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Soil zoology: an indispensable component of integrated ecosystem studies

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Abstract

Society is faced with environmental issues that exceed the level of local governments, but which need to be dealt with at international or even global scales. These issues include nature conservation and management, development of a more sustainable agriculture, effects of environmental pollution, biodiversity, and effects of global change. The development of political and technical protocols necessary to control the future state of such environmental issues requires a detailed knowledge of the structure and functioning of the world's ecosystems. Studies that integrate the interpretation of results from (detailed) community and ecosystem process and pattern studies and that, moreover, include social and economic aspects might be defined as 'integrated ecosystem studies'. Four examples of integrated ecosystem studies are presented, and it is concluded that a full understanding of the contribution of soil zoology to such studies requires detailed analyses of interactions of fauna with other system components. If not, analyses can result in superficial conclusions that possibly underestimate the vulnerability of ecosystems to disturbances or their sensitivity to management.

Keywords: Agriculture; Biomonitoring; Desert; Ecosystem studies; Soil ecology; Termites; Tropics

1. Introduction

Society is faced with environmental issues that exceed the level of local governments, but which need to be dealt with at international or even global scales. These issues include nature conservation and management, development of a more sustainable agriculture, effects of environmental pollution, biodiversity, and effects of global change. The development of political and technical protocols necessary to control the future state of such environmental issues requires a detailed knowledge of the structure and functioning of the world's ecosystems.

The classical definition of an ecosystem is the biological community together with its physical environment [2,35]. The study of ecosystems is focused on the description of the structure of the biological community and its physical environment and the dynamic interactions (processes) between these ecosystem components. According to Mooney et al. [20], ecosystem structure or pattern can be divided into community patterns which describe the abundance and spatial distribution of species in an ecosystem, and ecosystem patterns. The latter include quantities and configuration of water, energy, and materials in biotic and abiotic components of the system. Similar to ecosystem patterns, ecosystem processes also can be divided into community and ecosystem processes [20]. Community processes involve species interactions, such as competition, predation and mutualism, whereas ecosystem processes are flows of water, energy, and materials within and among ecosystems. Examples of ecosystem processes are primary production, decomposition, microbial immobilization, and nutrient leaching.

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It can be questioned whether a full knowledge of these community and ecosystem patterns and processes is necessary in order to understand ecosystem function. What knowledge is necessary to understand biological succession, nutrient cycling, food-web and food-chain interactions, disease suppressiveness, soil formation, or the significance of biodiversity? In our opinion many, if not all, such topics need a research approach that integrates the interpretation of results from community and ecosystem processes and pattern studies. Knowledge generated by such integrated ecosystem studies will shed light on global issues that are related to, for example, nature conservation and management, development of a more sustainable agriculture, effects of environmental pollution, biodiversity, and effects of global change. Moreover, studies on such issues addressing questions on (inter)national or global scales should be linked to human society and the political agenda by including social and economic aspects.

What is the contribution of soil zoology to such integrated ecosystem studies? Each ecosystem comprises terrestrial, aquatic and/or atmospheric compartments. The terrestrial compartment can be divided into above-ground and below-ground parts. The below-ground part of the terrestrial compartment is essential for life in controlling 'life-support functions' [21] such as decomposition of organic material, release and recycling of nutrients, availability of nutrients for plants, formation of soil structure and the stability of the soil ecosystem. These life-support functions are regulated by processes such as fragmentation and transformation of organic substrates, nitrogen mineralization, bioturbation and formation of soil aggregates, etc., which primarily depend on microbial and faunal activity in soils [6,10]. We have selected a number of case studies that will underscore the importance of soil biology, in particular soil zoology, in ecosystem studies.

2. Case studies

2.1. Ecosystem function and management of the Negev desert, Israel

The Negev desert in Israel is a mosaic of macrophytic patches, consisting of shrubs and annual plants growing in a soil mound, and microphytic patches, consisting of algae, cyanobacteria, bacteria, mosses, and lichens growing on a soil crust [27]. For the management, protection and sustainable use of the area, it was necessary to understand the mechanisms by which a relatively diverse community of microbes, plants and animals could coexist. The cyanobacteria in the microphytic patches can secrete polysaccharides that bind the soil [9] and thus form crusted soil patches. With a long-term annual average precipitation of only 200 mm (occurring between November and March), such crusts have large impacts on the spatial distribution of rainwater owing to a reduced infiltration rate. Non-crusted soil immediately down-slope of the crust patches receives more rainwater resulting in patches with higher soil moisture. In such patches, macrophytic vegetation can develop because here seeds and other plant propagules have a higher chance of successful settlement. The macrophytic patches attract many organisms including herbivorous snails and vertebrates. Snails, such as *Trochoidea seetzenii* and *Euchondrous albulus*, can reach densities of 20–26 individuals m^{-2} and can produce up to about 20 mg feces d^{-1}, which is a significant contribution to the total litter production, soil formation, and nitrogen supply for the vegetation [37]. Moreover, the atmospheric deposition of especially coarse particles that are primarily composed of organic material from plant detritus rich in carbon and nitrogen is higher in macrophytic patches compared to the microphytic crusts [27]. This results in a very slow, but for the system extremely important formation of soil mounds which support the highest annual plant germination and growth rates of the local vegetation. The impacts of the disturbance of the soil mounds on local patch dynamics and biodiversity are not unambiguous, but it is clear that recovery will be a long-term process as a typical soil mound requires at least 180–290 years to develop [27]. Several of the larger vertebrates concentrate their feeding activity on these macrophytic patches. The Indian crested porcupine (*Hystrix indica*), for example, feeds on bulbs and tubers which are dug up mainly in the space between the shrubs [25]. Plant biomass, density and species richness in such porcupine diggings appeared higher than in the direct surroundings and this was explained by relatively higher runoff absorption and seed trapping in the diggings [3,28]. Similar effects were found for large herbivores, such as goats that feed on the above-ground parts of the macrophytic vegetation. However, they disturb the crusted microphytic patches with their hooves creating small pits in which seeds and runoff water are trapped [9]. The system as described so far appears to show a delicate interaction between the biotic and abiotic components of which the spatial organization in or at the soil surface seems crucial for the maintenance of productivity and biodiversity. Too high levels of, for example, the microphytic crust destruction due to overgrazing can affect water distribution such that it can result in a negative impact on productivity, whose recovery depends on the slow-growing crust organisms [9]. Besides the 'part-time' inhabitants of the soil system, such as porcupines, desert isopods (*Hemilepistus reaumuri*), are among the 'full-timers'! They are soil-dwelling animals of about 2 cm long (fresh weight of c. 200 mg) that live in monogamous families (80–120 individuals) in burrows of 50–70 cm deep, and represent a total biomass of about 13 kg fresh weight ha^{-1} [26]. Together with 'rock-eating' snails (*Euchondrus albulus* and *E. desertorum*), they significantly contribute to the erosion and patch dynamics in the desert soil [27,29]. One family of desert isopods can consume up to about 250 g soil $year^{-1}$ corresponding to 250–350 cm^3 soil. The soil is casted at the soil surface in fecal pellets that are very sensitive to erosion. Desert isopods thereby produce 170 ± 109 kg erodible soil ha^{-1} $year^{-1}$, which is about 60% of the total erodible soil production in the area [26]. Shachak and Jones [26] presented an ecological interaction web for the desert isopod that describes its effect on landscape level patch dynamics. Soil moisture controls the settling behavior of the isopod families [1,5,7,24] that in turn controls the production of erodible soil. The amount of runoff controls the proportion of soil that will erode, and this affects the soil-to-rock ratio and thereby runoff, which finally (or better, again) controls soil-moisture distribution and isopod settling. The rock-eating snails feed on endolithic lichens living in limestone rock. With a feeding rate of 9–15 mm^3 d^{-1} $animal^{-1}$ the snails are responsible for 0.7–1.1 mg limestone-rock erosion ha^{-1} $year^{-1}$, which is in the range of the total fine-dust deposition in the area [29].

The studies in the Negev desert ecosystem showed very complicated ecological relationships that significantly contributed to ecosystem function. The processes related to soil formation and the availability of water and nutrients were controlled not only by soil fauna but also by 'part-time' soil inhabitants such as porcupine, 'rock-eating' snails, and large vertebrate herbivores. Knowledge of these complicated ecological interactions which needed > 20 yearrs of detailed research resulted in management methods for a sustainable use of the area for, e.g., livestock grazing, (fire)wood collection, and tourism, which increased the value of the land for the local population [30].

2.2. *Contribution of interactions between above-ground and below-ground biota to vegetation succession and mosaics*

Bush lupine (*Lupinus arboreus*) is a rapidly growing, nitrogen-fixing shrub that can dominate the vegetation of Bodega Head, 73 km north of San Francisco on the California coast. It forms a vegetation comprising a mosaic of large round canopies of bush lupine surrounded by low-growing grasses and forbs [32]. The spatial cover of bush lupine in six stands appeared to show large year-to-year fluctuations (0–90% cover) within stands, and these were found to be positively correlated with the densities of caterpillars of the ghost moth (*Hepialus californicus*) [33]. In 1993, for example, in areas with an average of about 38 (maximum 62) caterpillars per root about 40% of the mature lupine bushes died, whereas this was only about 2% in areas with no more than six caterpillars per root [32]. Ghost moths are strong flyers that can disperse widely. They deposit their eggs (up to 2000) around and beneath the bush lupine. After hatching, the larvae burrow into the soil and feed upon the exterior of the lupine roots, whereafter they bore inside the root. The prepupal larvae bore upwards into the shoot and leave the plant as an adult Ghost moth through a self-made exit hole. Field observations showed that when feeding on the root exterior, the caterpillars were vulnerable to the entomopathogenic nematode, *Heterorhabditis hepialus*. In some stands, 65–80% of the caterpillars found on the bush lupine roots had been killed by this nematode [34]. However, at the same time, in other stands, no killing was observed. Also later on in the season, in summertime, when the caterpillars had bored inside the root, no killing by nematodes was observed. Clear negative correlations were found between the number of caterpillars per root, the fraction of rhizosphere occupied by *H. hepialus*, and the survival of bush lupine stands [34]. Moreover, the observations suggested that this was related to long-term site-specific vegetation dynamics in the study area. In areas with large long-term (1955–1994) fluctuations in bush lupine cover, a relatively high caterpillar density (16–38 $root^{-1}$; study year 1994–1995) coincided with low densities (5–6% of rhizosphere occupied) of *H. hepialus*, whereas the opposite was the case (6–12 caterpillar $root^{-1}$ and 45–78% of rhizosphere occupied by *H. hepialus*) in stands with constant or increasing cover [34]. These data suggest that species-specific interactions between a soil-dwelling root herbivore and its parasite, an entomopathogenic nematode, can influence above-ground vegetation dynamics. The herbivore–parasite interaction, however, appeared part of a complicated interaction web including nematophagous fungi predating on the entomopathogenic nematode, above-ground herbivores and granivores affecting the flowering, reproduction, and seed dispersal of bush lupine, and competition between forbs and grasses and seedlings of bush lupine, each directly or indirectly contributing to the survival of the bush lupine [32]. Moreover, in their turn, the activities of the caterpillar of the foliar-feeding tussock moth (*Orgyia vetusta*), which can periodically defoliate the lupine were, like the entomopathogenic nematodes, found to be controlled by predators and parasitoids (refs in [32]). Also, competition of lupine seedlings with other plant species is likely to be controlled by vertebrate herbivores grazing on the grasses [32]. Thus, a complex web of interactions between above-ground and below-ground biota was shown to affect spatial and temporal vegetation dynamics.

2.3. *Use of soil-dwelling termites and mulches in the rehabilitation of the crusted Sahelian soils*

Soil degradation in the semi-arid Sahelian zone is an enormous environmental problem for human society, especially the local inhabitants of the area, jeopardizing the potential of the agricultural system to meet the food, fuel and clothing needs of the increasing population [11]. Mismanagement of the ecosystem has resulted in large areas with crusted soils [31] that are characterized by low-infiltration capacity, nutrient imbalance, reduced biodiversity, and zero-to-very-low primary production. There is an urgent need to find management strategies that can contribute to the rehabilitation of these soils. Mando and coworkers developed an ecological technology that helped to improve the water infiltration and restored nutrient cycling. They applied mulch to the soil surface which attracted soil-dwelling termites such as *Odontotermes smeathmani* and *Microtermes lepidus*. The termites acted as ecosystem engineers [9]. They perforated the sealed, crusted soil surface resulting in 86 surface macropores m^{-2} compared to none in the absence of termites. Moreover, their digging activity significantly increased soil porosity (Table 1), and their channels and chambers accounted for > 60% of the total macroporosity in the 0–10 cm soil [15]. This significantly ($P < 0.05$) affected water-infiltration rate (infiltration per rain shower in the presence and absence of termites was 9.2–12.9 and 4.5–5.3 mm, respectively) resulting in higher levels of soil-water content, even at 60 cm soil depth [18]. Already one year after mulching, cumulative drainage was significantly increased in the presence of termites and the effect increased during the next two years of the study [12]. The increased soil porosity due to termite activity also resulted in a significant reduction of the resistance to cone penetration (RTCP) [13], a measure for plant-root growth potential. In soils without mulch or with mulch but without termites (termites were excluded by the application of the insecticide dieldrin) RTCP exceeded the capacity of the penetrometer (10 Mpa). In the mulched soils where termites were present RTCP was significantly lower and ranged between 1 and 4 Mpa for the 0–50 cm layer depending on the type of mulch applied [13]. Such values are within the range for penetration by roots for most plant species [16], which was supported by the observations on vegetation development on these soils (Table 2). Soils with mulch and termites had significantly higher plant cover, biomass, and diversity compared to soils with mulch but without termites and those without mulch [19]. On the latter soils, no vegetation developed. Termite activity also accounted for a significant loss of *Penisetum pedicellatum* straw (C–N ratio, 120) from litterbags that were placed on the soil surface [14]. In the absence of termites, 88–92% of the straw remained in the litterbags after one year, whereas in the presence of termites this was 38–72% indicating that termite activity contributed 71–80% of the total weight loss [14], probably contributing to an improved nutrient availability. Studies on the crusted soils of the semi-arid region of Sahel showed that soil-dwelling termites can play a key role in the rehabilitation of these degraded soils. Mando and Van Rheenen [17] concluded that after the establishment of termite populations a minimum biomass production of 2–4 t ha^{-1} will be possible. This can only be achieved by an initial investment in organic matter that can be applied as mulch, which might be problematic as a result of the poor economical situation in this part of the world. Also an evaluation program for farmers is necessary to assess the possibility of implementation of the technology in local farmers' practice and to convey the message that termites in the Sahel can be a friend and not an enemy. In fact, farmers can make the 'pest' work for them [17].

Table 1
Percentage of voids expressed as % of the total porosity calculated from bulk density data in the 0–7 cm soil of termite plots (mulched) and in non-termite plots (bare)

Void size class	Percentage of voids	
	With termites	Without termites
> 3 mm	38.6	0.0
> 0.1 mm	59.1	14.9

After [15].

2.4. *The Dutch national soil-quality monitoring network*

In 1993, the RIVM (National Institute for Public Health and the Environment) started the National Soil-quality Monitoring Network (LMB) on the request of the Dutch government. Its objectives are to monitor changes in soil quality over time and to establish the actual quality of the soil and upper groundwater [8]. The monitoring is focused on the rural part of the Netherlands. A total of 200 locations representing ten characteristic combinations of soil type and land use (dairy-cattle farms on sand (three levels of fertilizer application, $n = 60$), river clay (20), marine clay (20), and peat (20), arable farms on sand (20) and clay (20), market gardens on sand or clay (20), and forest on sand (20)) were selected. Every year, a selection of 40 locations (two combinations of soil type and land use) is sampled and sampling is repeated every 5 years. Initially, soil analyses were focused primarily on soil-chemical analyses including basic soil characteristics (pH, clay content, organic matter, CEC), nutrients (phosphorus), heavy metals (Cd, Cr, Cu,

Table 2
Effects of termites and mulch on vegetation cover, biomass, number of herb species, vegetation diversity (Shannon–Weaver index), and rainfall use efficiency in crusted soils in the semi-arid Sahel area 1–3 years after the start of the experiment.

	Cover (%)	Biomass (t ha^{-1})	No. of herb species	Diversity	RUE
Year 1					
NT	0.0 a	–	0 a		–
MNT	5.1 a	–	0–8 a	0.42–0.65 a	–
MT	14.4 b	–	1–15 a	0.39–1.02 a	–
Year 2					
NT	0.3 a	0.0 a	0–2 a		0.0 a
MNT	28.4 a	1.3 a	2–14 a	0.55–0.60 a	1.4 b
MT	86.8 b	3.1 a	5–25 a	0.65–0.73 a	3.9 c
Year 3					
NT	0.0 a	0.0 a	0 a		0.0 a
MNT	62.7 b	1.0 a	6–24 a	0.41–0.70 a	2.1 a
MT	144.3 c	3.3 b	18–35 a	0.84–0.91 b	6.8 b

After [19]: NT no mulch and no termites, MNT mulch but without termites, MT mulch with termites; – data not available; means within years followed by the same letter(s) are not statistically different.

Rainfall use efficiency (RUE): kg biomass production mm^{-1} rain.

Table 3
Biotic components that are monitored in the National Soil Quality Monitoring Network together with the life-support functions of ecosystems for which their diversity, mass and/or numbers are used as indicators.

Life-support function	Indicator variable (taxonomic group)
Decomposition of organic material	1. Earthworms + enchytraeids 2. mites 3. genetic diversity microflora, mushrooms
Recycling of nutrients	4. Bacteria + fungi 5. protozoa 6. nematodes 7. springtails 2. mites 8. Trophic interactions = 1+2+4+5+6+7
Availability of nutrients for plants	9. Mycorrhiza 10. Nitrifying bacteria 1. Earthworms + enchytraeids
Formation of soil structure Stability soil ecosystem	11. Structure community = 1+2+4+5+6+7

Modified from [21].

Hg, Pb, Zn), polycyclic aromatic hydrocarbons, and organochlorine pesticides. These measurements are compared with the Dutch guidelines for soil and groundwater quality, the so-called ‘target values’. However, the effects of pollutants or disturbances and the consequences of political measures to reduce various types of environmental pollution on ecosystem function might not be deduced easily from such measurements only. Only after extensive discussion, was it decided to include also a biotic component into the LMB project. Therefore, in each of the 200 sites the composition of the nematode fauna, a soil-organism group with a well-established bioindicator potential [4] has been monitored since 1993 as well [36]. Since 1997, the biotic component of the monitoring project has been substantially extended in order to include a biological indicator system (Table 3). This coincided with a shift in the focus of the Dutch environmental policy towards the ecosystem health and the sustainable use of ecosystems and maintenance of functions in biodiversity [21–23]. The data will be used to calculate a soil-quality index facilitating ecological soil assessment. Moreover, the data provide information for the calculation of response models for soil properties and soil pollutants which will be part of a decision-support system for the Dutch government.

3. Conclusions

The case studies on the Negev desert ecosystem, dynamics in the bush lupine vegetation, and the rehabilitation of the crusted Sahelian soils show that soil fauna can significantly contribute to ecosystem function and development and, therefore, should be a part of integrated ecosystem studies that aim at understanding ecosystem function. In particular, the ‘ecosystem engineers’ among the soil fauna can be key organisms that trigger new directions of ecosystem development. In this respect, it is interesting that organisms that are usually not classified as typical representatives of the soil community (porcupines, rock-eating snails, but also ground-nesting ants and bees) can also contribute to such soil processes. The ecological interaction web in the bush lupine vegetation made Strong [32] conclude that natural enemies of root-feeding insects may prove to be as important to plants as are the enemies of those insects that feed upon above-ground plant parts. Recent developments in both tropical [11] and temporal regions (pers. observ.) made farmers and scientists recognize the usefulness of calling in soil fauna to improve agricultural practices which can add to a more sustainable agriculture. Also among policy makers there is a growing awareness of the importance of soil biodiversity (Dutch LMB program and Soil Biological Indicator). However, the case studies also show that a full understanding of the contribution of soil zoology to such ‘integrated ecosystem studies’ requires detailed analyses of interactions of fauna with other system components. If not, analyses may result in superficial conclusions that possibly underestimate the vulnerability of ecosystems to disturbances or their sensitivity to management.

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