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Long-term dynamics and interrelationships of soil Collembola and microorganisms in an arable landscape following land use change

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Abstract

An arable landscape (150 ha) comprising a broad variety of soil types had been cultivated conventionally for many years. A small section had been intensively managed (hops), while another had been used as grassland. For 2 years at the beginning of our study, all arable land was cultivated with cereals only. After that, management was changed to integrated or organic farming, grassland or fallow land. Within a group of sites representing the variety of soil types and management systems, the development of soil microorganisms and Collembola was monitored every spring during an 8-year period. The microbial biomass compared to initial conditions under uniform management increased, particularly in land that had been set aside. General Collembola abundance slightly decreased, except for areas that had been converted to integrated farming. *Protaphorura armata* and *Lepidocyrtus cyaneus* decreased over the entire area, whereas the *Isotoma viridis* group was positively affected by conversion to integrated farming. Although recorded only once per year, the main results were comparable to data recorded in this area at higher temporal or spatial resolution. Nevertheless, site conditions may influence the reactions of soil organisms to land use change, and should be taken into account for evaluation. Biota resident in the upper 0–10 cm of the soil reflected current management practice, whereas those at greater soil depth reflected instead management history and soil properties. The microbial biomass and abundance of selected Collembola taxa were modeled using artificial intelligence methods (regression trees). Land management type was the most important factor determining soil biota performance. The variation of Collembola abundance depended additionally on microbial biomass.

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When supported by a sufficiently large data set, regression trees are powerful tools for explaining complex non-linear relationships. Finally, suggestions for the sampling design in future long-term studies at the landscape scale are given.

Keywords: Agricultural soils; Soil biota; Collembola; Modeling; Regression trees; Sampling strategy

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1. Introduction

Soil organisms are important components of agroecosystems. Although they also include a large number of pests (fungal diseases, root herbivores), the majority is essential for nutrient turnover and soil structure, in particular in systems with reduced management intensity (Hendrix et al., 1990). Although conventional farming is not necessarily detrimental to soil organisms, numerous studies have shown that, on average, biomass and abundance of most groups react positively to reduced tillage and pesticide use or to increased soil organic matter input. Herbicides have only a slight stimulating or no effect, and mineral fertilizers increase in most soils the biomass of the decomposer community (recently reviewed by Zwart and Brussaard, 1991; Wardle, 1995; Mäder et al., 1997). With few exceptions (Krogh, 1991; Çilgi et al., 1993; Wardle et al., 1999a, b; Fließbach and Mäder, 2000), these studies covered only short time periods, not exceeding 2 or 3 years. Most investigations were restricted to a single soil type (or a very small selection of crops) and typically conducted as plot experiments. The small size of these plots (e.g. 3 × 6 m) have raised skepticism since edge effects and disturbance by sampling may cause artifacts. In addition, the influence of soil type and climate on decomposer food webs remains unclear (Hendrix et al., 1986). Consequently, the necessity for long-term investigations, which are extremely scarce, as well as for studies at a spatial scale relevant to farming practice has been repeatedly pointed out (Paoletti et al., 1991; Wardle et al., 1999a).

Holland et al. (1994) reviewed a dozen recent studies carried out on experimental plots between 1 and 16 ha in size, most of which also considered soil microorganisms, earthworms or non-target invertebrates. Reduced input was generally beneficial for soil animals and often, but not always, for microorganisms. However, in these studies, the fields were mostly distributed over large distances and the management systems not strictly replicated, so that confounding of agricultural farming practice with soil properties or climatic conditions could have occurred, thus rendering the findings difficult to interpret. To our knowledge, the FAM Research Network on Agroecosystems is the first project of its kind that unifies different management systems, a large variety of crops, soil properties and realistic experimental plot sizes within a 150-ha area. Although neither strict replication nor direct comparisons of management systems is possible, the FAM field project provides a sound base for monitoring soil organism development following conversion to site-specific management over a longer period of time.

In order to realistically monitor and evaluate soil organism reactions to land use change, selected indicators should be representative of the community, react to environmental changes and have limited powers of dispersal (Paoletti et al., 1991; Holland et al., 1994). In order to apply the results of such investigations to a wide range of crops, soil and climatic conditions, these indicators should be appropriate for extrapolation to the landscape level by means of modeling, using basic pedological and agricultural farming information. We surveyed microorganisms because they are the dominant biota in soil nutrient turnover. Collembola, the most abundant and diverse arthropods in arable soils, were selected because they are important regulators of activity and composition of microorganisms. Extensive data collections during the initial phase of this study revealed that both organism groups were preferentially influenced by management history rather than by site properties (Fromm et al., 1993; Filser et al., 1995). Collembola species living deeper in soil appeared to be influenced by site properties to a larger extent than species living closer to the surface (Filser and Fromm, 1995). A first overview on the effects of land use change according to site-specific conditions (which can be roughly characterized as "reduced input", compared to previous conventional farming) revealed an increase of earthworm and microbial biomass over the entire farm area, whereas Collembola abundance tended to decrease (Filser et al., 1999). The purpose of the present study was to analyze the (i) spatial patterns of microbial biomass, (ii) reactions of different Collembola species to new land management, and (iii) interrelationships between management, microorganisms and Collembola. In addition to standard uni- and multivariate statistical procedures, we used artificial intelligence methods to model the observed changes. Such methods have proven useful for the description and analysis of non-linear ecological relationship, and are becoming increasingly popular in environmental modeling (e.g. artificial neural networks (Recknagel et al., 1997) and automated tree induction (Kompare and Dzeroski, 1995)). Moreover, these methods have been also recently applied in soil ecology (Kampichler, 1998a,b; Kampichler et al., 2000).

2. Material and methods

2.1. Soils and management

The FAM Research Station Scheyern comprises a 150-ha area in Southern Germany, and covers a wide range of soil types, mainly loamy cambisols derived from tertiary sediments. Texture (mean particle diameter between 9 and 424 μm) and carbon (C) content (between 1.15% and 2.42%) are the most variable properties of these soils. Eleven (13 for microorganisms) selected long-term observation areas (LOA, size: 25 × 20 m) representing the most important soil types were investigated at high temporal and small scale spatial resolution in 1991 and 1992, and annually in spring thereafter. LOA codes are coordinates increasing by 10 every 50 m, the first three numbers towards east, the last three numbers towards north; field number is given in pointed brackets. A map detailing the area, field numbers, management history and more detailed descriptions of the LOA can be found in Winter (1998) and in Schröder et al. (2001, this issue).

Before beginning of our study, the farm consisted of grassland, arable land (conventional farming with cereals, oilseed rape and maize), and small areas with intensive management (hops, LOA 160–240 ⟨A6⟩), resulting in high copper contamination (Filser et al., 1995). To achieve uniform conditions, all arable land was cultivated conventionally with winter wheat (1991) and spring barley (1992) during the first 2 years of this study. In autumn 1992, the area was subdivided into smaller fields and two different crop rotations were established. In the integrated system consisting mainly of fine-loamy Dystric Eutrochrepts, wheat, corn and potatoes were grown, after harvest of each crop catch crops were sown. In the organic system (predominantly coarse-loamy Dystric Eutrochrepts or Typic Udifluvents), white clover, potatoes, wheat, rye, lupine and sun flowers were cultivated. Parts of the farm area were left to natural succession (set-aside land, 140–200 ⟨F5⟩: fine Vertic Eutrochrept, 170–140 ⟨F21⟩: fine-loamy Typic Udifluvent), sown with a mixture of herbaceous plants and mulched annually (220–120 ⟨F24⟩, fine-loamy Endoaquept), or sown with grass (180–220 ⟨W19⟩, sandy Arenic Eutrochrept). In grassland (170–280 ⟨W6⟩, 330–180 ⟨W24⟩; fine-loamy Dystric Eutrochrept), fertilization was reduced from 1991 onward.

2.2. Methods

For each LOA, samples were taken at random within the upper 20 cm of soil. Soil microorganisms were recorded annually between 1991 and 1997 in early spring from a bulk sample of six soil cores (diameter: 6.8 cm). Substrate-induced respiration was measured according to Anderson and Domsch (1978), using a continuous-flow analyzer (Heinemeyer et al., 1989). Biomass was calculated according to Kaiser et al. (1992). Collembola were recorded in June 1991, and annually between 1994 and 1997 in early spring. Samples were taken with a cylindrical corer (diameter: 7.8 cm, 5 replicates each) and 5-cm sections of the cores were extracted over 6 days with a modified Macfadyen extractor; ethylene glycol served as collection fluid. The Collembola were identified according to Gisin (1960), Palissa (1964), Fjellberg (1980) and Zimdars and Dunger (1994). *Isotomurus fucicolus* (formerly: *I. palustris*) was identified according to Carapelli et al. (1999). Since many of the juveniles could not be identified, some taxa were grouped (within most of which only one or two species dominated and are thus marked in bold) as follows: *Folsomia quadrioculata* group (***F. quadrioculata***, *F. manolachei*), *Isotoma viridis* group (*I. anglicana*, *I. viridis*), *Protaphorura armata* group (***P. armata***, *P. campata*, *P. cancellata*, *P. subarmata*, *P. tricampata*, *P. vanderdrifti*), *Mesaphorura krausbaueri* group (*M. florae*, *M. hylophila*, ***M. krausbaueri***, ***M. macrochaeta***, *M. sylvatica*, *M. tenuisensillata*), *Pseudosinella* sp. (*P. alba*, *P. cf. decipiens*), *Sminthurinus* sp. (*S. aureus*, *S. elegans*). To maintain simplicity, the name of the dominant species (or genus) was used when referring to these groups. We refrained from recording data in 1993 in order to avoid artifacts caused by extreme oscillations of the biota due to the major disturbances (caused by altering the land use).

2.3. Statistics and modeling

Statistical calculations were done with SPSS ver. 6.1. Pairwise comparisons of the biota before and after management conversion were calculated for all management types, using the Student's *t*-test for the microbial biomass and the Mann–Whitney *U*-test for the Collembola. Each dataset and management type (1–3 LOAs per type) was subdivided into unequal subunits: (a) before and (b) after management conversion. For pairwise comparisons of (a) and (b), all replicates, LOAs and sampling dates within one management type were pooled. [Example: Collembola, integrated farming: 3 LOA, 1 sampling before, 4 samplings after conversion with 5 replicates each → $n = 3$ LOA by 1 date by 5 replicates = 15 (before) and $n = 3$ by 4 by 5 = 60 (after conversion). Several LOA were excluded from the statistics, namely LOA 160–240, organic (extraordinary situation due to copper contamination to be dealt with elsewhere: Albrecht et al., in preparation); LOA 170–140, fallow (no sampling before conversion); LOA 180–220 (Collembola only sampled in 1991 and in 1997)]. Multiple comparisons within each management type were Bonferroni-corrected with the Dunn–Šidák method (Ury, 1976). In a similar manner, hierarchical cluster analyses (method: cosine/average linkage) were conducted for Collembola dominances.

Microbial biomass and numbers of dominant collembolan species were analyzed by means of regression trees (Breiman et al., 1984). Briefly, tree-structured regression is based on the assumption that the functional dependence of a variable y on an array of independent variables x_i is not uniform throughout the entire domain but can be approximated as such on smaller subdomains. The tools developed for regression-tree induction search for these subdomains automatically and characterize them with regression functions or constants of y. Thus, they construct a piecewise linear model to explain the dependent variable. A tree consists of branches, nodes (the branching points) and leaves (the terminal nodes). Given an example for which the value of y should be estimated knowing the values of x_i, the tree is interpreted from its uppermost node. In each branching point, the left or right branch is selected until a leaf is reached. A value is computed at that point according to the model in that leaf. To maximize interpretability, a regression tree can be also represented as a set of *if–then* rules that define subdomains for which a functional dependence between x_i and y exists (e.g. *if* some x_i are in a certain range, *then* y is explained by a certain linear model or takes a certain constant value; cf. Table 2).

We used the program Cubist 1.05 (available at the URL http://www.rulequest.com) for building rule-based predictive models. This program is based on a top-down-induction of decision trees (TDIDT) algorithm. It divides the dataset into several subsets from which it recursively forms subtrees. The Cubist 1.05 algorithm maximizes the expected error reduction when splitting the data (for additional information on the algorithm, see Quinlan, 1992, 1993).

3. Results

In comparison to initial conditions under uniform management (conventional farming), the following changes after land use change were observed: the microbial biomass had increased over the entire area, particularly in set-aside land (Fig. 1). The increase in microbial biomass was significant for the upper 10 cm only and all management types (organic: $p < 0.05$, integrated: $p < 0.001$, fallow: $p < 0.01$, Student's t-test) except for grassland. The statistics indicate a more pronounced concentration of the microbial biomass in the upper centimeters of the soil in the integrated farming system (with reduced tillage) and in set-aside land compared to the organic farming system. Throughout the entire observation period, the copper-contaminated site, LOA 160–240, had the lowest microbial biomass (Fig. 1).

The development of total Collembola has already been addressed by Filser et al. (1999) and will only be dealt with briefly here. Over the entire area, abundance decreased from 35,456 individuals m^{-2} in 1991 to 20,337 individuals m^{-2} on average during 1994–1997. Based on mean values ($n = 5$) per LOA and taking the LOAs as replicates ($n = 11$), this decrease was significant (U-test, $p < 0.01$) in 1997 as compared to 1991, and showed a similar tendency ($0.05 < p < 0.1$) in 1994 and 1995. In most LOAs, the temporal variability of Collembola was very high. Following management conversion, individual numbers did usually not exceed 35,000 m^{-2}, except for areas with integrated management and one of the fallows (LOA 220–120). Looking at single management types, the overall decrease in total individual numbers was highly significant except for conversion to integrated farming (Table 1). The entire area was dominated by three taxa, namely *F. quadrioculata*, *P. armata* and *M. krausbaueri* (Fig. 2a). During 1991, the sum of these made up between 60% and 90%

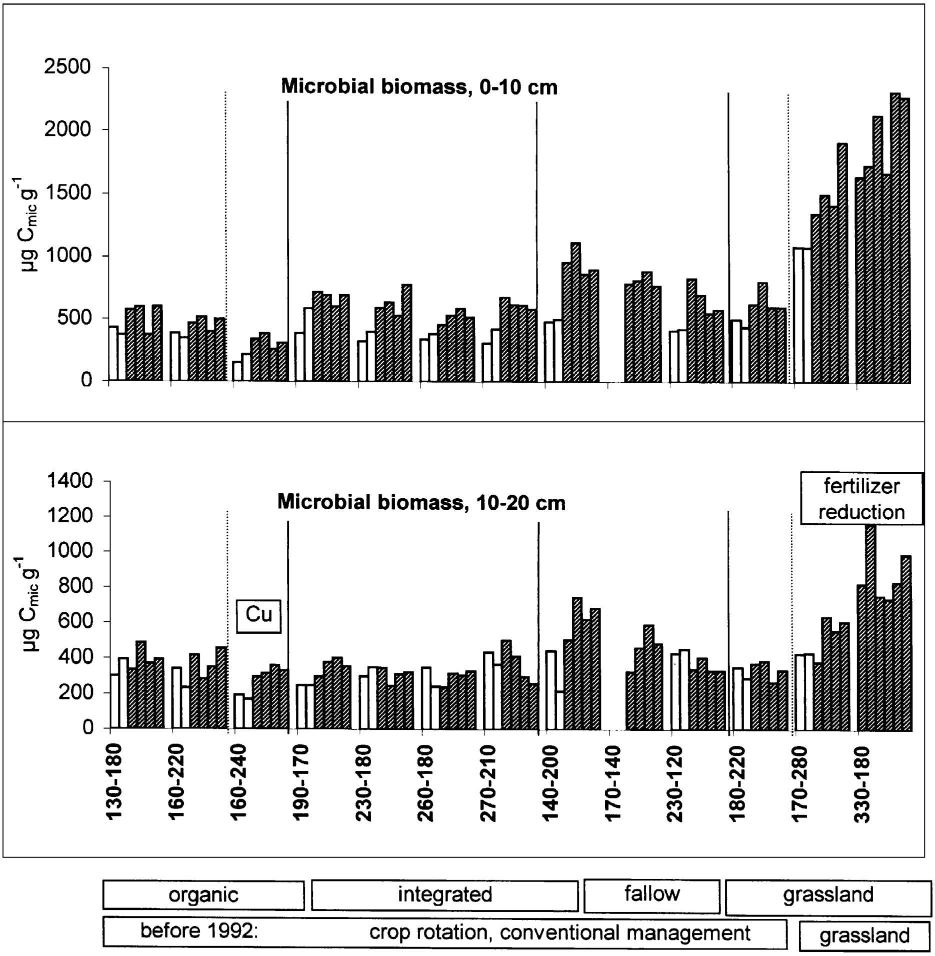


Fig. 1. Temporal development of soil microbial biomass in different management types. Numbers along x-axis denote LOA codes, "Cu" the Cu-contaminated site. Open bars: 1991–1992 (before management conversion); hatched bars: 1994–1997, subsequent years after conversion. For the statistics, see text.

of the Collembola community in any LOA. After conversion, this percentage decreased to 50% and 70%; in LOA 170–280 (grassland, no conversion, reduced fertilization) to less than 40%.

The abundance of *P. armata* and *Lepidocyrtus cyaneus* was negatively affected by management conversion or reduced fertilization in grassland, whereas the response of other species varied between sites (Fig. 2a,b; Table 1). Setting arable land aside had a negative effect on *F. quadrioculata* and *I. notabilis* abundance. The only species observed to significantly increase was *I. viridis* in the integrated farming system (Fig. 2a,b; Table 1).

Table 1
Significant differences (*U*-test; $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$; Bonferroni correction for $p < 0.05$, in parentheses: $p < 0.1$) in Collembola individual numbers (others = sum of rare species) according to management conversion, based on sampling in June, 1991 and early spring between 1994 and 1997 (one sampling before, four samplings after conversion)

	1991/1992 > 1994–1997 (decrease after conversion)				1991/1992 < 1994–1997 (increase after conversion)			
	o	i	f	g	o	i	f	g
F. quadrioculata group			**	(**)				
P. armata group	***	**	**	***				
M. krausbaueri group								
I. notabilis			***					
I. fucicolus								
I. viridis group						(**)		
L. cyaneus		***	***	***				
Isotomiella minor								
Sminthurinus sp.								
F. fimetaria								
Pseudosinella sp.								
Neotullbergia crassicuspis								
Others								
Total individual numbers	***		**	(**)				

o = conversion to organic farming, 2 LOA; i = conversion to integrated farming, 3 LOA; f = conversion to fallow land, 2 LOA; g = grassland, reduced fertilization, 1 LOA. For details concerning statistics, see Section 2.3.

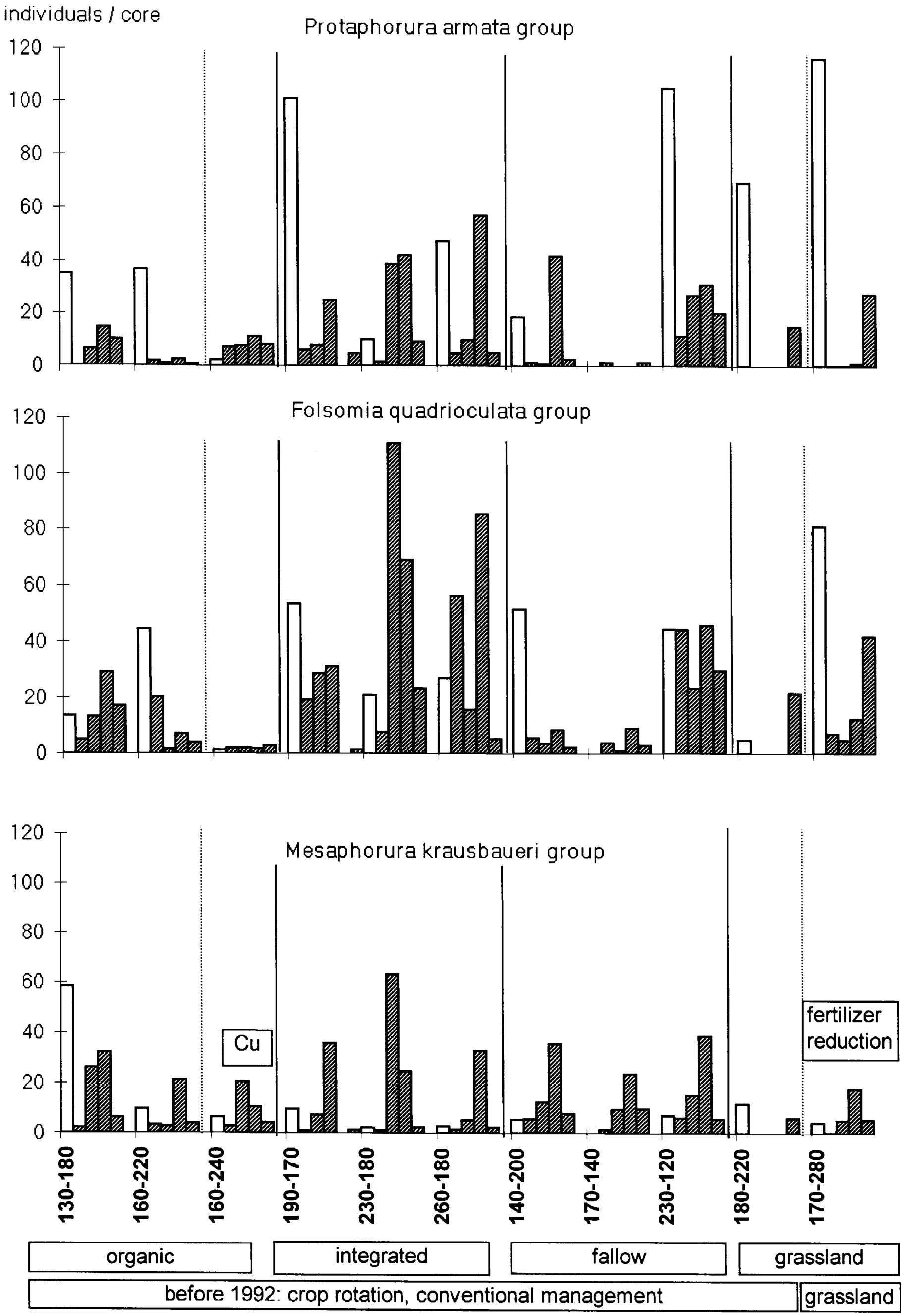
Arable land converted to grassland (LOA 180–220) had been sampled only in 1997, and increases in observed abundance of *N. crassicuspis*, *F. fimetaria* (data not shown) and *I. viridis* (Fig. 2b) were significant, as compared to 1991 (*U*-test, $p < 0.05$).

Due to high fluctuations in total abundance, the effects of management conversion appeared much more pronounced when considering the dominance structure of the Collembola community. Based on relative percentages of the single taxa, a cluster analysis revealed clear differences between Collembola before and after management conversion (Fig. 3a,b). In 1991, the single LOAs were highly similar, except for the copper-contaminated site and the very stony LOA 130–180 ⟨A3⟩, which differed from the other sites (Fig. 3a). After management conversion, the overall similarity was considerably lower, with the Euclidian distance of the Cu-contaminated site being the highest. The other sites formed three clusters: the first gathered the fields of the organic system and the fallow left to natural succession; the second a field of the integrated system and the grassland. The last group contained two sites of the integrated farming system and the mulched fallow (Fig. 3b).

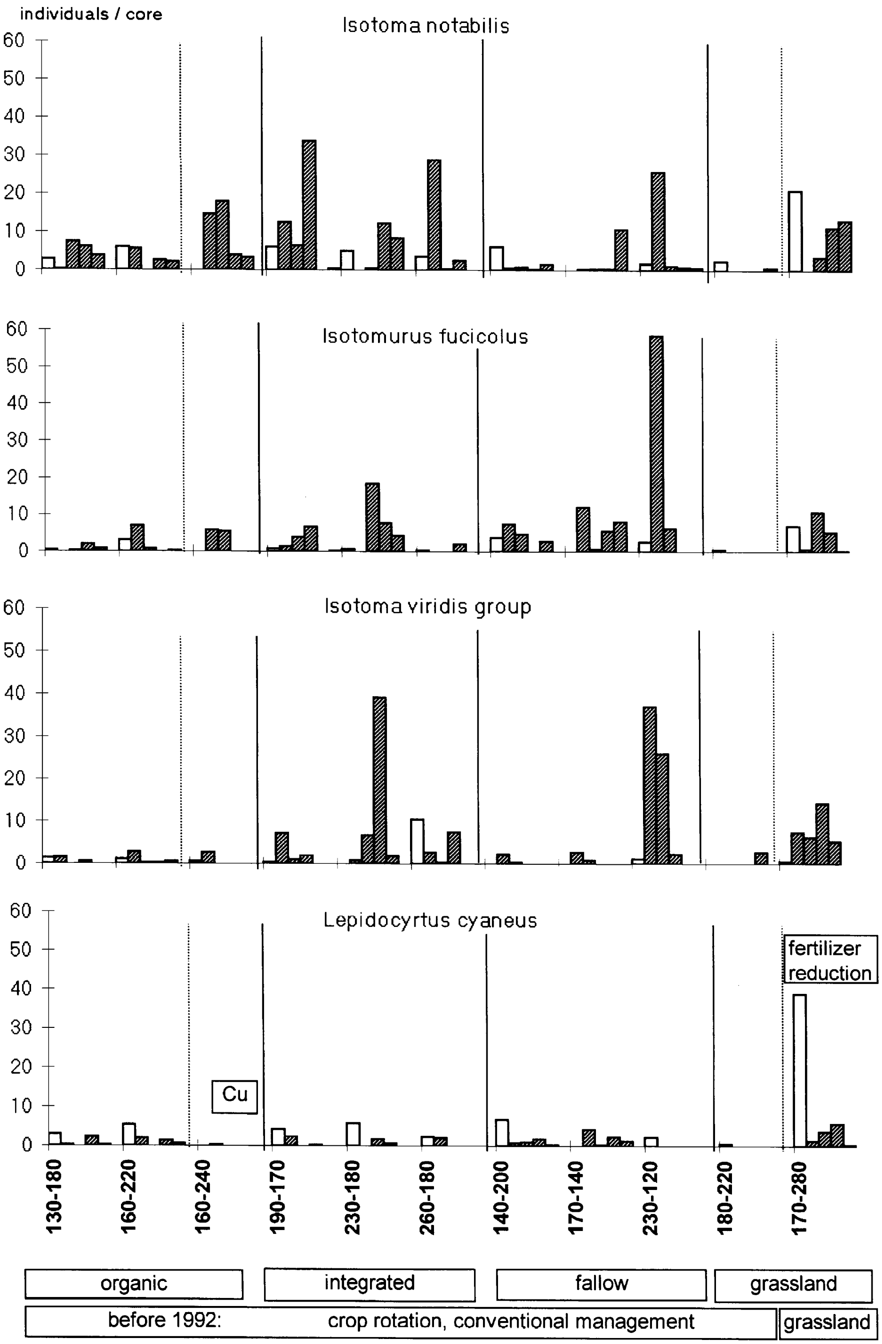
Modeling results are shown in Table 2. The regression trees identified management and year of sampling as the most important factors determining microbial biomass and Collembola abundance. In order to make the reader familiar with regression trees, the first model is explained. The last two columns show the summary statistics (C_{mic}, 0–10 cm) from the training data (left) and the remaining data after cross validation (right). The columns to the left contain the model rules, numbered according to importance, and the range of values within each rule. The first rule explains 54 cases ranging from 149 to 1730 μg C_{mic} g soil^{-1} ("*if* management conventional or organic, *then* the average value for C_{mic} is $471 + 13 \times$ year", i.e. here, a number between 0 and 6). In the subsequent rules, all calculated values are higher, which means not only that C_{mic} in grassland > fallow > integrated > organic/conventional, but also that the increase with time (factor with which "year" is multiplied) has the same order. Forty percent of the variability of microbial biomass was explained by management only (see last column), clearly distinguishing grassland (man = 4),

Fig. 2. (a) Temporal development of the dominant Collembola species (mean values in soil cores, volume = 728 cm^3, $n = 5$) in different management types. Numbers along *x*-axis denote LOA codes, "Cu" the Cu-contaminated site. Open bars: 1991 (before management conversion); hatched bars: 1994–1997, subsequent years after conversion (LOA 180–220 was only sampled in 1997). For the statistics, see Table 1. (b) Temporal development of the subdominant Collembola species (mean values in soil cores, volume = 728 cm^3, $n = 5$) in different management types. Numbers along *x*-axis denote LOA codes, "Cu" the Cu-contaminated site. Open bars: 1991 (before management conversion); hatched bars: 1994–1997, subsequent years after conversion (LOA 180–220 was only sampled in 1997). For the statistics, see Table 1.

fallow land (man = 3) and integrated farming (man = 2). Interestingly, the situation before conversion (man = 0) and the LOAs from organic farming (man = 1) were covered by the same rule (No. 1). For any rule, the model



indicated a pronounced increase with time. For the microbial biomass between 10 and 20 cm, model results were less clear and explained only 13% of variation (also expressed by a relatively large number of rules and comparably few cases



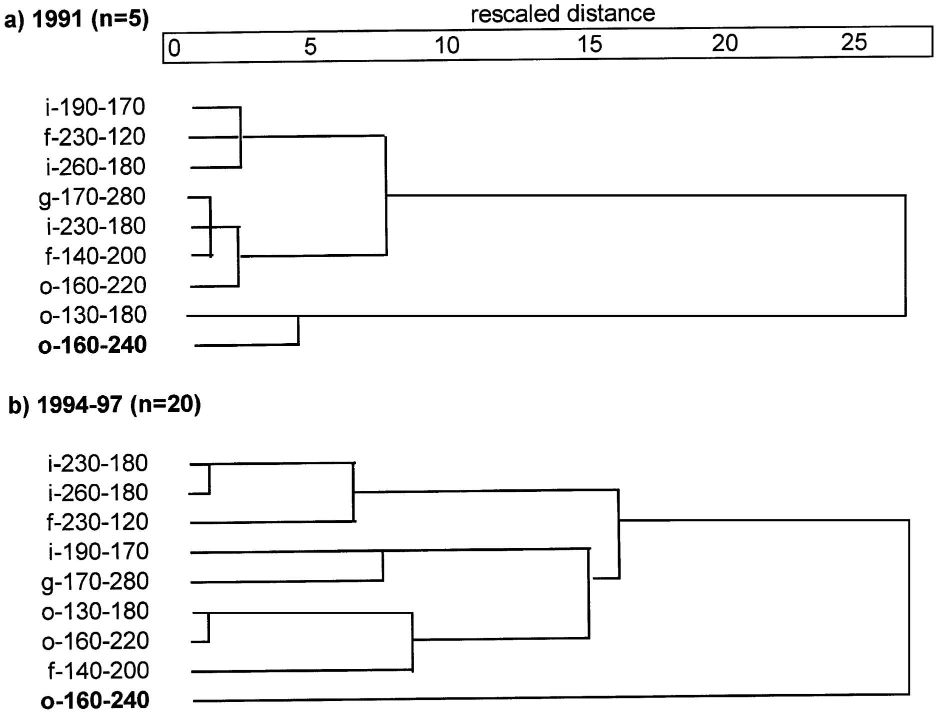


Fig. 3. Cluster analysis based on mean values ($n=5$) of Collembola dominance and taxa as in Table 1. For better overview, management abbreviations referring to the situation after conversion (o = organic, i = integrated, f = fallow, g = grassland) have been added to LOA numbers. (a) 1991, before management conversion; (b) 1994–1997, after management conversion (mean of all sampling occasions).

within the first rule). In rules 1 and 2, another general rule type is visible, namely, the double condition "*and*", read, e.g. "*if* year later than 1995 *and* management conventional or integrated, *then*...."

For total Collembola, evaluation on training data (data set used for the generation of the model) and evaluation by a fivefold cross validation explained 35% and 11% of the variation, respectively, indicating a heterogeneous dataset. Also here, management was important, with increasing abundance in the organic system, fallow land and grassland after management conversion but decreasing abundance in the integrated system. As a second factor, the model identified microbial biomass being positively related to Collembola numbers. Microbial biomass was also important for *P. armata*, but in this case, the relation was negative. Rules 1 and 4 clearly separated the situation before management conversion from the time after, with a sharp decline in abundance. Following conversion, rule 1 explains that the abundance found in the organic system and in grassland decrease with time; rules 2 and 3 explain the development in the

Table 2
Regression trees on factors determining microbial biomass (C_{mic}) and median values ($n = 5$) of Collembola abundances (a)

Rule	Cases	Range	*if*	then		Train	Cross
Model: C_{mic}, 0–10 cm (114 cases)							
1	54	149–1730	man in {0, 1}	$C_{mic} = 471 + 13$ year	ae	206.7	220.3
2	20	455–840	man = 2	$C_{mic} = 552 + 16$ year	r	0.66	0.64
3	12	526–1118	man = 3	$C_{mic} = 753 + 16$ year	ve	0.44	0.40
4	28	551–2321	man = 4	$C_{mic} = 1148 + 18$ year			
Model: C_{mic}, 10–20 cm (114 cases)							
1	10	261–405	year > 4	$C_{mic} = 305.5 + 2.9$ year	ae	98.8	106.6
			man in {0, 2}		r	0.42	0.36
2	10	241–503	1 < year ≤ 4	$C_{mic} = 352.3 + 2.9$ year	ve	0.17	0.13
			man in {0, 2}				
3	30	170–1163	year ≤ 1	$C_{mic} = 365.1 - 30.9$ year			
4	24	186–707	man = 1	$C_{mic} = 364.4 + 2.9$ year			
5	40	269–987	man in {3, 4}	$C_{mic} = 480 + 4.8$ year			
Model: total Collembola, 0–20 cm (50 cases)							
1	29	12–135	man in {1, 3, 4}	$a = 44.4 + 1.4$ year	ae	35.13	42.69
2	11	10–179	man in {0, 2}	$a = 66.8 + 0.085$	r	0.61	0.33
			$C_{mic} \leq 426$	$C_{mic} - 3.2$ year	ve	0.35	0.11
3	8	9–302	man in {0, 2}	$a = 3 + 0.181$			
			$C_{mic} > 457$	$C_{mic} - 3.2$ year			
4	2	180–207	man in {0, 2}	$a = -39.8 + 0.414$			
			$426 < C_{mic} \leq 457$	$C_{mic} - 3.2$ year			
Model: P. armata group, 0–20 cm (50 cases)							
1	17	0–21	year > 0	$a = 6.7 - 0.42$ year	ae	11.25	13.00
			man in {1, 4}	$- 0.0008\ C_{mic}$	r	0.64	0.52
2	14	0–32	man in {2, 3}	$a = 10.5 - 0.0116$	ve	0.40	0.25
			$C_{mic} > 503$	$C_{mic} + 0.27$ year			
3	10	2–47	man in {2, 3}	$a = 18.8 - 0.0094$			
			$C_{mic} \leq 503$	$C_{mic} + 0.69$ year			
4	9	1–107	year ≤ 0	$a = 44.2 - 0.0018\ C_{mic}$			

Factors used for calculation of the models: (1) man = management (0 = conventional, 1 = organic, 2 = integrated, 3 = fallow, 4 = grassland); (2) year = years after beginning of study (0 = 1991, 1 = 1992, before management conversion, 2–6 = 1993–1997, after conversion); (3) before/after conversion; (4) former hop-field (yes/no); (5) site (LOA code). For Collembola, factor no. 5 was replaced by "C_{mic}" (microbial biomass, measured at the respective LOA and sampling date in 0–20-cm depth). Rule = rule number, train = evaluation on training data, cross = cross validation, ae = average |error|, ve = proportion of variance explained.

integrated system and in fallow land with a slight increasing tendency from 1994 onwards. Models were also calculated for *M. krausbaueri* and *F. quadrioculata* but revealed no significant results after cross validation.

4. Discussion

4.1. Response to land use change

Microbial biomass is not necessarily low in high-input farming systems (Zwart and Brussaard, 1991; Wardle, 1995; Wardle et al., 1999b). In the present study, microorganisms showed an overall increase in biomass after conversion from conventional farming to integrated farming, organic farming or fallow land but not in grassland, where fertilization had been reduced. Alternative agricultural systems, such as organic farming, promote microbial biomass and activity (Wardle, 1995; Fließbach and Mäder, 2000), irrespective of climate and soil conditions (Mäder et al., 1997). Microbial biomass is favored by both organic and mineral fertilization, it is positively related to soil organic matter content and weed biomass, and is usually higher in undisturbed, native soils than in arable soils (Brussaard et al., 1990; Zwart and Brussaard, 1991; Houot and Chaussod, 1995; Jordan et al., 1995; Wardle et al., 1999b). The concentration of microbial biomass in the uppermost 10 cm soil in all land use types, except for organic farming, can be related to a spatial distribution according to soil tillage (Wardle, 1995), which took place almost exclusively in the latter. Tillage per se has been reported to be positive, to have no effect or even reduce microorganisms (Zwart and Brussaard, 1991; Holland et al., 1994; Jordan et al., 1995; Wardle, 1995; Wardle et al., 1999b).

Although tillage or pesticides may sometimes have a negative effect (Hendrix et al., 1986; Zwart and Brussaard, 1991; Çilgi et al., 1993), Collembola can create large populations under high management intensity (Heimann-Detlefsen, 1991; Filser, 1995) and are less affected by farming practice than are most other soil animals, in particular earthworms and epigeic predators (Andrén and Lagerlöf, 1983; Hendrix et al., 1990; Holland et al., 1994; Wardle, 1995; Sabatini et al., 1997; Wardle et al., 1999a). We observed Collembola abundance to decrease considerably, except in the integrated farming system, i.e. the most intensive. These data contradict those of Andrén and Lagerlöf (1983), Mäder et al. (1997) and Wardle et al. (1999a), who found arthropod taxa to be generally high at high weed biomass, high organic matter input or in organic farming systems. Conversely, Collembola abundance was markedly higher in highly degraded soil with low organic matter content than with high SOM content (Hendrix et al., 1990). Competition or predation may explain the decrease of Collembola population densities following reduction of management intensity, despite increases in microbial biomass. Earthworm populations strongly increased, particularly in the organic system and in fallows (Filser et al., 1999). Earthworms may have competed with Collembola which are thought to be resource-controlled (Wardle et al., 1999a). In a field experiment, epigeal predators substantially reduced Collembola populations (Lang, 1998; Angermayr, unpublished data). A higher proportion or diversity of predators in low-input systems has been well documented (Wardle, 1995; Krooss and Schaefer, 1998; and references therein).

Since the total number of Collembola is highly variable, it cannot be a sensitive indicator of environmental change (Filser et al., 1999; Wardle, 1995; Wardle et al., 1999a). Although some considerable differences between single LOAs within one management type (cf. Fig. 2) existed, a number of effects were consistent at the species level. Under the conventional farming system in 1991, *P. armata* and *F. quadrioculata* dominated the Collembola community, whereas the population sizes of *I. fucicolus* and *I. viridis* were very low. With few exceptions, conversion resulted in a general decrease of *P. armata* and *L. cyaneus*. Under integrated management, *F. quadrioculata* dominated and *I. viridis* increased in abundance.

The *I. viridis/I. anglicana* group and *I. fucicolus* are typical of wet grassland and arable land with green manure or underseeds (Heimann-Detlefsen, 1991; Filser, 1995, 1999). *P. armata* is abundant in arable land with high organic matter content, even in intensively managed fields (Brussaard et al., 1990; Krogh, 1991; Filser, 1995). *L. cyaneus* occurs both in grassland and in arable land with high nitrogen availability (Gisin, 1960; Mebes, 1999). The *F. quadrioculata* group is sensitive to fungicides, in particular copper (Krogh, 1991 and personal communication, Filser et al., 1995). Within this group, differences between species exist: *F. quadrioculata* thrived very well in the integrated farming system, whereas *F. manolachei* was strongly augmented in fallow land (Filser, 1996; Mebes, 1999).

According to Heimann-Detlefsen (1991) and Çilgi et al. (1993), high management intensity should negatively affect mainly epigeal and hemiedaphic Collembola species, and species with a low dispersal ability should take a long time to recover. However, our data demonstrate this approach to be too simplistic. Indeed, large epigeal taxa, such as *I. viridis*, were favored and the euedaphic *P. armata* decreased when management intensity was reduced or areas were set aside. Under the same conditions, however, one epigeal species, *L. cyaneus*, decreased and euedaphic taxa with low dispersal ability such as *M. krausbaueri* flourished.

4.2. Site effects and sampling strategy

The cluster analysis indicated management-induced changes within the Collembola community. The clear separation of the Cu-contaminated site from all other LOAs confirmed the long-lasting effect of heavy metals on Collembola (Filser et al., 1995). However, intermixing of grassland, mulched fallow and integrated farming sites demonstrated that effects other than management, such as soil type or vertical distribution (Andrén and Lagerlöf, 1983), also determine species dominance. Euedaphic Collembola appear to be more sensitive to soil properties than epigeal or hemiedaphic ones (Fromm et al., 1993; Filser and Fromm, 1995; Fromm, 1998; Mebes, 1999). In this study, differences in microbial biomass due to management were found only at the 0–10-cm soil depth. Mulching can result in microorganism concentration close to the soil surface (Wardle et al., 1999b). In studies reviewed by Mäder et al. (1997), soil microbial biomass also increased in deeper layers, yet in all these studies, the various management systems were conducted for at least 10 years. Thus, organisms living close to the soil surface seem to reflect actual management rather than euedaphic ones. Nevertheless, processes in arable soils do not only take place in the uppermost centimeters and, if indication should not only describe differences between sites but reflect processes important for nutrient turnover and plant nutrition, the indicators should be recorded in the relevant horizons, i.e. in the rooted zone.

Within-year temporal variability and effects of the present crop may obscure management effects on soil organisms (Andrén and Lagerlöf, 1983) and was a reason to restrict sampling in our study to the spring. Our additional, extensive records prior to and following conversion have shown that the spring data generally represented the annual mean of both microbial biomass, and Collembola abundance and community structure (Fromm et al., 1993; Filser et al., 1995, Filser and Fromm, 1995; Fromm, 1998; Winter, 1998; Mebes, 1999; Palojärvi, unpublished data). Thus, we think that in long-term studies, sampling of microorganisms and Collembola can be restricted to the spring aspect (design suggestions see below), irrespective of high temporal fluctuations throughout the year. Resultant information may sometimes be biased or lost, but the general patterns occurring after land use change will remain unchanged.

4.3. Conventional statistics versus artificial intelligence methods

Simple statistical comparisons were sufficient to identify changes in the decomposer community as a function of land use change. Multiple regressions revealed that, for the variation of microbial biomass, soil nitrogen content and water holding capacity were more important than management, which contributed only 10–13% to the total variance (Filser et al., 1999). Other factors were year and silt content, where at least 50% of the variance remained unexplained at each depth, despite the extensive inclusion of additional information (soil pH, carbon content, C/N ratio, water holding capacity, bulk density, sand and clay content, temperature, precipitation, vegetation cover and intercrop). Although it has to be kept in mind that some of these variables are intercorrelated with “management” (e.g. due to higher carbon content in grassland), the power of the model trees becomes obvious when taking into account that a very limited set of variables (cf. Table 2) could explain approximately

40% of the microbial biomass variation, despite exclusion of soil water and nitrogen content (water content due to its strong dependence on actual climate, nitrogen content was not measured regularly as it will take decades to change).

Due to sandy or even stony soils and because the Cu-contaminated field was situated in this area, the average microbial biomass in the "organic" LOAs was generally lower than in the rest of Scheyern (cf. Fig. 1). Consequently, the model placed the organic farming system in one group with the whole arable land under conventional management. However, the factor "site" did not contribute to the models, showing that pedological differences within Scheyern exerted no significant influence on microbial biomass development. Although LOA 160–240 clearly differed from all other sites, also the factor "hop" ($\cong$ site property "Cu contamination") never occurred in the models, being perhaps overruled by the positive effect of the new management.

Correlations, regressions, factor analyses, etc. aid in interpreting results, but reveal only one single equation or ordination plot not permitting, e.g., unimodal relationships. The latter is possible with other procedures, such as canonical correspondence analysis (CANOCO). Using several of these techniques and only the 1994/1995 data, Mebes (1999) showed that dominant Collembola species were associated with certain environmental variables (mainly microbial parameters) and either less or more intensive management. However, the CANOCO model output disallows extensive interpretation as well since it only demonstrates the strength of the relationship between the variables and factors. The great advantage of model trees is their ability to split datasets according to defined variables by means of different rules, thus providing a maximum transparency for non-linear relationships. The model presented a more differentiated view of the data than conventional statistics, e.g. it can be seen from the rules that, after a pronounced drop following management conversion, *P. armata* showed an increasing trend between 1994 and 1997 in the integrated system and in fallow land but decreasing tendencies in the other management types (Table 2). Although this outcome fits the data (Fig. 2a), it was not revealed by "classical" statistics, which presented solely negative tendencies (Table 1).

Overall, the model fit for *P. armata* was comparable to the one achieved for the microbial biomass in 0–10 cm, but the cross validation strongly reduced the proportion of variance explained, indicating a more heterogeneous dataset than the microbial biomass data. A plausible explanation is that the latter dataset contained more than twice as many cases. We assume that the Collembola data set was too small to fully exploit the possibilities of regression trees. To avoid pseudoreplication (e.g. Lamont, 1995) in the present analyses, the replicates per plot and sampling date were pooled, thus reducing the total cases to one fifth of its original size (and even then the annual samplings per plot cannot be regarded as strictly independent data). The replication on selected plots had been necessary to produce reliable time series in each of them.

4.4. Conclusions

The present long-term study is one of very few existing on the reactions of soil organisms to land use change. Our conclusions are based on a large dataset, supported additionally by extensive records at high spatial and temporal resolution, comprising many crops and different soil types. Most of our data have confirmed findings by other authors based on plot experiments, but there were also new, partly unexpected, results. Figs. 1 and 2 clearly demonstrate the large differences existing between single plots within each management type. If our investigations had been restricted to a short time period or to only one soil type, as is commonly the case in replicated plot experiments, contradicting results to those presented here would have been obtained, especially concerning Collembola. Nevertheless, our report is valid only for comparable climatic conditions, soil types, and crop rotations. Even so, our study has pointed out the importance of investigating effects of land use change at the landscape level. In order to model the influence of environmental variables in a heterogeneous landscape, we suggest the following experimental design: (i) replicate sampling within one plot should be avoided. Instead, concurrently investigate a correspondingly larger number of plots. (ii) Avoid repeating measurements in one plot during subsequent years, but randomly select the plots to be sampled within a given area. The resulting dataset will be large and problems of independence and pseudoreplication are unlikely to occur.

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