academic Press, London: 203 - 214.

BOUDREAUX, B.H. (1979): Arthropod phylogeny with special reference to insects. − John Wiley & Sons, New York, 320 pp.

CLOUDSLEY-THOMPSON, J.L. (1962): Microclimates and the distribution of terrestrial arthropods. — Ann. Rev. Entomol. **7**: 199 - 222.

COLLINS, N.M. (1980): The distribution of soil macrofauna on the west ridge of Gunung (Mount) Mulu, Sarawak. — Oecologia (Berl.) **44**: 263 - 275.

CORNABY, B.W. (1973): Population parameters and systems models of litter fauna in a white pine ecosystem. — Ph.D. Thesis, Univ. of Georgia, Athens: 98 pp.

COTTON, M.J. & P.F. MILLER (1974): A population of *Cylindroiulus latestriatus* (CURTIS) on sand dunes. — In: BLOWER, J.G. (ed.), Myriapoda, 712 pp., Symp. Zool. Soc., Lond. **32**: 589 - 602.

CRAWFORD, C.S. (1976): Feeding-season production in the desert millipede *Orthoporus ornatus* (GIRARD) (Diplopoda). — Oecologia (Berl.) **24**: 265 -276.

— (1991): Macroarthropod detritivores. — In: POLIS, G.A. (ed.), Ecology of desert communities, Univ. Arizona Press, Tucson: 456 pp.

CRAWFORD, C.S., K. BERKOVITZ & M.R. WARBURG (1987): Regional environments, life-history patterns, and habitat use of spirostreptid millipedes in arid regions. — Zool. J. Linn. Soc. **89**: 63 - 88.

CROWSON, R.A. (1960): The phylogeny of Coleoptera. — Ann. Rev. Entomol. **5**: 111 - 134.

DAVIS, R.C., M. HASSALL & S.L. SUTTON (1977): The vertical distribution of isopods and diplopods in a dune grassland. — Pedobiologia **17**: 320 - 329.

DUNGER, W. & K. STEINMETZGER (1981): Ökologische Untersuchungen an Diplopoden einer Rasen-Wald-Catena im Thüringer Kalkgebiet. — Zool. Jb. Syst. **108**: 519 - 553.

DURDEN, C.J. (1969): Pennsylvanian correlation using blattoid insects. — Can. J. Earth Sci. **6**: 1159 - 1177.

EDNEY, E.B. (1977): Water balance in land arthropods. — Springer-Verlag, Berlin: 282 pp.

EDWARDS, C.A. (1974): Macroarthropods. — In: DICKINSON, C.H. & G.J.F. PUGH, (eds.), Biology of plant litter decomposition, Vol. 2. 850 pp., Academic Press, London: 533 - 554.

EDWARDS, C.A. & J.R. LOFTY (1977): Biology of earthworms, 2nd edition. — Chapman and Hall, London: 333 pp.

FAIRHURST, C. & M.L. ARMITAGE (1979): The British Myriapod Survey, 1978. — In: CAMATINI, M. (ed.), Myriapod biology, 456 pp., Academic Press, London: 183 - 194.

FRIEND, J.A. & A.M.M. RICHARDSON (1986): Biology of terrestrial amphipods. — Ann. Rev. Entomol. **31**: 25 - 48.

FRITZ, R.S., N.E. STAMP & T.G. HALVERSON (1982): Iteroparity and semelparity in insects. — Amer. Nat. **120**: 264 - 268.

GEOFFROY, J.-J. (1979): Les peuplements de chilopodes et de diplopodes d'une chénaie-charmaie (Station Biologique de Foljuif Siene & Marne). — Thesis, L'université Pierre et Marie Curie, Paris: 179 pp.

GHABBOUR, S.I. (1983): Population density and biomass of terrestrial isopods (Oniscoids) in the xero-mediterranean agro-ecosystems of Mariut region, Egypt. — Ecologia Méditerranea **9**: 3 - 18.

GILLON, D. & Y. GILLON (1979): Estimation du nombre et de le biomasse des iules (Myriapodes Diplopodes) dans une zone cultivée au Sénégal. — Bull. Ecol. **10**: 95 - 106.

GUPTA, A.P. (1979): Origin and affinities of Myriapoda. — In: CAMATINI, M. (ed.), Myriapod biology, 456 pp., Academic Press, London: 373 - 390.

HAWKINS, C.P. & J.A. MACMAHON (1989): Guilds: the multiple meanings of a concept. — Ann. Rev. Entomol. **34**: 423 - 451.

HOOGERKAMP, M., H. ROGAAR & H.J.P. EIJSAKERS (1983): Effect of earthworms on grassland on recently reclaimed polder soils in the Netherlands. — In: SATCHELL, J.E. (ed.), Earthworm ecology: from Darwin to vermiculture, 495 pp., Chapman and Hall, London: 85 - 105.

HOFFMAN, R.L. (1969): Myriapoda, exclusive of Insecta. — In: BROOKS, H.K.: Part R, Arthropoda 4. Treatise on Invertebrate Paleontology, 252 pp., Univ. Kansas Press, Lawrence: R 572 - 606.

— (1979): Classification of the Diplopoda. — Muséum d'Histoire Naturelle, Geneve: 237 pp.

IATROU, G.D. & STAMOU, G.P. (1989): Preliminary studies on certain macroarthropod groups of a *Quercus coccifera formation* (Mediterranean-type ecosystem) with special reference to the diplopod *Glomeris balcanica*. — Pedobiologia **33**: 301 - 306.

KRAUS, P. (1974): On the morphology of Paleozoic diplopods. — In: BLOWER, J.C. (ed.), Myriapods, 712 pp., Academic Press, London: 13 - 22.

KURIHARA, Y. & J. KIKKAWA (1986): Trophic relations of decomposers. — In: KIKKAWA, J. & D.J. ANDERSON (eds.), Community ecology: pattern and process, 432 pp., Blackwell, London: 127 - 160.

LABANDIERA, C.C., B.S. BEALL & F.M. HUEBER (1988): Early insect diversification: evidence from a Lower Devonian bristletail from Quebec. — Science **242**: 913 - 916.

LAMOTTE, M. (1989): Place des animaux détritivores et des microorganismes décomposeurs dans les flux d'én-

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ergie de savanes africaines. — Pedobiologia **33**: 17 - 35.

LAVELLE, P. & B. PASHANASI (1989): Soil macrofauna and land management in Peruvian Amazonia (Yuri-maguas, Loreto). — Pedobiologia **33**: 283 - 291.

LAWRENCE, J.F. & A.F. NEWTON Jr. (1982): Evolution and classification of beetles. — Ann. Rev. Ecol. Syst. **13**: 261 - 290.

LEVINGS, S.C. & D.M. WINDSOR (1982): Seasonal and annual variation in litter arthropod populations. — In: LEIGH, E.G. Jr., A.S. RAND, A.S. & D.M. WINDSOR (eds.), The ecology of a tropical forest — seasonal rhythms and long-term changes, 468 pp., Smithsonian Institution Press, Washington, D.C: 355 - 387.

— (1985): Litter arthropod populations in a tropical deciduous forest: relationship between years and arthropod groups. — J. Anim. Ecol. **54**: 61 - 69.

LEWIS, J.G.E. (1971): The life history and ecology of three paradoxosomatid millipedes (Diplopoda: Polyde-smida) in northern Nigeria. — J. Zool. Lond. **165**: 431 - 452.

LYFORD, W.H. Jr. (1943): The palatability of freshly fallen forest tree leaves to millipedes. — Ecology **23**: 252 - 261.

MEIDELL, B.A. (1979): Norwegian myriapods: some zoogeographical remarks. — In: CAMATINI, M. (ed.), Myriapod biology, 456 pp., Academic Press, London: 195 - 201.

MEYER, E. (1985): Distribution, activity, life history and standing crop of Julidae (Diplopoda, Myriapoda) in the Central High Alps (Tyrol, Austria). — Holarctic Ecology **8**: 141 - 150.

— (1990): Altitude-related changes in the life histories of Chordeumatida in the Central Alps (Tyrol, Austria). — In: MINELLI, A. (ed.), Proc. 7th Int. Cong. Myriapodology, 480 pp., E.J. Brill, Leiden: 311 - 322.

MEYER, E. & G. EISENBEIS (1985): Water relations in millipedes from some alpine habitat types (Central Alps, Tyrol) (Diplopoda). — Bijdr. Dierkunde **55**: 131 - 142.

MILLER, P.F. (1974): Competition between *Ophyiulus pilosus* (NEWPORT) and *Iulus scandinavius* LATZEL. — In: BLOWER, J.G. (ed.), Myriapoda, 712 pp., Symp. Zool. Soc. Lond. **32**: 553 - 574.

MOEED, A. & M.J. MEADS (1985): Seasonality of pitfall trapped invertebrates in three types of native forest, Orongorongo Valley, New Zealand. — N. Z. J. Zool. **12**: 17 - 53.

MORRIS, D.W. (1987): Ecological scale and habitat use. — Ecology **68**: 362 - 369.

NICOLSON, S.W. (1990): Water relations in the Namib Desert Beetles. — In: SEELY, M.K. (ed.), Current re-search on Namib ecology — 25 years of the Desert Ecological Research Unit. 230 pp., Transvaal Mus. Monogr. No. 8, Johannesburg: 173 - 178.

O'NEILL, R.V. (1967a): Behavior of *Narceus americanus* (Diplopoda) on slopes and its ecological significance. — Amer. Midl. Nat. **77**: 535 - 539.

— (1967b): Niche segregation in seven species of diplopods. — Ecology **48**: 983.

— (1969): Comparative desication tolerance in seven species of millipedes. — Amer. Midl. Nat. **82**: 182 - 187.

OLDROYD, H. (1964): The natural history of flies. — W.W. Norton, New York: 324 pp.

PERTTUNEN, V. (1953): Reactions of Diplopods to the relative humidity of the air. Investigations on *Orthomor-pha gracilis*, *Iulus terrestris* and *Schizophyllum sabulosum*. — Ann. Soc. Zool. Fenn. Vanamo **16**: 1 - 67.

PIMM, S.L. (1982): Food webs. — Chapman and Hall, London: 219 pp.

RANTALA, M. (1985): Hibernating Myriapoda in compost in Tampere (Finland) (Diplopoda; Chilopoda; Sym-phyla). — Bijdr. Dierkunde **55**: 171 - 176.

READ, H.J. (1988): The life histories of millipedes: A review of those found in British species of the order Julida and comments on endemic Maderian species. — Rev. Écol. Biol. Sol. **25**: 451 - 467.

RETALLACK, G.J. & C.R. FEAKES (1987): Trace fossil evidence for late Ordovician animals on land. — Science **235**: 61 - 63.

RICKLEFS, R.E. (1990): Ecology. Third edition. — W.H. Freeman and Co., New York: 896 pp.

ROGERS, L.E., N. WOODLEY, J.K. SHELDON & V.A. URESK (1978): Darkling beetle populations (Tene-brionidae) of the Hanford site in southcentral Washington. — Battelle Pac. Northw. Lab. Res. Report PNL-2465, Richland, Washington: 125 pp.

ROLFE, W.D.I. (1985): Aspects of the Carboniferous terrestrial arthropod community. — 9eme Congr. Int. Strati-graphie et de Geologie du Carbonifere, C. R. **5**: 303 - 316.

SAKWA, W.N. (1974): A consideration of the chemical basis of food preference in millipedes. — In: BLOWER, J.G. (ed.), Myriapoda, 712 pp., Symp. Zool. Soc. Lond. **32**: 329 - 346.

SATCHELL, J.E. (1983): Earthworm ecology in forest soils. — In: SATCHELL, J.E. (ed.), Earthworm ecology:

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from Darwin to vermicultre, 495 pp., Chapman and Hall, London: 161 - 170.

SCHRAM, F.R. (1986): Crustacea. — Oxford Univ. Press, New York: 606 pp.

SHAW, G.G. (1968): Population size, ecology and mineral reservoir of the millipede, *Narceus annularis* (RAF.). — Ecology **49:** 1163 - 1166.

SOLEM, A. (1985): Origin and diversification of pulmonate land snails. — In: TRUEMAN, E.R. & M.R. CLARKE (eds.), The Mollusca, Vol. 10, Evolution, 491 pp., Academic Press, Orlando: 269 - 293.

SOUTHWOOD, T.R.E. (1987): Habitat and insect biology. — Bull. Entomol. Soc. Amer. **33:** 211 - 214.

SPAULL, V.W. (1976): The life history and post-embryonic development of *"Spirobolus"bivirgatus* (Diplopoda: Spirobolida) on Aldabra, Western Indian Ocean. — J. Zool., Lond. **180:** 391 - 405.

STAMOU, G.P., S. SGARDELIS, S. & N.S. MARGARIS (1984): Arthropods distribution pattern on a mountain gradient (Mt. Olympus, Greece). — Rev. Écol. Biol. Sol. **21:** 491 - 505.

STRIGANOVA, B.R. & Z.G. PRISHUTOVA (1990): Food requirements of diplopods in the dry steppe subzone of the USSR. — Pedobiologia **34:** 37 - 41.

SWIFT, M.J., O.W. HEAL & J.M. ANDERSON (1979): Decomposition in terrestrial ecosystems. — Univ. California Press, Berkeley: 372 pp.

TAYLOR, E.C. (1982): Fungal preference by a desert millipede *Orthoporus ornatus* (Spirostreptidae). — Pedobiologia **23:** 329 - 334.

TOYE, S.A. (1967): Observations on the biology of three species of Nigerian millipedes. — J. Zool., Lond. **152:** 67 - 78.

VAN DER DRIFT, J. (1965): The effects of animal activity in the litter layer. — In: HALLSWORTH, E.G. & D.V. CRAWFORD (eds.), Experimental pedology, 413 pp., Butterworths, London: 227 - 235.

VISSER, S. (1985): Role of the soil invertebrates in determining the composition of soil microbial communities. — In: FITTER, A.H. (ed.), 451 pp., Blackwell Scientific Publ., Oxford: 297 - 317.

VOIGTLÄNDER, K. (1987): Untersuchungen zur Bionomie von *Enantiulus nanus* (LATZEL, 1884) und *Allajulus occultus* C.L. KOCH, 1847 (Diplopoda, Julidae). — Abh. Ber. Naturkundemuseums. Görlitz **60:** 1 - 116.

WALLWORK, J.A. (1970): Ecology of soil animals. — McGraw-Hill, London: 283 pp.

WARBURG, M.R. (1987): Isopods and the terrestrial environment. — Adv. Ecol. Res. **17:** 187 - 242.

WARBURG, M.R., K.E. LINSENMAIR & K. BERKOVITZ (1984): The effect of climate on the distribution and abundance of isopods. — Symp. Zool. Soc. Lond. **53:** 339 - 367.

WHITTAKER, R.H. (1975): Communities and ecosystems. — MacMillan Publ. Co., Inc., New York: 385 pp.

WISE, D.H. (1981): A removal experiment with darkling beetles: Lack of evidence for interspecific competition. — Ecology **62:** 727 - 738.

WOOD, T.G. and SANDS, W.A. (1978): The role of termites in ecosystems. — In: BRIAN, M.V. (ed.), Production ecology of ants and termites, 409 pp., Cambridge University Press, Cambridge: 245 - 292.

WOOTEN, R.C. Jr., C.S. CRAWFORD & W.A. RIDDLE (1975): Behavioural thermoregulation of *Orthoporus ornatus* (Diplopoda: Spirostreptidae) in three desert habitats. — Zool. J. Linn. Soc. **57:** 59 - 74.