Primary colonisation of newly formed soils by actinedid mites

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Abstract

In the brown-coal open-cast mining district near Cottbus, Germany, an artificial, experimental water-catchment system was constructed in 2005. The purpose of the experiment is to observe the development of the soil ecosystem during simulated primary succession. Within these studies the development of the soil fauna has been monitored since late 2005, of which the results regarding actinedid mites are presented here. Actinedida represented the major microarthropod group colonising the newly developing soils, having been present within months after exposition of the substrates to the surface, albeit in very low densities and only in sporadic samples. Initially, species richness was also extremely low, with practically only *Nanorchestes* sp. und *Speleorchestes* sp. present. Three years after site initiation, the abundances and species richness increased significantly, although they were still low compared to mature soils. The microarthropod communities continued to be strongly dominated by actinedid mites and colonisation of the soils remained spatially heterogeneous. The sporadic individual-richness was mostly caused by strong population development of single species in a few samples, e.g., *Siteroptes* sp. and *Bakerdania* sp. The abundance and distribution of *Nanorchestes* sp. originally increased strongly in the first two years. However, as many more species were found thereafter, the density of this species decreased briefly; dramatically in samples containing high densities of *Siteroptes* sp., indicating successional species replacement. Remarkable is the occurrence of species such as *Cheletomimus vescus*, *Hawaiieupodes thermophilus* and *Xerophiles ereynetoides*, which are rare, most likely xero-thermophilous species adapted to nutrient-poor soils. The results described here represent only those of the first 2.5 years and sampling and evaluation will continue.

Keywords: Actinedida, succession, sand, colonisation

1. Introduction

The soil fauna plays an important role in primary succession as it is present almost immediately after exposure of new land surfaces, facilitating the establishment of other biota (Hodkinson et al. 2004, Frouz et al. 2007, Wanner et al. 2008). On the other hand, vegetation development is an important determinant of the structure and function of the soil food web. Plant species' effects on soil development, decomposer organisms and processes are especially apparent in the course of ecosystem development (Wardle 2002). Changes in species composition during succession are controlled by biotic interactions, i.e. facilitation, competition and inhibition as well as tolerance. Many studies have followed secondary succession of soil-fauna (e.g. during recovery after disturbance), showing important effects of

regional species pool as well as species' disturbance tolerance and abiotic adaptation on colonisation, founder effects on community composition and structure etc. (Koehler & Born 1998, Dunger et al. 2002, Berg & Hemerik 2004, Wanner & Xylander 2005, Russell & Griegel 2006). However, very little is known about soil-faunal colonisation and community establishment during primary succession. In one of the few studies, Dunger et al. (2001, 2004) and Hohberg (2003) could show, in chronosequences of gradually reclaimed post-mining sites including initial substrates, regular patterns of colonisation by soil-faunal species as well as soil food-web development that paralleled soil maturation and was dependant on site conditions and amelioration (afforestation) methods. Even after 50 years of succession, initial ecosystem sites did not nearly approach soil-faunal climax conditions. Very few studies have investigated the interaction between vegetation and the soil food web or between soil food-web components during the initial stage of ecosystem development. This holds true, especially, with regard to the influence of interactions on the temporal and spatial variability of the soil fauna (Wardle 2002, Walker & del Moral 2003).
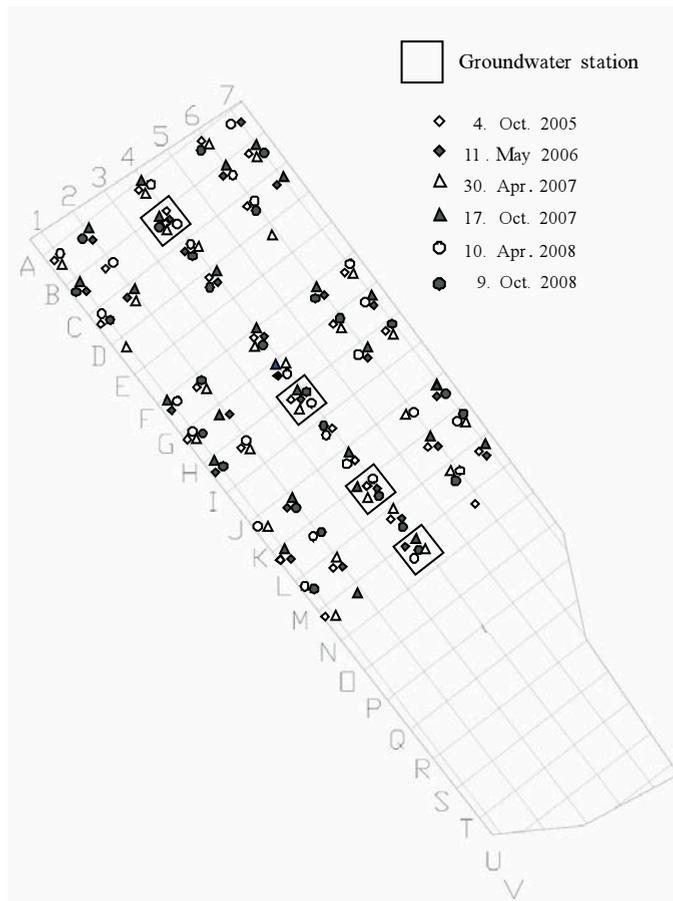

Fig. 1   Sketch of the study area with the plot coordinates and position of the individual samples at the different sampling dates.

Thus, within the framework of a multidisciplinary project of the BTU Cottbus, an artificial water-catchment area ('Chicken Creek') was created in order to study the ecological structures, processes and interactions during initial ecosystem development (Gerwin et al. 2009). In contrast to the study sites mentioned above, this area was left without further human interference, thus providing the opportunity to investigate undisturbed, natural primary succession during initial ecosystem development. The goal of this project is the study of the spatio-temporal succession of soils, soil microbiology, soil fauna, vegetation and their interactions during initial phases of ecosystem development.

Within these studies, the spatial and temporal development of several components of the soil-faunal food web is being investigated in detail during the initial stages of primary succession in the water-catchment area. Actinedid mites (in the sense of the paraphyletic group comprising Prostigmata and 'Endeostigmata'; OConnor 1984, Norton et al. 1993) are well known to be the dominant microarthropod group in nutrient- and structurally poor (e. g. sandy) soils around the world (i.e., Santos et al. 1978, Steinberger & Whitford 1984, Kinnear 1991, Cepada-Pizzaro et al. 1996, Noble et al. 1996). Therefore, this soil-animal group was expected to play an important role during initial developmental phases in the experimental ecosystem and is being intensively studied within the soil-biological investigations. Since only preliminary data regarding soils, soil microbiology and vegetation are becoming available and the soil-fauna studies are still ongoing, a comprehensive analysis of interrelations and interactions is not yet possible. Nonetheless, clear patterns of initial colonisation and community development are already emerging after only the first 2.5 years of primary succession. Therefore, the present report describes results concerning the actinedid fauna obtained during the initial period of soil-faunal colonisation and establishment in the artificial water-catchment area 'Chicken Creek'.

2. Materials and methods

The study was carried out at the artificial, approximately 6-ha large catchment area 'Chicken Creek' (Fig. 1). The site is located in the open-cast mine site Welzow-South (20 km south of Cottbus, Lower Lusatia, Germany; 51°36'18" N; 14°15'58" E). The catchment was constructed as a small hill with an altitude difference of approximately 10 m and an approximate slope of 2 %. In the winter of 2004/2005, a packed bed was produced and covered with a 2- to 3-m basal layer of clay to allow development of a groundwater table. Sandy quaternary substrate (85 % sand, 9 % silt, 6 % clay) taken from 20- to 30-m depth were then deposited on the surface to create a 2- to 3-m deep initial surface substrate (Gerwin et al. 2009). Construction of the area was finished in September 2005 and subsequently fenced to prevent disturbance by large vertebrate animals. Besides levelling and planning the area, no amelioration measures were taken and the area was allowed to undergo primary succession. For further information of the site see Gerwin et al. (2009). Soil parameters were measured by the BTU Cottbus for initial site conditions (in 2005), which are given in Tab. 1.

Tab. 1   Mean values and standard deviations of various soil parameters of the upper 30 cm of substrate after construction of the 'Chicken Creek' catchment area. From Gerwin et al. 2009.

Parameter	pH (H₂O)	Gravel (%)	Sand (%)	Silt (%)	Clay (%)	C_{tot} (mg g⁻¹)	C_{org} (mg g⁻¹)	N_{tot} (mg g⁻¹)	$CaCO_3$ (%)
Mean	8.05	14.5	84.8	9.1	6.1	2.7	1.6	0.1	0.87
Std Dev.	0.43	6.6	5.4	3.4	2.1	1.5	1.0	<0.01	0.66

Vegetation was allowed to spontaneously colonise the 'Chicken Creek' site with no anthropogenic influence. Floral monitoring (by the Tech. Univ. Munich) documented a rapidly increasing vegetation cover and number of plant species. In the first year, a total of 18 plant species was found. The number of species increased to 130 in 2008. The two most dominant plant species were *Cirsium arvense* and *Chenopodium album* (2005), *Ch. album* and *Conyza canadensis* (2006), *C. canadensis* and *Echinochloa crus-galli* (2007) and *Trifolium arvense* with *Tussilago farfara* (2008). As one of the first woody plants, *Robinia pseudoacacia* was represented by a total of 88 individuals in 2008. Other pioneer tree species were also present in the catchment, e.g. *Pinus sylvestris*. However, their abundances and growth was much weaker than *Robinia* (Gerwin pers. comm.).

Sampling of the endogeous soil microarthropods took place via soil cores (6.4 cm in diameter, 5 cm depth) from the catchment area. Preliminary sampling was undertaken in October 2005 and May 2006 to assess initial soil-fauna development. Regular soil-faunistic sampling began in 2007 and took place at usual times of peak abundances, namely in April and October of each year. At each sampling date, 27 soil cores, distributed evenly throughout the catchment area, were taken. To prevent undue emphasis of single coordinate points as well as to avoid undue destructive sampling, the sampled points were rotated slightly from sampling date to sampling date (see Fig. 1). Solely permanent groundwater measurement stations were sampled at every date to ensure direct correlations between soil-fauna and hydrological or soil data. The cores were removed intact, transferred to size-matched transportation containers and taken to the laboratory, where the animals were driven from the cores via an increasing temperature and desiccation gradient in a Macfadyen-type, high-gradient extractor (Macfadyen 1961, Bieri et al. 1978).

Extraction took place with soil cores placed intact and inverted onto metal nets (2 mm mesh size) above funnels and continued for an average of 10 days. Temperatures in the heating chamber continually increased from approximately 20 °C to 50 °C with a temperature gradient within the cores increasing from approximately 5 °K to 20 °K. Extraction ended with total desiccation of the soil. The animals were caught in 30-ml reception jars containing von-Törne's conservation medium (50 % isopropanol with 3 % glacial acetic acid and 0.3 % formalin; Dunger and Fiedler 2000).

After extraction, the collected animals were transferred sample-specifically into 70 % ethanol and stored for approximately three weeks to allow total fixation and conservation. The microarthropods were subsequently sorted into higher-level taxon groups under a stereomicroscope at maximally 50× magnification, individual mites then mounted in Hoyer's medium and determined to species or generic level under a differential-interference microscope at up to 1000× magnification. Determination of Actinedida followed, e.g., Kazmierski (1998), Kethley (1990, and unpubl. manuscript), Khaustov (2008), Savulkina (1981), Volgin (1989), Zacharda (1978) as well as original descriptions and taxonomic generic and family reviews. However, due to lack of determination keys or unavailability of all species descriptions for some genera, not all taxa could be confidently determined to species level. As of yet, only the Actinedida from samples taken until April 2008 have been completely determined.

The number of individuals as well as of species present in each sample was summed into sampling-date averages for the total catchment area in order to assess temporal faunistical development during primary succession. Average densities were calculated and standardised

into individuals m^{-2} from the total individuals of all 27 samples per sampling date. Total species numbers were determined as sampling-date sums. In order to characterise the actinedid communities, the community composition (= species composition) and community structure (= relative proportion of each species in the total community; 'dominance' in %) was determined.

To test for significant temporal developments in the actinedid communities, the data were submitted to a variance analysis with sampling date as the main factor. Due to the non-normal distribution of soil animals, differences in the densities and species richness (as individuals and species per sample, respectively) between sampling dates were tested for significance using a non-parametric one-way ANOVA for multiple observations (= samples) per cell (= sampling date) (modified Friedman test; Zar 1999, Schöps and Russell 2004). This ANOVA is based on ranked per sample data for each sampling date and on the χ_r^2 rather than the F distribution. A post-hoc Tukey-like multiple comparison procedure for this non-parametric ANOVA (Zar 1999) tested for significant differences between sampling dates.

In a first step towards evaluating possible interactions with soil or vegetation parameters during temporal changes of the actinedid fauna, for each species non-parametric Spearman correlations were carried out between total individual numbers occurring in a sample and data for soil parameters of the same sample. Core-by-core soil data was available particularly for soil moisture and pH. Contents of C and N apparently did not change appreciably during this initial study period. However, slight increases were associated with developing vegetation structures – resulting in, i.e., patchy colonisation processes of protists (Wanner & Elmer, 2009). The correlations were undertaken for all sampling dates together as well as for each sampling date individually. Furthermore, correlations were carried out between species abundance and vegetation ground cover (as an indicator of ecosystem development during primary succession). However, this was only carried out for data from 2007, after vegetational succession had noticeably progressed and for which comprehensive vegetational data were available. Vegetation ground cover was estimated in categories as 0 %, 10 %, 20 % or 50 %.

3. Results

At all sampling dates, Actinedida represented the absolutely dominant group, often constituting more than 90 % of all microarthropods (Fig. 2). During initial development from 2005 to early 2007, only very low densities were registered (< 5000 ind. m^{-2}; Fig. 3). Distribution was very heterogeneous especially in the years 2005 and 2006, where many samples (25–50 %) contained only single individuals or no Actinedida at all. Accordingly, the variability of densities was very high, extraordinarily so in 2007, when single samples contained more than 2000 individuals, while others contained none. The number of samples with actinedid mites increased steadily from sampling date to sampling date until 2008, when numerous Actinedida were present in every sample and total variability was much lower. The increases in density were significant as of autumn 2007 (Xr^2 = 51.226; P < 0.001; Fig. 2). Although the highest average densities were found in October 2007, the statistically highest densities were recorded in April of 2008, due to very high individual numbers in only single samples in 2007 and a more homogeneous distribution among the samples in 2008.

Total species numbers were also very low (3–4 species) during initial ecosystem development (Fig. 4), with most individuals representing *Nanorchestes* sp. und *Speleorchestes* sp. (s. Appendix). Total species richness increased significantly as of October 2007
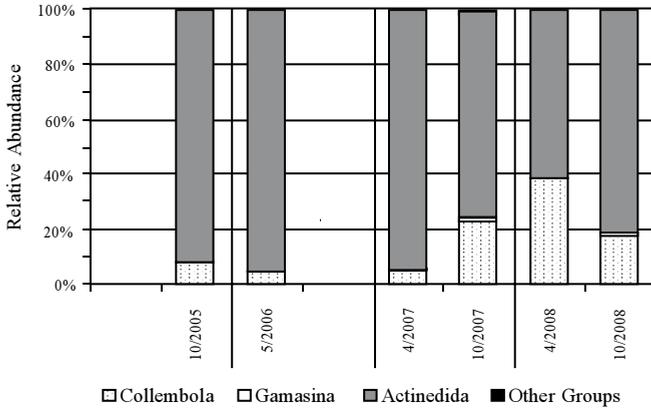
Fig. 2   Composition of the major microarthropod groups found in the experimental catchment area
          'Chicken Creek' at the various sampling dates.
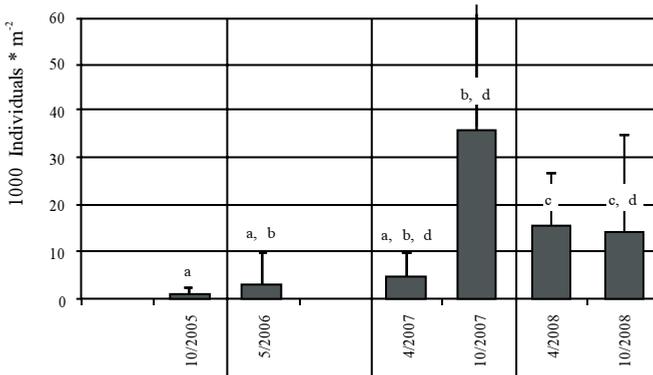

Fig. 3   Temporal development of actinedid species richness in the study site (total registered
          species number as well as average species number per sample + standard error at the
          different sampling dates). Different letters denote significantly different species richness
          between sampling dates.
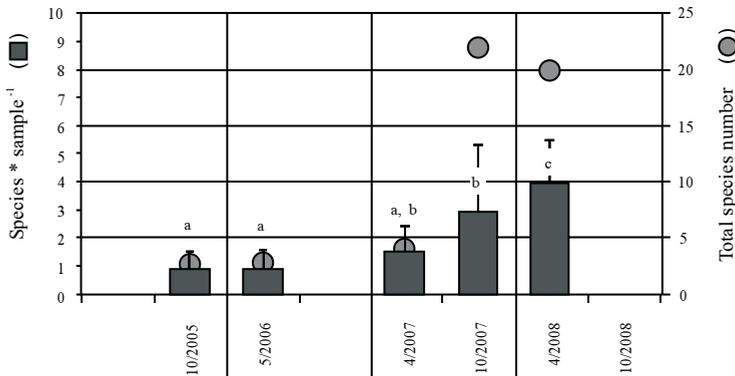

Fig. 4   Temporal development of actinedid species richness in the study site (total registered
          species number as well as average species number per sample + standard error at the
          different sampling dates). Different letters denote significantly different species richness
          between sampling dates.

(Xr^2 = 60.206; P < 0.001; Fig. 4), when 23 (October 2007) and 19 different taxa (April 2008) were identified. Except for heterostigmatid taxa (i.e., *Siteroptes* sp. and *Bakerdania* sp.), most of the additional species in October 2007 were only registered as one or two individuals. The exceedingly high densities in single samples in October 2007 were mostly caused by highly individual-rich populations of *Siteroptes* sp. in these samples. This taxon was no longer registered in April 2008 (but again in October 2008, data not shown), where the populations of many other species were found to be somewhat more individual-rich.

Whereas the most common taxon, *Nanorchestes* sp., was found in only 75 % of the samples in low individual numbers in 2005, its abundance and spatial distribution (= occurrence in number of samples) increased steadily from 2005 to 2008. Its population densities were then significantly higher at each sampling date as of 2007 (Xr^2 = 50.994; P < 0.001) and it was found in all samples in high individual numbers in 2008. Its densities decreased briefly only in autumn 2007, dramatically in samples containing high densities of *Siteroptes* sp. Also *Speleorchestes* sp. was registered at every sampling date, albeit in very low individual numbers in 2005 and 2006 (< 5). Its densities similarly increased significantly as of 2007 (Xr^2 = 40.999; P < 0.001), but also with a reduction in October 2007.

Remarkable was the occurrence of species such as *Xerophiles ereynetoidales* (2006–2008), *Cheletomimus vescus* (2007 and 2008) as well as *Hawaiieupodes thermophilus*, *Claveupodes delicates* or Iolinidae taxa (all in Oct. 2007 and 2008). Although most were only found in few individuals, the populations of these species all increased in the later sampling dates. Especially the development of *Xerophiles ereynetoidales* was conspicuous. Found only as occasional individuals as of 2006, its density and distribution increased sharply as of October 2007 (Fig. 5). In general, with increasing species richness, the proportion of purely carnivorous species (i.e., species of Rhagidiidae, Cunaxidae, Bdellidae, Stigmaeidae, Cheyletidae) also increased. Whereby no exclusively carnivorous taxa were registered in 2005 and 2006, they accounted for > 25 % of all species as of October 2007, albeit still less than 5 % of all individuals.

The changes described above did not relate to changes in soil parameters. Only soil moisture correlated with a few species (Tab. 2). However, this appears to be a statistical artefact occurring when all sampling dates are taken into account: these species increased in density only at later sampling dates, when higher soil moistures were also measured (Fig. 5). A true parallelism between species' densities and soil moisture could not be observed and no significant correlations were present at single sampling dates. Furthermore, it must be noted

Tab. 2   Spearman correlations of species' abundances and soil moisture (all sampling dates) as well as vegetation cover (data from October 2007). Only significant correlations are shown. * P<0.05; ** P<0.01

Taxon	Correlation coefficient (Spearman's R) Soil moisture
Alicorhagia sp.	0.291**
Xerophiles ereynetoidalis	0.252**
Speleorchestes sp.	0.188*
Claveupodes delicatus	0.183*
Tydaeolus sp.	0.179*
Ground vegetation cover	
Siteroptes sp.	0.572**
Tydeus sp.	0.503**
Xerophiles ereynetoidalis	0.399*

that the occurrence of all these species was in cores with very low soil moistures (i.e. 2–6 %). However, three species, *Siteroptes* sp., *Tydeus* sp., and *Xerophiles ereynetoidalis*, did correlate with vegetation ground cover when the data of single sampling dates was analysed (Tab. 2). Higher densities or a more frequent occurrence were observed for these species in cores taken from areas with a higher vegetation cover (Fig. 6).
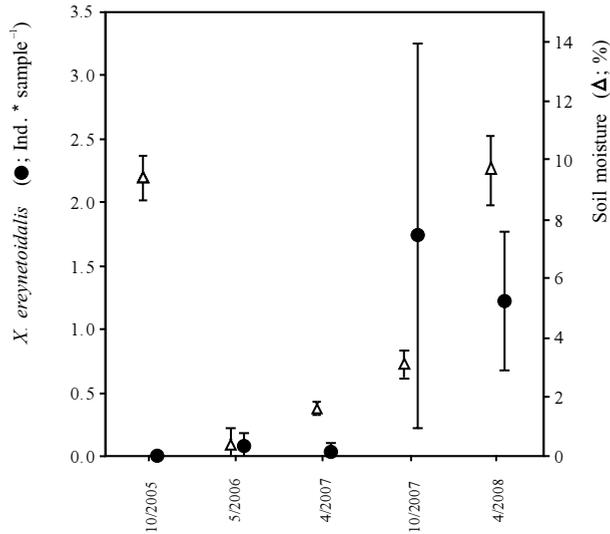

Fig. 5   Development of individual richness of *Xerophiles ereynetoidalis* and soil moisture at the different sampling dates. Although both increase with time and thus are positively correlated (see text), a strict parallelism suggestive of a causal relationship is not observable.
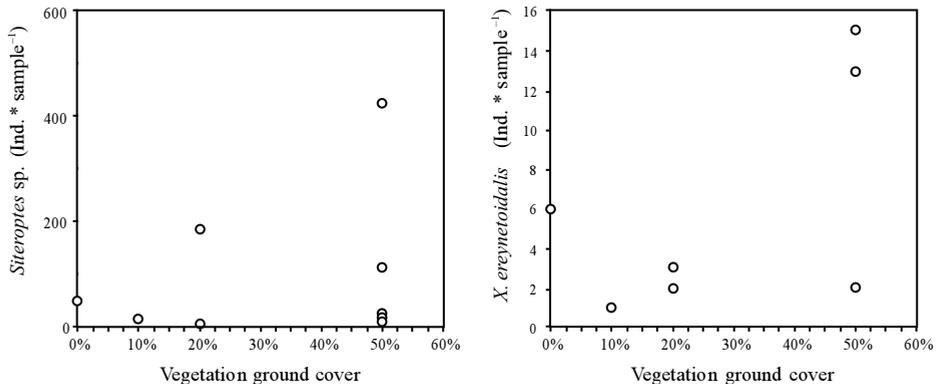

Fig. 6   Densities in individual samples of *Siteropes* sp. and *Xerophiles ereynetoidalis* in relationship with the vegetational ground cover of the respective sample (data from October 2007). Only samples with individuals of the respective taxon are shown. Higher individual densities or more samples containing individuals were found in cores taken under higher vegetation cover.

4. Discussion

It is most remarkable that one month after construction of the artificial catchment the initial substrates were already colonised by Actinedida, even if by only two major species in only few, very patchily distributed individuals. It could not be ascertained whether these species were already present in the deep sands before being transported to the surface, were anthropogenically introduced during site construction or were passively transported to the site by wind or animals. Active immigration is highly unlikely since developed soils were many kilometres distant from the study site.

The early presence of these species makes obvious that nutrient resources needed for population establishment were almost immediately available in the newly formed soils. Single-celled algae were observed in substrate samples and an individual-rich nematode fauna predominated by bacterial feeders as well as a strong development of algal-feeding tardigrades were recorded in the study site during early succession (Elmer et al., in press; Hohberg et al., in press). This is indirect proof that microbial and soil-algal communities were present early in ecosystem development and were available as faunal nutrient resources.

The two main, early colonising taxa, *Nanorchestes* sp. und *Speleorchestes* sp., are common throughout the world in sandy or newly formed soils poor in organic matter (Franco et al. 1979, Whitford & Santos 1980, Santos & Whitford 1983, Steinberger 1990, Kinnear 1991, Cepeda-Pizzaro et al. 1996) and are most likely microbivore, algivore and possibly nematophageous (Walter 1988).The study area was also colonised early by the widespread, microbivore/algivore collembolan *Mesaphorura macrochaeta* in a similarly individual-poor, patchy manner (Elmer et al., in press). Thus, in the first two years, the catchment area was only sporadically colonised by few individuals of common microarthropod species that occupy basal positions in the soil food web and are known to regularly inhabit primary soils and nutrient-poor conditions.

Throughout the first years, all of these species steadily increased their populations and distribution throughout the study site until, after 2.5 years, a 'homogeneous' distribution was attained. Their populations can thus be considered to have become established during early succession. Ufer (1993) observed recolonisation of totally defaunated agricultural soils by endogeous species to proceed via 'initial nuclei', spreading throughout a site from there. Thus, this form of colonization mechanism appears to be common among endogeous microarthropods in newly formed soils.

In late 2007, two years after site construction, individual densities and species richness increased dramatically, indicating a successional jump in the development of the actinedid communities. Data are not yet available to ascertain whether this was due to a qualitative change in the soil conditions, allowing colonisation by further actinedid species. That the few species correlating positively with vegetation cover first occurred in higher densities or at all on this date is, however, indicative of this. Alternatively or concurrently, species previously present and already finding adequate conditions increased their population size and spatial distribution throughout the site. Furthermore, the increased number of predator species observed in 2007 indicate a successional development of the trophic complexity in the communities.

The variances of the abundances were very high during early succession, due to many samples containing few individuals while some included many hundreds or even thousands. This indicates that colonisation of the soils was still very heterogeneous. This sporadic

individual-richness in October 2007 was mostly caused by strong populations of single species, e.g., the heterostigmate species *Siteroptes* sp. and *Bakerdania* sp. These species are probably microbi- und fungivore (Suski 1973, Greenslade & Cliff 2004) and can be distributed phoretically (Rack & Vercammen-Grandjean 1979, Masan 1993, Kurosa 2002), allowing strong population development if appropriate habitat and nutritional resources are found. Interestingly, *Nanorchestes* decreased dramatically at this date in samples containing high densities of *Siteroptes* sp., indicating first successional species replacement. However, especially Siteroptes was not found in spring of the following year (although individuals were again recorded in the following autumn; data not shown), showing that an overwintering was not yet assured and that population establishment of these species had not yet fully occurred. In 2008 *Nanorchestes* again increased in abundance, indicating an oscillation in species occurrence and population sizes during these early successional stages.

In 2008, based on reduced abundance variability and steadying species numbers, the densities and species richness of the actinedid communities apparently began to stabilise. Compared to mature soils, however, where total actinedid densities can reach 50-200,000 individuals m^{-2} (Peterson & Luxton 1982, Curry 1994), the densities found in the 'Chicken Creek' catchment area must still be considered low. Nonetheless, the communities attained densities commonly found in sandy, nutrient-poor xerothermic habitats (1000-32,000 ind. m^{-2}; Lussenhop 1970, Wood 1971, Edney et al. 1975, Franco et al. 1979, Steinberger et al. 1990), indicating that colonisation and succession had attained a stage common for nutrient-poor, xerothermic habitats less than three years after site initiation.

Notable was the occurrence of species such as *Cheletomimus vescus*, *Hawaiieupodes thermophilus*, *Xerophiles ereynetoides* and *Neonanorchestes ammolitoreus*, which are all rare, often xero-thermophilous species probably adapted to sandy and/or nutrient-poor soils (McDaniel & Bolen 1981, Jesionowska 2003, 2008). Almost all of these species are reported here for the first time in Germany; *C. vescus* has only been recorded in desert habitats of Iran or Pakistan (Bochkov et al. 2005). This raises important questions regarding the distribution and means of dispersal of these species. It is likely that these species are more widely distributed than presently known, but have not been recorded due to the lack of studies of Actinedida in such habitats. Although still present in low densities in the study area, the populations of these species have been steadily increasing from sampling date to sampling date, indicating population establishment also of these species. The established presence of these species – together with *Nanorchestes*, *Speleorchestes* etc. suggests an actenidid community specialised to xero-thermophilic habitat conditions already 2.5 years after ecosystem initiation.

Thus, as of October 2007, a marked development in the actinedid communities could be observed. Beyond increased densities and species richness, the proportion of purely carnivorous species also increased as of late 2007, although their populations are most likely not thoroughly established. Whereby microbivore species originally represented almost 100 % of the community, in autumn 2007 and spring 2008 (2–2.5 years after ecosystem initiation) purely predaceous species accounted for more than 25 % of the species, if still less than 1–5 % of the individuals. At this time, also the first gamasid species began to show established populations, albeit still in very low individual numbers (Elmer et al., in press). This indicates a development of the soil food web beyond basal trophic levels of microbi- and algivore species, which alone were found in 2005 and 2006. This concurs with the herbaceous plant

society becoming richer and more diverse, thus providing an increasing supply of nutrient resources and niches. Nonetheless, according to the microarthropod fauna (within which Oribatida were still lacking), 'Chicken Creek' soil food webs in 2008 were apparently still poorly structured, species-poor and dominated by basal trophic levels (Elmer et al., in press). It is expected that, during soil succession, the food web structure should further increase from basal food webs, where only generalists can survive and reproduce, to mature food webs with a higher trophic diversity and multitrophic interactions.

A comprehensive analysis of the species of all faunal groups and their small-scale spatio-temporal distribution in relation with soil and vegetation parameters still remains to be undertaken in order to fully understand these developmental patterns. Especially in such nutrient-poor initial habitats, minor differences in vegetation, soil organic matter and the related nutritional resources can play an important role in colonisation, the population development of individual species and community assembly. As the background data become more available for the study site and the soil-faunistic studies progress, a spatial point-by-point analysis of all these factors should help understand the ecosystem interactions structuring community establishment, assembly and succession in the study area.

5. Acknowledgements

6. References

Berg, M. P. & L. Hemerik (2004): Secondary succession of terrestrial isopod, centipede, and millipede communities in grasslands under restoration. – Biology and Fertility of Soils **40**: 163–170.

Bieri, M., V. Delucchi & C. Lienhard (1978): Ein abgeänderter Macfadyen-Apparat für die dynamische Extraktion von Bodenarthropoden. – Bulletin de la Société Entomologique Suisse **51**: 119–132.

Bochkov, A. V., M. Hakimitabar & A. Saboori (2005): A review of the Iranian Cheyletidae (Acari: Prostigmata). – Belgian Journal of Entomology **7**: 99–109.

Cepeda-Pizzaro, J. G. & W. G. Whitford (1989): Spatial and temporal variability of higher microarthropod taxa along a transect in a northern Chihuahuan Desert watershed. – Pedobiologia **33**: 101–111.

Cepeda-Pizzaro, J. G., J. R. Gutiérrez, Valderrama & H. Vasquez (1996): Phenology of the edaphic microarthropods in a Chilean coastal desert site and their response to water and nutrient amendments to the soil. – Pedobiologia **40**: 352–363.

Curry, J. P. (1994): Grassland Invertebrates. Ecology, Influence on Soil Fertility and Effects on Plant Growth. – Chapman & Hall, London, UK: 437 pp.

Dunger, W. & H.-J. Fiedler (2000): Methoden der Bodenbiologie. – Gustav Fischer, Stuttgart New York: 432 pp.

Dunger W., H.-J. Schulz & B. Zimdars (2002): Colonization behaviour of Collembola under different conditions of dispersal. – Pedobiologia **46**: 316–327.

Dunger, W., H.-J. Schulz, B. Zimdars & K. Hohberg (2004). Changes in collembolan species composition in Eastern German mine sites over fifty years of primary succession. – Pedobiologia **48**: 503–517.

Dunger, W., M. Wanner, H. Hauser, K. Hohberg, H.-J. Schulz, T. Schwalbe, B. Seifert, J. Vogel, K. Voigtländer, B. Zimdars & K. P. Zulka (2001). Development of soil fauna at mine sites during 46 years after afforestation. – Pedobiologia **45**: 243–271.

Edney, E. B., P J. Franco & J. F. McBrayer (1975): Abundance and distribution of soil microarthropods in Rock Valley, Nevada. – US/IBP Desert Biome Research Memorandum 76-24, Reports of 1975 Progress, Vol. 3, Invertebrate Section: 11–27.

Elmer, M., K. Hohberg, D. J. Russell, A. Christian, H.-J. Schulz & M. Wanner (in press): Succession of the soil faunal community during initial ecosystem development. – Ecosystem Development.

Franco, P. J., E. B. Edney & J. F. McBrayer (1979): The distribution and abundance of soil arthropods in the Northern Mojave desert. – Journal of Arid Environments **2**: 137–149.

Frouz, J, V. Piᴄl & K. Tajovský (2007): The effect of earthworms and other saprophagous macrofauna on soil microstructure in reclaimed and un-reclaimed post-mining sites in Central Europe. – European Journal of Soil Biology **43**: 184–189.

Gerwin W., W. Schaaf, D. Biemelt, A. Fischer & S. Winter (2009): The artificial catchment 'Chicken Creek' (Lusatia, Germany) – A landscape laboratory for interdisciplinary studies of initial ecosystem development. – Ecological Engineering **35**: 1786–1796.

Greenslade, P. & A. Clift (2004): Review of pest arthropods recorded from commercial mushroom farms in Australia. – The Australasian Mycologist **23**: 77–93.

Hohberg, K. (2003): Soil nematode fauna of afforested mine sites: genera distribution, trophic structure and functional guilds. – Applied Soil Ecology **22**: 113–126.

Hohberg, K., D. J. Russell & M. Elmer (in press): Mass occurrence of algal-feeding tardigrade *Apodibius confusus* Dastych, 1983 in the young soils of a post-mining site. – Journal of Zoological Systematics and Evolutionary Research.

Hodkinson, I. D., S. J. Coulson & N. R. Webb (2004): Invertebrate community assembly along proglacial chronosequences in the high Arctic. – Journal of Animal Ecology **73**: 556–568.

Jesionowksa, K. (2003): *Xerophiles ereynetoidalis*, a new mite genus and species of the family Eupodidae (Actinotrichida, Actinedida, Eupodoidea) from Poland. – Acta Biologica Cracoviensia **45**: 11–18.

Jesionowksa, K. (2008): Redescription of *Hawaiieupodes thermophilus* Strandtmann et Goff, 1978 (Acari: Prostigmata: Eupodoidea: Penthalodidae) from Hawaii, with a discussion of the systematic status of the taxon. – Annales Zoologica **58**: 337–346.

Kaźmierski, A. (1998): Tydeinae of the world: generic relationships, new and redescribed taxa and keys to all species. A revision of the subfamilies Pretydeinae and Tydeinae (Acari: Actinedida: Tydaidae) – part IV. – Acta Zoologica Cracoviensia **41**: 283–455.

Kethley, J. (1990): Acarina: Prostigmata (Actinedida). - In: Dindal, D. L. (ed.) Soil Biology Guide. – J. Wiley & Sons, New York Chichester Brisbane: 667–756.

Khaustov, A. A. (2008): Mites of the family Scutacaridae of Eastern Paleaearctic. – Akadem-periodyka, Kiev: 290 pp.

Kinnear, A. (1991): Acarine communities of semi-arid soils from the Eastern Goldfields region of Western Australia. – Pedobiologia **35**: 273–283.

Koehler, H. & H. Born (1998): Secondary succession of soil mesofauna: a thirteen year study. – Applied Soil Ecology **9**: 81–86.

Kurosa, K. (2002): A new genus and species of Pygmephoridae (Acari: Heterostigmata) associated with *Onthophagus* (Coleoptera: Scarabaeidae) in Japan. – Journal of the Acarological Society of Japan **11**: 27–36.

Lussenhop, J. (1972): Distribution and phenology of a prairie soil arthropod population. – Mid-West Prairie Conference **2**: 60–72.

Macfadyen, A. (1961): Improved funnel-type extractors for soil arthropoda. – Journal of Animal Ecology **30**: 71–184.

Masan, P. (1993): Mites (Acarina) associated with species of *Trox* (Coleoptera: Scarabaeidae). European Journal of Entomology **90**: 359–364.

McDaniel, B. & E. G. Bolen (1981): A new genus and two new species of Nanorchestidae from Padre Island, Texas (Acari: Prostigmata). – Acarologia **22**: 253–256.

Noble, J. C., W. G. Whitford & M. Kaliszweski (1996a): Soil and litter microarthropod populations from two contrasting ecosystems in semi-arid eastern Australia. – Journal of Arid Environments **32**: 329–346.

Norton, R. A., J. B. Kethley, D. E. Johnston & B. M. OConner (1993): Phylogenetic perspectives on genetic systems and reproductive modes of mites. – In: Wrensch, D. & M. Ebbert (eds): Evolution and Diversity of Sex Ratio in Insects and Mites. – Chapman & Hall, London, UK: 8–99.

OConnor, B. M. (1984): Phylogenetic relationships among higher taxa in the Acariformes, with particular reference to the Astigmata. – In: Griffiths, D. A. & C. E. Bowman (eds): Acarology VI, Vol. 1. – Ellis Horwood, Chichester, UK: 19–27.

Petersen, H. & M. Luxton (1982): A comparative analysis of soil fauna populations and their role in decomposition processes. – Oikos **39**: 284–422.

Rack, G. & P. H. Vercammen-Grandjean (1979): *Siteroptes* (*Siteroptoides*) *trombidiphilus* sp. n. (Acarina: Pygmephoridae) phoretisch auf einem Weibchen der Familie Trombidiidae (Acarina) aus Ostafrika. – Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg **6**: 217–220.

Russell, D. J. & A. Griegel (2006): Influence of variable inundation regimes on soil Collembola. – Pedobiologia **50**: 165–175.

Santos, P. F. & W. G. Whitford (1983): Seasonal and spatial variation in the soil microarthropod fauna of the white sands national monument. – Southwestern Naturalist **28**: 417–421.

Santos, P. F., E. DePree & W. G. Whitford (1978): Spatial distribution of litter and microarthropods in a Chihuahuan desert ecosystem. – Journal of Arid Environments **1**: 41–48.

Savulkina, M. M. (1981): The system, ecology and distribution of the mite family Pygmephoridae [in Russian]. – Entomological Review (St.-Petersburg) **60**: 434–450.

Schöps, F.-R. & D. J. Russell (2004): Ein modifizierter Friedman-Test (nicht-parametrische ANOVA) für quantitativen Auswertungen von Bodenmesofauna-Daten. – Mitteilungen der AG Bodenmesofauna **20**: 31–35.

Steinberger, Y. (1990): Acarofauna of a Negev desert loess plain. – Acarologia **31**: 313–319.

Steinberger, Y. & W. G. Whitford (1984): Spatial and temporal relationships of soil microarthropods on a desert watershed. – Pedobiologia **26**: 275–284.

Steinberger, Y., E. F. Aldon & W. G. Whitford (1990): Soil microarthropod fauna of four habitats of the Rio Puerco watershed, New Mexico. – Southwestern Naturalist **35**: 279–284.

Suski, Z. W. (1973): A revision of *Siteroptes cerealium* (Kirchner) complex (Acarina, Heterostigmata, Pyemotidae). – Annales Zoologici Warszawa **30**: 509–535.

Ufer, A., F. Schmider & G. Alberti (1993): Auswirkungen einer Bodenentseuchung auf die Populationen von Collembolen in Ackerbiozönosen. – In: Ehrnsberger, R. (ed.): Bodenmesofauna und Naturschutz. – Güner Runge, Cloppenburg: 355–367.

Volgin, V. I. (1989): Acarina of the Family Cheyletidae of the World. – Brill Archive, Leiden: 532 pp.

Walker, L. R. & R. del Moral (2003): Primary succession and ecosystem rehabilitation. – Cambridge University Press, Cambridge New York Port Melbourne Madrid: 442 pp.

Walter, D. E. (1988): Predation and Mycophagy by Endeostigmatid Mites (Acariformes: Prostigmata). – Experimental & Applied Acarology **4**: 159–166.

Wardle, D. A. (2002): Communities and ecosystems – linking the aboveground and belowground components. – Monographs in Population Biology **34**: 392 pp.

Wanner, M. & M. Elmer (2009): 'Hot spots' on a new soil surface – How do testate amoebae settle down? – Acta Protozoologica **48**: 281–289.

Wanner, M. & W. E. R. Xylander (2005): Biodiversity development of terrestrial testate amoebae: is there any succession at all? – Biology and Fertility of Soils **41**: 428–438.

Wanner, M., M. Elmer, M. Kazda & W. E. R. Xylander (2008): Community assembly of terrestrial testate amoebae: How is the very first beginning characterized? – Microbial Ecology **56**: 43–54.

Whitford, W. G. & P. F. Santos (1980): Arthropods and detritus decomposition in desert ecosystems. – In: Dindal, D.L. (ed.): Soil Biology as Related to Land Use Practices. – EPA, Office of Pesticide and Toxic Substances, Washington DC, USA: 770–778.

Wood, T. G. (1971): The distribution and abundance of Folsomides deserticola (Collembola: Isotomidae) and other micro-arthropods in arid and semi-arid soils in Southern Australia, with a note on nematode populations. – Pedobiologia **11**: 446–468.

Zacharda, M. (1978): Soil mites of the family Rhagidiidae (Actinedida: Eupodoidea). Morphology, Systematics, Ecology. – Acta Universitatis Carolinae Biologica **5-6**: 489–790.

Zar, J. H. (1999): Biostatistical Analysis. 4th Edn. – Prentice Hall, London Sydney Toronto: 663 pp.

Appendix List of the registered taxa with their observed densities (in average ind. * m^{-2} [rounded values]) at the different sampling dates. Dominant taxa in bold type.

	10/2005	05/2006	04/2007	10/2007	04/2008
Endeostigmata					
Nanorchestidae					
Nanorchestes **Topsent & Trouessart, 1890 sp.**	990	3,170	3,780	1,120	12,790
Neonanorchestes ammolitoreus McDaniel & Bolen, 1981					35
Speleorchestes **Trägårdh, 1909 sp.**	60	25	830	265	1,290
Alicorhagiidae					
Alicorhagia **Berlese, 1910 sp.**					450
Prostigmata					
Bdellidae					
Bdella Latreille, 1795 sp.					10
Spinibdella Thor, 1930 sp.				25	
Cunaxidae					
Pseudobonzia Smiley, 1975 sp.				10	10
Eupodidae					
Claveupodes delicatus **Strandtmann & Prasse, 1976**	10			10	115
Cocceupodes Thor, 1934 sp.					25
Eupodes C. L. Koch, 1835 sp.				25	25
Hawaiieupodes thermophilus Strandtmann & Goff, 1978				10	35
Protereunetes Berlese, 1923 sp.				10	
Xerophiles ereynetoidalis **Jesionowska, 2003**		25	10	540	380
Penthalodidae					
Penthalodes ovalis (Dugès, 1834)				10	
Rhagidiidae					
Parallelorhagidia evansi Strandtmann & Prasse, 1976				10	10
Gen. II sp. juv.				10	
Iolinidae					
Coccotydaeolus Baker, 1965 sp.					12
Tydaeolus Berlese, 1910 sp.				100	90
cf. *Tyndareus* Livshitz & Kuznetzov, 1972 sp.				10	
Tydaeidae					
Pseudolorryia Kazmierski, 1989 sp.				10	
Tydeus C. L. Koch, 1835 sp.				60	
Stigmaeidae					
Gen. sp. LV				10	
Cheyletidae					
Cheletomimus cf. *vescus* Qayyum & Chaudhri, 1979			10	25	70
Siteroptidae					
Siteroptes **Amerling, 1861 sp.**				31,900	
Pygmephoridae					
Bakerdania **Sasa, 1961 sp.**				1,390	25
Brennandania **Sasa, 1958 sp.**				207	80
Pediculaster Vitzthum, 1931 sp.					10
Scutacaridae					
Scutacarius cf. *wasyliki* Mahunka, 1977				50	50
Tarsonemidae					
Dendroptus Kramer, 1876 sp.				25	