Temporal predictability of soil microarthropod communities in temperate forests

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Summary

The temporal predictability of soil microarthropod communities in stable forest ecosystems was analysed using data gathered from the literature and original data. Four studies were found with time series of at least five consecutive years; they all reported data on Collembola from temperate forests (as do the original data included). We applied the time lag analysis (regressions of Euclidian distance between communities on time lag) for detecting directional change of community composition, the partial rate autocorrelation function for detecting density dependence, and we regressed standard deviations of the logarithms of abundance on observation period for detecting the colour of the time series. Collembolan communities did not show directional change over time, and the composition of the community appeared to be predictable at a gross qualitative level: dominant species tend to stay dominant over time. A high degree of density dependence could be detected, which might be responsible for the observed temporal stability of community composition. Intra- and interspecific competition and/or predation may cause deterministic community structure and the results of this study support the increasing body of evidence that Collembola communities are structured by intensive biotic interactions. Collembolan populations did not show any fluctuations characterised by scaling laws. Either there actually exist point attractors and stable equilibria in Collembola (brought about by non-overcompensating density-dependent interactions), or Collembolan community trajectories are restarted every year by external forces. Due to the large time-scale of environmental variation in forests,

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low-frequency noise in Collembola may be recognisable only in time series spanning at least some decades.

Introduction

The analysis of variability and constancy in ecological populations and communities has been a focus of ecological research for decades and still is of the utmost importance for understanding the complexity of intrinsic and extrinsic forces that influence their temporal dynamics (e.g. Pimm and Redfearn, 1988; Micheli et al., 1999; Lundberg et al., 2000; Bjørnstadt and Grenfell, 2001). During the 1980s, questions such as whether communities are in equilibrium or not dominated the search for patterns in ecological time series (e.g. Rahel et al., 1984; Lawton and Gaston, 1989). More recently, the identification of chaotic dynamics has led to the question whether the erratic fluctuations and reddened spectra (amplitudes of time series increase approximately as 1/(frequency)) often observed in ecological populations are caused by extrinsic or intrinsic forces (e.g. Costantino et al., 1997; Miramontes and Rohani, 1998).

These questions have been very rarely addressed to below-ground biota: whereas several above-ground systems are well studied (e.g. Tanner, 1966; Peterson et al., 1984; Royama, 1992), there is a dearth of data on the development of below-ground microarthropod populations and communities over time. Although being extremely numerous, with abundances of up to 500,000 individuals per square metre in suitable habitats (Petersen and Luxton, 1982), being amongst the most species-rich components of terrestrial ecosystems, with up to 200 species within $1\,m^2$ of woodland soil (Giller, 1996), and being suspected of considerable importance for influencing soil-biological processes relevant for entire ecosystems (Lussenhop, 1992), soil microarthropods are among the least studied arthropods regarding their temporal dynamics. This is due to a number of facts: (i) they are inconspicuous and tiny; (ii) their habitat (air-filled pores below the soil surface) is an extremely opaque system that renders non-destructive methods of observation almost impossible, and (iii) their communities consist of numerous species that present considerable (and, therefore, time-consuming) taxonomical difficulties. The only comprehensive work on the temporal aspects of soil microarthropods was published by Bengtsson (1994), who presented an analysis of the predictability of forest soil communities using data gathered from the literature. However, he applied only non-parametric correlation statistics based on the ranked abundances of species, which did not allow a closer insight into possible mechanistic relationships influencing the temporal dynamics of communities.

Soil arthropod communities are frequently used as bioindicator systems (but see Geissen and Kampichler, 2004). If this is to be successful, community composition should be stable in time as long as environmental conditions remain constant (van Straalen, 1997). In the present paper, we thus analyse data collected from published studies reporting time series of soil microarthropod abundances of at least five consecutive years in stable ecosystems without obvious directional change. It is a non-trivial task to decide when an ecosystems can be called 'stable' (Grimm and Wissel, 1997) and long-term changes in habitats due to the impact of climatic change or air-borne nutrient emissions, however, can never be ruled out. In this study, therefore, we considered habitats without short-term disturbances as 'stable', but successional studies on e.g. the development of communities on abandoned fields, spoil heaps or mine sites (e.g. Dunger, 1991) and studies monitoring change after experimental human impact, e.g. long-term studies of pesticide application, were not considered. We also did not include papers reporting on single species or total microarthropod densities only. The aim of this paper is to analyse how far soil microarthropod communities from stable ecosystems are predictable over time. To achieve this goal, we analysed the community dynamics as well as the dynamics of their constituent populations and asked three specific questions, namely (i) whether time series of soil microarthropod abundance show directional changes in community patterns over time, (ii) whether time series of single populations and total abundance show any indications of density-dependence, and (iii) whether time series of single populations or total abundance are characterised by a reddened spectrum, that is by frequency-dependent noise (Gisiger, 2001).

Materials and methods

Data origin

We found four studies that matched our search template (at least five consecutive years, stable

ecosystem, community data), namely the papers by Takeda (1987), Kaczmarek (1995), Wolters (1998) and Chernova and Kuznetsova (2000). All of them deal exclusively with Collembola and include data on the dominant species from six temperate forest ecosystems in Germany, Poland, Russia, and Japan. No published study on soil mites met the restrictions; they either reported on annual changes in a successional context (Koehler, 1998) or presented long-term data with large time-lags of several years (Hoy, 1990). When reported, we used abundance data measured at a fixed point in time each year (e.g., late autumn data), thereby avoiding noise by within-year demographic fluctuations, which can be considerable in microarthropod populations (van Straalen, 1997); otherwise, we used annual mean abundances. Characteristics of the included studies are shown in Table 1.

In addition to literature data, we also present original data on Collembola from a central European mixed forest ('Kottenforst') near Bonn, Germany, rendering this study exclusively to an investigation of Collembolan temporal dynamics. The forest had an extent of 3700 ha at an elevation between 145 and 175 m a.s.l. Mean annual precipitation and mean annual air temperature were 680 mm and 10.3 °C, respectively. The most abundant soil types in the forest were Stagnic Alisols on loess. The humus form in the stands dominated by spruce (*Picea abies* (L.) Karsten) was moder to raw humus, while the stands dominated by oak (*Quercus robur* L.) and hornbeam (*Carpinus betulus* L.) had mull to moder humus. We present data from five consecutive years (1993–1997) from the 2500 m^2 control plots of a long-term liming and fertilisation experiment, one stocked with oak and hornbeam, the other with spruce (Geissen, 2000). Undergrowth was only weakly developed in the oak–hornbeam stand; the spruce stand had a dense understory composed of raspberry (*Rubus fruticosus* L.) and bracken (*Pteridium aquilinum* (L.) Kuhn).

Collembola were sampled at the end of October each year by taking eight to 10 soil-cores (diameter: 5 cm; depth: litter layers and the uppermost 10 cm of the mineral soil) in a 100-m^2 area in the middle of the plots. Microarthropods were extracted in standard Tullgren funnels, sorted under a dissecting microscope, cleared by lactic acid, and identified according to the keys of Gisin (1959–1967, 1960), Fjellberg (1980, 1995) and Dunger and Zimdars (1995). For this study, we considered those of the 41 (oak–hornbeam stand) and 50 (spruce stand) species that accounted for >3% of individuals of the entire five-year sample at each stand; this left the species *Mesaphorura macrochaeta* Rusek, *Protaphorura armata* (Tullberg), *Supraphorura furcifer* (Börner), *Protaphorura quadriocellata* (Gisin), *Folsomia quadrioculata* (Tullberg), *Parisotoma notabilis* (Schäffer) and *Isotomiella minor* (Schäffer) (oak–hornbeam stand) and *Micranurida pygmaea* Börner, *Friesea mirabilis* (Tullberg), *Xenylla tullbergi* Börner, *M. macrochaeta*, *Paratullbergia callipygos* (Börner), *F. quadrioculata*, *P. notabilis* and *I. minor* (spruce stand) in the analysis. These species accounted for >78% and >87% of the total Collembola abundance in the oak–hornbeam and spruce stand, respectively.

Table 1. Characteristics of the studies included in the analyses of Collembolan abundance time-series in temperate forest ecosystems and parameters of the time-lag analyses

Habitat	L	S	Data	Authors	TLA		
					Slope	P	R^2
Red pine forest	15[*]	8	December data	Takeda (1987)[†]	592	0.605	0.00
Beech forest	10	6	Annual mean abundance	Wolters (1998)	877	0.292	0.03
Pine–oak forest	7	7	Annual mean abundance	Kaczmarek (1995)	19	0.237	0.07
Pine–oak forest[‡]	6	7	Annual mean abundance	Kaczmarek (1995)	96	0.066	0.24
Spruce forest[§]	5	5	August data	Chernova and Kuznetsova (2000)	−350	0.317	0.12
Spruce forest[¶]	5	3	August data	Chernova and Kuznetsova (2000)	−77	0.570	0.04
Oak–hornbeam forest	5	7	October data	Original data	−8622	0.354	0.11
Spruce forest	5	8	October data	Original data	−2258	0.606	0.03

TLA, regression of the square root of time-lag on squared Euclidian distance. L, length of the time series in years; S, number of species in the analyses; P, significance level of the slope; R^2, explained variance.
[*]Two years missing.
[†]For the time-lag analysis, a year had to be left out due to the mass occurrence of a single species, which eliminated the requirements for regression analysis.
[‡]Occasionally flooded.
[§]Mosses dominating on the forest floor.
[¶]Common wood sorrel (*Oxalis acetosella*) dominating on the forest floor.

Statistical analysis

The available time series on soil microarthropods were extremely short and even shorter than that normally encountered in ecological datasets (Perry et al., 2000), setting hard limits to the possibilities of statistical analysis. We examined change of community composition over time by the time-lag analysis (TLA) presented by Collins et al. (2000). Briefly, for all possible pairs of years, jk, the Euclidean distance ED between their communities was calculated as

$$ED = \left(\sum_{i=1}^{S} (x_{ij} - x_{ik})^2 \right)^{1/2} \qquad (1)$$

where x_{ij} is the abundance of the ith species in the jth year, and x_{ik} is the abundance of the ith species in the kth year, and S is the total number of species. The ED values were plotted against time lag for all lags, and a linear regression was calculated for ED as a function of the square root of the time lag. The square root transformation corrects for the fact that the smaller number of points at larger time lags potentially bias the regression analysis. TLA allows for the discrimination between different patterns of community change: significantly positive regression-lines (ED increases with time lag) imply directional change; non-significant slopes imply stability or stochastic variation (ED does not change with time-lag); significantly negative slopes imply convergence of communities (ED decreases with time-lag). No attempt was made to force the collected data into a unified measure (e.g. individuals m^{-2}) due to different sampling regimes and data processing in the included papers. Consequentially, the ED values and the slopes of the regression lines cannot be directly compared across studies.

The two longest available time series (Takeda, 1987; Wolters, 1998) were checked for indications of density-dependence according to the partial rate correlation function (PRCF) introduced by Berryman and Turchin (2001). Briefly, PRCF is a further development of the conventional way of determining density-dependence: the partial autocorrelation function (PACF) by Box and Jenkins (1976). The PRCF model can be written as

$$R_t = a_0 + a_1 L_{t-1} + a_2 L_{t-2} + \cdots + a_d L_{t-d} + \varepsilon, \qquad (2)$$

where R_t is the per-capita rate of change $\ln(N_t/N_{t-1})$, $L_{t-\tau}$ is the log-transformed population density N at time $t - \tau$ (where $\tau = 1, 2, \ldots, d$ is the time lag), $a_0, a_1, \ldots, a_d$ are the regression coefficients, and ε is an exogenous error term. First, R_t is regressed on L_{t-1}, the correlation coefficient yields PRCF[1]. Next, R_t is regressed on L_{t-1} and L_{t-2} and

PRCF[2] is the partial correlation coefficient between R_t and L_{t-2} given that L_{t-1} is already in the model. Subsequently $L_{t-3}, L_{t-4}, \ldots, L_{t-d}$ are added to the model, yielding PRCF[3], PRCF[4], $\ldots$, PRCF[d]. This model has the advantage over PACF that the null model is more adequate for biological systems: while in PACF the system goes to a fixed point when the dependent variable is unaffected by the independent variables ('perfect compensation'), the null model in PRCF is either a continually increasing, a continually decreasing, or a constant population. The practical difference is that PRCF[1] can have negative values, which indicates direct density dependence. In contrast, even in unregulated populations, PACF[1] can have strong positive spikes, potentially obscuring effects of negative feedback. Coefficients of PRCF are assumed to be statistically significant when they are larger than $2/n^{1/2}$ ('Bartlett's criterion', Berryman and Turchin, 2001), with n being the length of the time series. Since the 15-year time series by Takeda (1987) lacks values for two years (Table 1), the number of data varied between lags (for example, n was only 10 for the correlation between R_t and L_{t-1}) and significance limits had to be conservatively set at $2/10^{1/2} = 0.632$ (for an unbroken series of 15 years, Bartlett's criterion would be $2/15^{1/2} = 0.516$). As in TLA, the original measures of the data were retained for the analysis.

The available time series are much too short for a sensible spectral analysis. Thus, for the eight consecutive years within the 15 year time series by Takeda (1987) and for the entire 10 year time series by Wolters (1998), we estimated the colour of their noise by plotting the standard deviations of the logarithms (SDL) of density against the period over which the calculation was made and computing a linear regression, a simple approach introduced by Pimm and Redfearn (1988) for the analysis of skylark time series. SDL was calculated for nested periods of 2, 4 and 8 years (that is for the years x and $x + 1$, x to $x + 3$ and x to $x + 7$). This 8-year window was shifted along the 10-year study period of Wolters (1998); we averaged the values of the resulting three regression analyses. If SDL increases with observation period, this indicates long-term trends in abundance: what might appear to be an equilibrium over a number of years is really a level cycling over longer time periods. Power spectras of such time series are proportional to $1/f$ ('$1/f$-noise' or 'red noise') (Gisiger, 2001). If the time series are characterised by white noise, in contrast, the regression between SDL and observation period does not differ from 0. As in TLA and PRCF, the original measures of the data were retained.

Results

None of the slopes of the TLA deviated significantly from 0. Thus, no directional change of community composition of soil Collembola could be identified in the time series (Table 1, Fig. 1). There was high scatter in the ED values, and the regression models explained only a few percent of their variance (Table 1). The occasionally flooded site of Kaczmarek (1995) showed the highest R^2 (0.24) and a positive slope close to formal significance ($p = 0.07$), indicating a trend towards directional change in the community.

No evidence could be found for the existence of reddened spectra in the time series of soil Collembola: only two of the 15 regressions of the standard deviations of the logarithms of density against observation period were statistically significant, one each for the data of Takeda (1987) and of Wolters (1998) (Fig. 2), contrary to expectations showing a negative slope. However, since these were multiple analyses ($n = 8$ for Takeda (1987), $n = 7$ for Wolters, 1998), the probability that at least one regression line was significant by chance alone was 0.34 (for Takeda, 1987) and 0.30 (for Wolters, 1998).

All species from the data of Takeda (1997) and four of the six species from the data of Wolters (1998) showed statistically significant PRCF coefficients for lag 2 (*F. quadrioculata*) or lag 1 (remaining species) (Fig. 3), thus strongly indicating a density-dependent structure of the time series of the soil Collembolan populations. In contrast to single-species data, the density of total Collembola (available only for Wolters, 1998) did not show signs of density-dependence.

Discussion

Although data are scarce and time series for soil microarthropods usually only span two or three years, the view exists that their populations are rather stable over a number of years, in particular for species with high abundances (van Straalen, 1997). For soil fauna communities in general, Bengtsson (1994) states that, in stable, unchanging habitats, they are quite predictable, based on the concordance of the relative abundances of the constituent species over time. Compared with the data for aquatic invertebrates or terrestrial plants, the interannual fluctuations of Collembolan species are in fact quite moderate when measured by the standard deviation of the logarithmically transformed population abundances; Takeda (1987) and

Chernova and Kuznetsova (2000) report values between 0.1 and 0.5 and between <0.1 and 0.3, respectively. Vegter et al. (1988), in a study of Dutch forest Collembola, found values between 0.3 and 0.9. Moreover, Takeda (1987) and Chernova and Kuznetsova (2000) determined a high degree of concordance in species ranks over their observation times of 15 years (Kendall's $W = 0.8$) and five years (Kendall's $W = 0.8$ in both spruce stands), respectively. This observation was also made by Kaczmarek (1995), although she did not formally test concordance. Only Wolters (1998) describes his data as varying remarkably from year to year with respect to which species were dominant.

TLA grossly supports this view, showing that, in unchanging habitats, soil Collembolan communities are constant insofar as a directed change in community structure was not detectable. However, ED showed a wide scatter in most of the data sets; for Takeda (1987), for example, minimum (2051) and maximum (35,765) values of ED differed by a factor of 17.4, for Wolters (1998) ED varied between 2009 and 12,694, supporting his observation of interannual variability. The lag between years has no explanatory power at all for ED, except for the data of the wet spruce stand by Chernova and Kuznetsova (2000). They remark in their paper that the site is occasionally flooded. Obviously, these perturbations tend to induce a directed change of the community as shown by the nearly significant slope of TLA and a larger ratio of signal versus noise, as indicated by its R^2.

The lack of directional change alone does not imply a stability, it could also suggest stochastic change. However, PRCF shows that a high degree of density-dependence in Collembolan communities might be responsible for the observed stability of community composition. Wolters (1998) reported inconclusive evidence for a density-dependent structure of Collembolan time series based on the randomization procedure by Pollard et al. (1987). He stated, however, that at least part of the community may be exposed to processes leading to density dependent regulation. Also, Takeda (1987) supposed density-dependent regulation to be the cause for the consistency of temporal organisation patterns of the studied Collembolan community, yet without testing this hypothesis by formal analysis. Recently, Ferguson and Joly (2002) presented evidence for endogenous control of springtail numbers on forest soils in intra-annual time series by finding negative correlations between population growth rate and 1-week lagged density. It has been suggested that intra- and interspecific competition and/or predation may lead to the deterministic community structure of the soil fauna
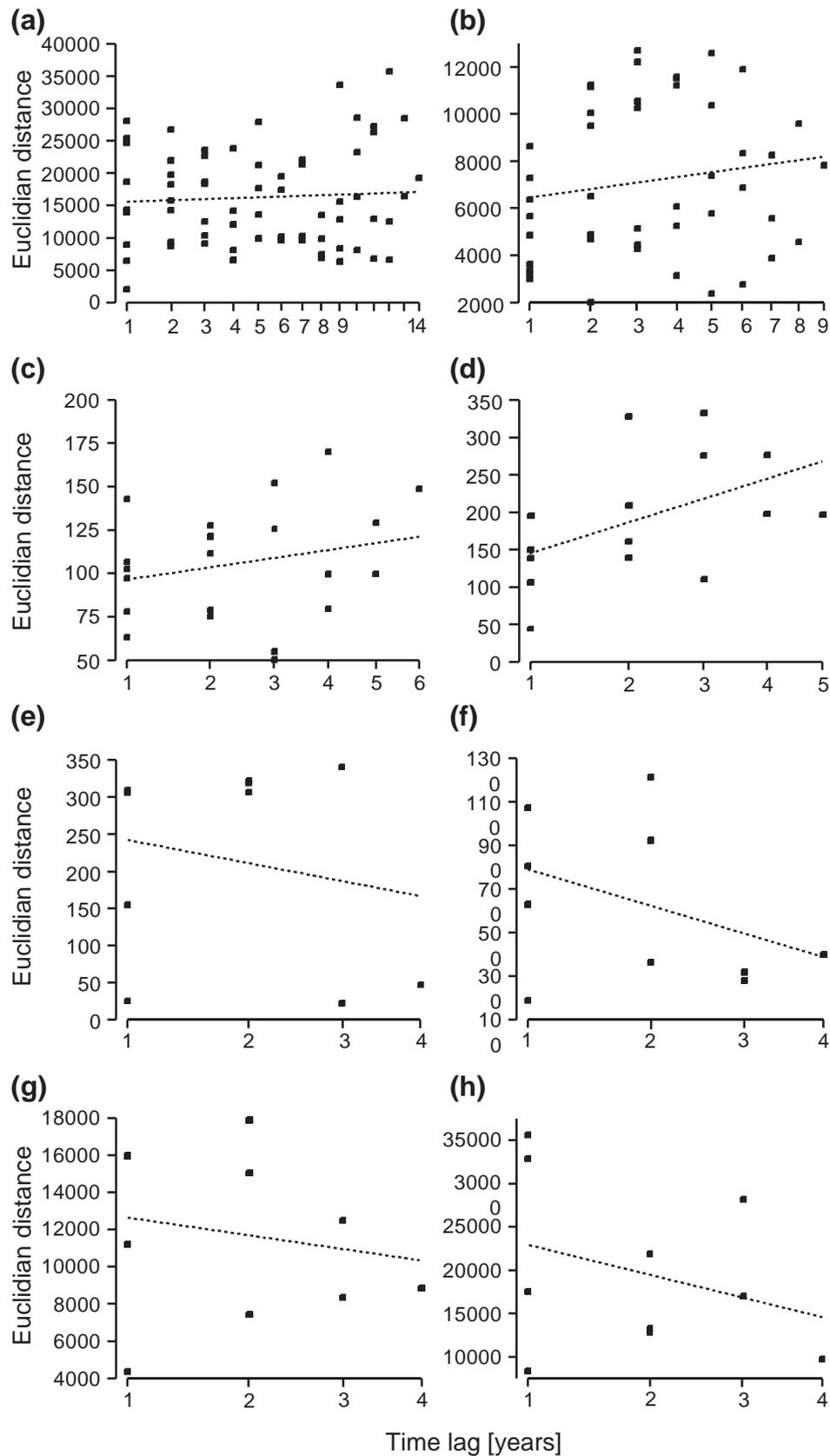
Figure 1. Time-lag analysis (regression of the square root of time-lag on Euclidian distance) of Collembolan abundance dynamics in temperate forests: (a) red pine forest (Takeda, 1987), (b) beech forest (Wolters, 1998), (c) spruce forest and (d) occasionally flooded spruce forest (Kaczmarek, 1995), (e) spruce forest with dominate wood sorrel and (f) mosses on the forest-floor, respectively (Chernova and Kuznetsova, 2000), (g) spruce forest and (h) oak–hornbeam forest (original data). See Table 1 for slopes and significance levels of the regression lines.
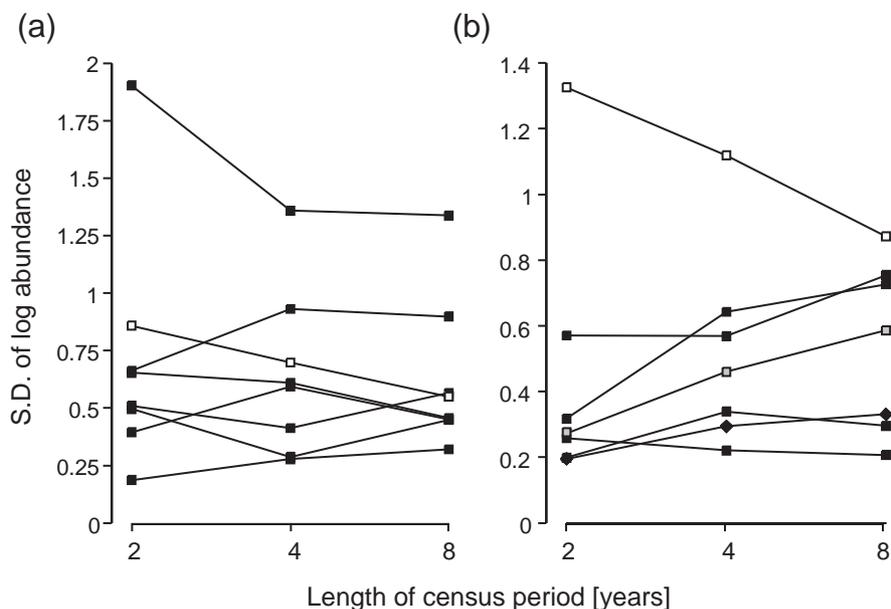
Figure 2. Standard deviations of the logarithms of density plotted against the period over which the calculation was made: (a) red pine forest (Takeda, 1987), (b) beech forest (Wolters, 1998). Single species are represented by squares, total Collembola by diamonds. Black symbols: slope is different from 0 with $P>0.1$; grey symbols: $P<0.1$; white symbols: $P<0.05$.

(Bengtsson, 1994), and the evidence that Collembolan communities in particular are structured by intensive biotic interactions has been growing during the last 15 years. First, a number of early laboratory experiments had demonstrated considerable biotic interactions between Collembolan populations (Christiansen, 1967; Culver, 1975; Longstaff, 1976; Christiansen et al., 1992), including direct interaction, substrate conditioning and airborne allomones. Second, Collembolan populations are food-limited and their density in the field could be increased by 3–4 times in a food-enhancement experiment (Chen and Wise, 1997). Third, abundance profiles of Collembolan field populations are quite similar across studies and resemble straight lines if plotted as rank versus log abundance (for example in Takeda, 1987; Vegter et al., 1988; Kampichler, 1992; Giller, 1996), commonly explained by a strong degree of dominance and pre-emptive competition along a joint niche-axis (Magurran (1988); but see Hubbell (2001) for an alternative explanation by the Unified Neutral Theory). Vegter et al. (1988) argue that, in contrast to conventional theory, this hierarchical structure of Collembolan communities does not characterise assemblages in an early successional state but that it is typical for developed communities where more and more species are forced into secondary roles. Fourth, while most studies addressing the relationship between local and regional diversity detected proportional sampling (Cornell

and Karlson, 1997), that is, the number of locally coexisting species is a constant proportion of the regional species-pool and increases with its size (Cornell and Lawton, 1992), Collembola show a hard upper limit to local species richness independent of the size of the regional pool (Winkler and Kampichler, 2000). Although none of these observations in isolation can prove that Collembolan field populations are actually structured by internal biotic forces, the sum of empiric data along with the results of this study strongly suggest this.

The reddened spectra of ecological time series have conventionally been interpreted as being driven by external environmental forces. However, even laboratory populations under constant experimental conditions can produce coloured time series, as shown by Miramontes and Rohani (1998). They suggest that chaotic dynamics may simply arise naturally from the interaction between demographic stochasticity and density dependence. What then could be the reason that the Collembolan field populations in this study did not show reddened spectra? First, the time series simply could have been too short for being able to detect red noise, even when using SDL analysis. However, since there was not the slightest trend for positive relationships between observation period and the standard deviation of log abundance, and since the only significant slopes showed the opposite trend of decreasing standard deviation with increasing time period, these results must be
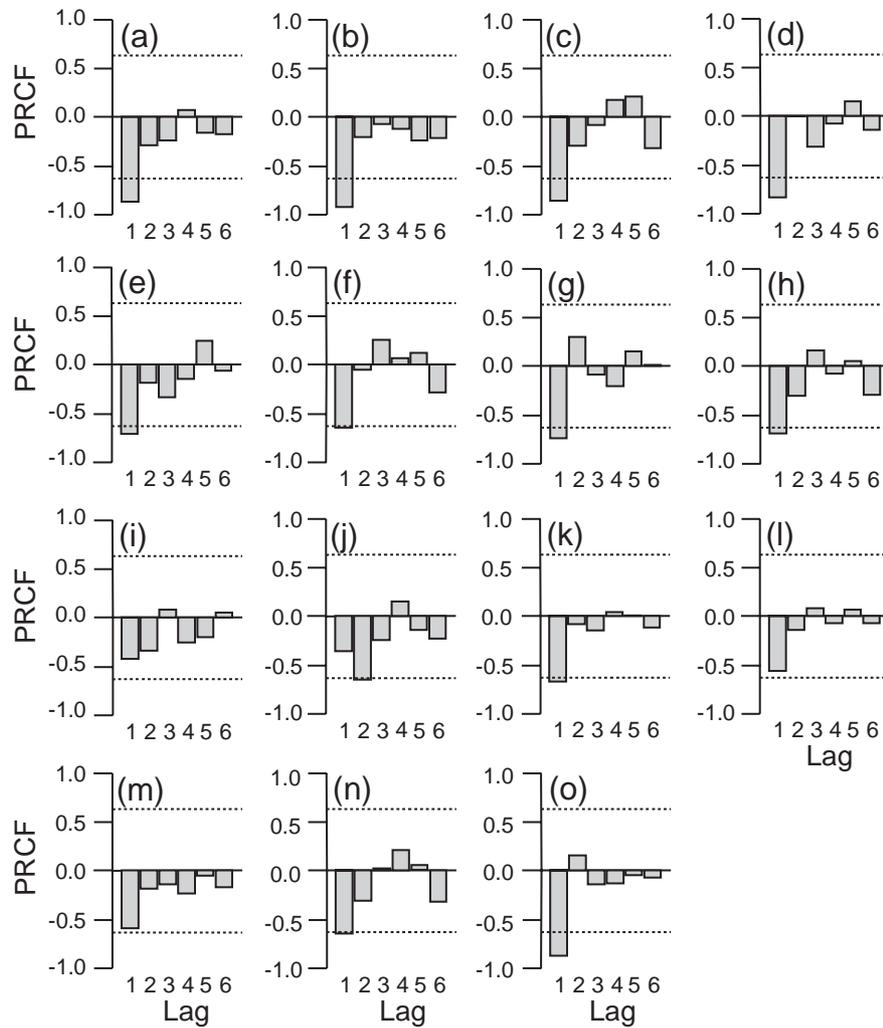
Figure 3. Partial rate correlation function (PRCF) for the time series of (a) *Folsomia octoculata* Handschin, (b) *Tullbergia yosii* Rusek, (c) *Tetracanthella sylvatica* Yosii, (d) *O. decemsetosus* Yosii, (e) *Isotoma carpenteri* Börner, (f) *Tomocerus varius* Folsom, (g) *Isotoma sensibilis* Tullberg, (h) *Folsomina onychiurina* Denis in a Japenese red pine forest (data from Takeda, 1987), and of (i) total Collembola, (j) *F. quadrioculata*, (k) *Mesaphorura krausbaueri* Börner, (1) *I. minor*, (m) *Lepidoyrtus lignorum* (F.), (n), *P. notabilis* and (o) *Sminthurinus flammeolus* (Gisin) in a Central European beech forest (data from Wolters, 1998). Dotted lines indicate limits for statistical significance (values >0.632) according to Bartlett's criterion (see Material and Methods for explanations).

taken seriously. Second, density-dependent inter-actions can potentially stabilise fluctuations in density unless they are strongly overcompensatory, resulting in point attractors and stable equilibria (Bjørnstadt and Grenfell, 2001). Third, we return to the argument by Vandermeer (1990) that temperate time series can be prevented from showing chaotic behaviour by mortality factors related to distinct seasonality (for example, winter frost or summer drought), which "restart" com-munity trajectories each year. Wolters (1998), in fact, made the observation that population den-sities of some species were related to the tem-perature conditions of the previous year and

discussed possible effects on overwintering eggs or on the number and/or fertility of overwintering adults. Bengtsson (1994) found only a small increase of variability in soil fauna populations with time, which did not translate into decreased predictability. He explains this pattern by the larger time-scale of environmental variation in forests (related to the turnover of trees and soil organic matter) compared with the length of the available time series, resulting in small changes in community composition. According to this view, low-frequency noise in soil Collembolan dynamics should be recognisable only in time series spanning at least some decades. Thus, using a metaphor by

Vandermeer (1990), Collembola communities in temperate forest may be 'like the climate, predictable at a gross qualitative level'.

Finally it must be stated that the data basis on microarthropod temporal dynamics is very poor and hampers a consistent interpretation of their patterns. We conclude cautiously that density-dependent dynamics tend to stabilize time series of Collembola and prevent directional change of community composition. Density-dependent dynamics could also be responsible for the observed lack of reddened spectra of the time series, alternative explanations, however, have to be kept in mind. We urgently need more and longer time series on microarthropods and other soil fauna to understand their temporal dynamics.

Acknowledgements

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