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Effects of decomposing cadavers on soil nematode communities over a one-year period

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ABSTRACT

In terrestrial ecosystems decomposing cadavers act as resource patches affecting nutrient cycling and soil communities, but the effects on soil communities are not well known. In this study we investigated nematode community response to decomposing pig cadavers (*Sus scrofa*) over a one-year period. As nematodes play key roles in soil food webs and are known to respond to disturbances and nutrient enrichment, we hypothesised that they would respond to decomposing cadavers and that this response would change over time. We compared the temporal patterns of nematode density and community structure under pig cadavers, either placed directly on the ground or hung 1 m aboveground (for effects of cadaveric fluids only), with two controls, i.e., bare soil and bags filled with soil placed on the ground (fake pigs – for microclimatic effects only). In the control and fake pig treatments nematode densities, community patterns and maturity indices did not change significantly. In contrast, density increased significantly underneath the ground and hanging pigs two weeks after the beginning of the experiment, and nematode family richness, Simpson diversity and maturity index were significantly reduced in the cadaver treatments. Most nematode families responded negatively to cadavers with the notable exceptions of Rhabditidae, Neodiplogasteridae and Diplogasteroididae. The latter two were found exclusively underneath the decomposing cadavers and are promising bioindicators of vertebrate cadaver decomposition. Even though diversity, density and communities were recovering after one year, the impact of cadavers was still significant for the maturity index. These contrasting patterns illustrate how decomposing cadavers contribute to increasing local biodiversity and suggest that soil nematodes could be used as a tool to document the presence of a decomposing cadaver, or to estimate the time elapsed since death (post-mortem interval). Patterns should, however, be compared in different settings and seasons before such a tool can be validated.

1. Introduction

Decomposing cadavers represent an important natural resource in terrestrial ecosystems. By providing food for scavengers (ranging from microbes to vertebrates), they contribute to the heterogeneity of the soil ecosystem at different spatial and temporal scales, depending on the size of the cadaver (DeVault et al., 2003; Carter et al., 2007). A large number of mammals die from other causes than predation, e.g., injuries, starvation, extreme weather conditions, parasites or diseases (Carter et al., 2007; Parmenter and MacMahon, 2009), and their cadavers strongly affect biotic communities and nutrient cycling (Beasley et al., 2012; Barton et al., 2013). Cadavers can be described as patchy "resource pulses" for local consumers, being rare, brief and intense episodes of increased resource availability in space and time (Payne, 1965; Schoenly and Reid, 1987; DeVault et al., 2003; Yang, 2008).

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Previous cadaver research has mainly focused on the post-mortem interval (PMI), or time since death, and other aspects directly useful in criminal investigations (Barton et al., 2013), while detailed studies on the impact of cadavers on the diversity and community structure of soil organisms are rare (Carter et al., 2007; Metcalf et al., 2013, 2016). Thus, cadavers offer opportunities to explore natural disturbance patterns, succession and, more generally, soil biodiversity. However, it is often not obvious that cadavers should be left to decompose naturally, at least not close to where humans or farm animals may be exposed to the transmission of diseases (Fielding et al., 2014).

Decomposing cadavers are sources of water (60–80%), lipids, proteins, carbohydrates, and microorganisms (including pathogens) (Spray and Widdowson, 1950; Swift et al., 1979; Clark et al., 1997; Tortora and Grabowski, 2000). Through decomposition they release large amounts of nutrients and organic carbon (Putman, 1978; Vass et al., 1992; Hopkins et al., 2000; Towne, 2000; Carter et al., 2007; Benninger et al., 2008; Forbes, 2008). The resulting chemical changes in soil may remain measurable for several years (Towne, 2000).

Vertebrate cadaver decomposition can be divided roughly into six stages: fresh, bloated, active decay, advanced decay, dry and remains (Payne, 1965). Directly after the fresh stage the bloated stage begins, characterized by a tightening of the skin and inflation, due to an accumulation of gases (Vass et al., 1992, 2002). In the active decay stage blood and body fluids escape from body orifices, the skin begins to crack, and the body deflates releasing cadaveric fluids, allowing oxygen to enter the cadaver which stimulates aerobic microbial activity. In the advanced decay stage, most of the flesh is removed and the cadaver begins to dry. When only dry skin, cartilage and bones remain, the dry stage begins. At the remains stage, only bits of skin, hair, bones and teeth are left (Payne, 1965; Vass, 2001; Carter and Tibbett, 2008). The duration of the various stages depends on temperature and insect access to the cadaver (Vass et al., 1992; Campobasso et al., 2001; Megyesi et al., 2005).

This “island of fertility” associated with increased nutrient content, soil microbial biomass and activity on a small terrestrial area has been described as the “Cadaver Decomposition Island” (CDI) (Carter et al., 2007; Benninger et al., 2008). The CDI receives additional organic and inorganic materials, brought by scavengers, grazers and predators (Towne, 2000; Carter et al., 2007). It serves as a food source and a resource for reproduction of blow flies and carrion beetles (Smith and Merrick, 2001; Carter et al., 2007; Hall et al., 2011) within a spatially discrete area. Being a specialised habitat for these organisms, which in turn may affect other trophic levels (bacteria, fungi, protozoa, nematodes) the CDI contributes to overall biodiversity (Carter et al., 2007). Among these groups nematodes have been shown to be stimulated by the increase of bacteria responding to the cadaver nutrient pulse (Metcalf et al., 2013; Carter et al. 2015; Weiss et al., 2016).

Nematodes are one of the most abundant groups of soil metazoans with densities reaching up to 50 million m^{-2} (Bongers and Bongers, 1998; Bongers and Ferris, 1999). They are ubiquitous (Ritz and Trudgill, 1999) and diverse with ca. 30,000 described species, but a total diversity estimated at > one million species (Hugot et al., 2001). Nematodes are recognized as useful biological proxies (bioindicators) of soil conditions (Ritz et al., 2009) due to their abundance, diversity and short generation time (Bongers, 1990; Ettema and Bongers, 1993; Neher and Campbell, 1994; Yeates, 1999; Yeates et al., 2009). Soil nematodes are known to respond to changes in food resource availability and environmental conditions (Boag and Yeates, 1998; Yeates, 1999; Zhang et al., 2012). They can be classified according to feeding types and “colonizer—persister” (c-p) functional groups (Bongers, 1990; Yeates et al., 1993; Bongers and Bongers, 1998; Yeates, 2003). The c-p groups are based on the life strategies of nematodes ranging from c-p 1 i.e. “colonizers” enrichment opportunists, with an immense population growth under food-rich conditions, to c-p 5 “persisters” with a low reproduction rate and a high sensitivity to disturbance (Bongers and Bongers, 1998). This classification facilitates the interpretation of changes in nematode community structure at family level (Korthals et al., 1996). The use of the c-p classification overcomes a main limitation of the trophic group approach, namely the fact that different responses to stress may exist within a given trophic group (Cesarz et al., 2015).

The response of soil nematodes to a range of perturbations has been studied in various natural and agro-ecosystems (Weiss and Larink, 1991; Korthals et al., 1996; Georgieva et al., 2002) and pasture (Bardgett et al., 1994; Yeates et al., 1994, 1995). However, the impact of vertebrate cadavers on soil nematodes is not well known. In a previous experiment focusing on testate amoebae, Szelecz et al. (2014) anecdotally observed major changes in nematode abundance and community structure in response to cadaver decomposition (the nematode data were not published). In this new study we therefore investigated the temporal patterns of nematode density and community structure associated with the decomposition of pig cadavers over a one-year period. Given the responses of nematodes to perturbations and vertebrate decomposition in soils, we firstly expected to find shifts towards bacterial feeding c-p 1 nematodes during the peak of nutrient input along with a decline of other feeding groups and more sensitive nematodes. We then expected that over time community structure and density would gradually return to the pre-disturbance status.

2. Materials and methods

2.1. Study site and experimental setup

The experiment was conducted in a small spruce (*Picea abies*) forest near Neuchâtel, Switzerland (47°01′05.01 N, 6°52′27.76 E, 775 m a.s.l.). The study site was almost flat and covered an area of 1200 m^2. Mean annual temperature and total precipitation (measured in-field with a Decagon Em50 digital data logger) were 10.2 °C and 978 mm (Fig. 1). The topsoil consisted of a litter layer (spruce needles and mosses), a fragmentation layer and a humification layer (O horizon, up to 1 cm), and an umbric horizon with a dark brown colour (A horizon, 1–17 cm).

In total 20 plots (ca. 4 m distance from each other) with four treatments (five replicates each) were set up randomly: 1) control (bare soil), 2) fake pigs (cotton bags of the same size as the pig cadavers), 3) ground pigs (cadavers directly placed on the ground for microclimatic and cadaveric fluids effects), and 4) hanging pigs (cadavers hanging 1 m above ground). The fake pigs served as an additional control for microclimatic effects (e.g. temperature, humidity, solar insolation). The bags covered an area of the same size, but without any cadaveric fluids seeping into the ground. They were filled with soil of the same weight as the cadavers and were gradually emptied to match the average weight loss of the ground cadavers. The hanging pigs provided cadaveric fluids, but without any direct contact to the soil or covering of an area, and thus with no or very minimal microclimatic effect.

Ten domestic pigs (*Sus scrofa domestica*), eight females and two males, 10 weeks old, were bought at a local farm. They were sedated with Stresnil® (Azaperone) and euthanized with T61® by a veterinarian, immediately transported to the experimental site, weighed and placed on the plots. The average cadaver weight was 28 kg ± 2.5 kg (SD). All cadavers were placed in cages (140 cm × 95 cm) surrounded by wire mesh fences to keep scavengers and larger animals away. The experimental area was surrounded by an electric fence for additional protection. Control and fake pig plots were marked with sticks and cords. Fences and cages could be opened at one side for soil sampling and weighing of the cadavers. At each sampling time, soil from inside the fake pig bags was removed to match the weight loss of the pig cadavers.

2.2. Decomposition stages, sampling and laboratory analyses

Decomposition stages were estimated using the definitions provided by Payne (1965) for arthropod-exposed carrions. From the first day of cadaver placement (July 01, 2013) until the beginning of the dry stage, each pig cadaver was examined daily to record the state of decomposition (including photographs and written reports) according to physical characteristics and arthropods present. After the beginning of the dry stage the cadavers were examined at longer intervals (>9 days).

On 11 sampling days from June 2013 until July 2014 a total of 220 soil samples (11 days x 4 treatments x 5 replicates) were collected. Samples were initially taken shortly before the placing of the cadavers (D0), then at one-week intervals i.e. on days D8, D15, D22, and thereafter at increasing intervals on days D36, D59, D84, D123, D263, D331 and D367. A wooden frame, identical in size to the experimental cages, with x (letters A-N) and y (numbers 1–8) coordinates was placed on the ground at each site to ensure random sampling based on the coordinates. Before sampling, coordinates for 10 subsamples per plot were selected with raffles, avoiding resampling the same place. Subsamples were taken with a bulb planter to a depth of 10 cm, pooled and mixed to obtain one soil sample from each plot at each sampling day. Samples were stored at 4 °C until further processing.

Nematodes were extracted from 100 g soil using a modified Baermann funnel technique (Brown and Boag, 1988). Nematodes from all 220 samples were enumerated live using a dissecting microscope (Olympus SZ51), fixed with heated formaldehyde (4%) and heat-killed at 65 °C for 3 min. A subset of three replicates per treatment were used for community analysis ($n = 132$) and one hundred randomly chosen nematodes per sample were identified to family level (Bongers, 1994; Scholze and Sudhaus, 2011) using an upright light microscope at ×400 magnification (Axio Lab. A1, Zeiss). All densities were given as mean ± standard deviation (SD) $100\ \mathrm{g}^{-1}$ dry soil. For this calculation 10 g of each sample were dried in a drying oven (105 °C, 24 h) to determine soil moisture.

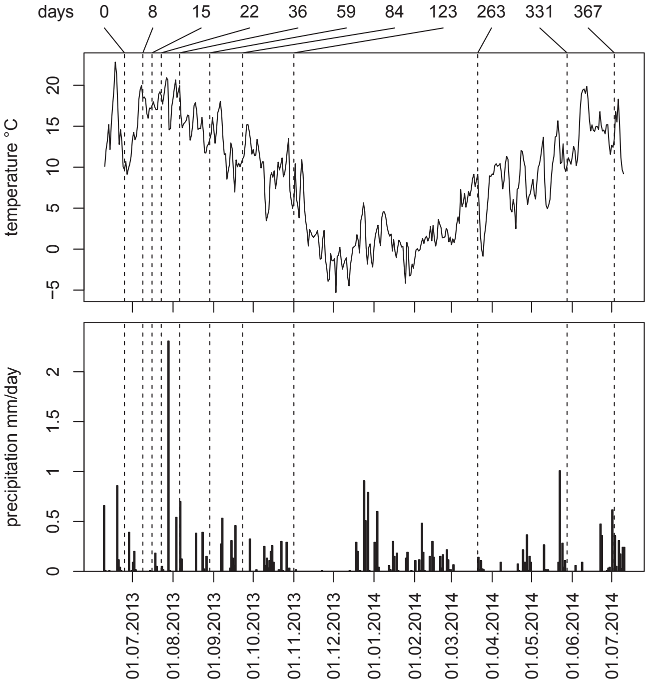

Fig. 1. Climatic data measured at the Bois-du-Clos experimental site (Neuchâtel, Switzerland) over the course of the experiment from June 10, 2013 to July 10, 2014: Air temperature (top) in °C, precipitation (bottom) in mm h^{-1} (grey columns). Days (top) indicate the days elapsed since placing the cadavers on July 01, 2013. Day 0 data was taken on June 26, 2013.

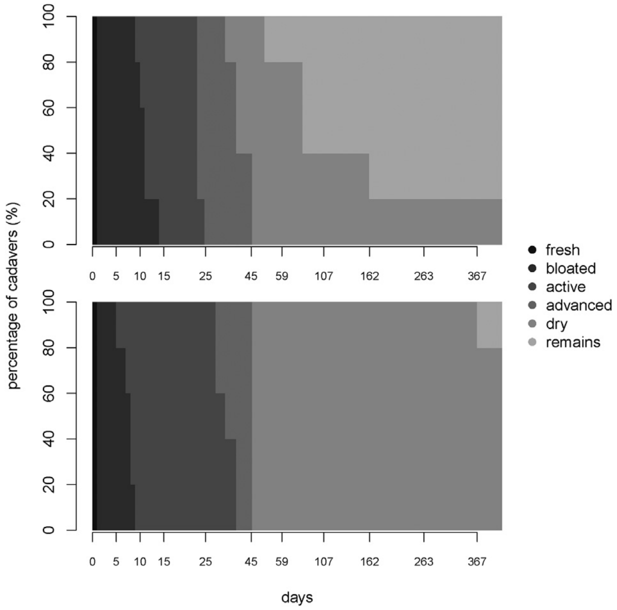

Fig. 2. Duration of decomposition stages, and percentage of cadavers representing a given decomposition stage, in the ground (top) and hanging pig (bottom) cadaver treatments over time at the Bois-du-Clos spruce forest experimental site (Neuchâtel, Switzerland). Decomposition stages are shown in different shades of grey.

Soil samples were analysed for selected chemical markers known to vary in response to decomposing cadavers. Soil pH was measured after diluting the sample in water in a 1:2.5 proportion. Ammonium and nitrate analyses were performed directly after sampling using colorimetric determination (Scheiner, 2005). Total nitrogen was determined using a CHN (Carbon, Hydrogen, Nitrogen) analyser (Thermo Finnigan Flash EA 1112) on dry, ground soil. Bioavailable phosphorus content was determined by colorimetric analysis (Olsen, 1954).

2.3. Data analyses

The duration of each decomposition stage was tested according to treatment (*t*-test adjusted according to Holm) to determine whether the length of the decomposition stages differed between hanging and ground pigs. Nematode data were analysed based on the following metrics 1) functional composition according to trophic grouping (Yeates et al., 1993), 2) colonizer-persister (c-p) life-strategy groups (Bongers, 1990), 3) taxonomic composition (family-level community structure) and 4) Simpson diversity, richness, Hill's evenness and the maturity index (MI), calculated as the weighted mean of the individual c-p values (Bongers, 1990). The c-p structure and MI were calculated using NINJA, the Nematode Indicator Joint Analysis software (Sieriebriennikov et al., 2014).

Temporal patterns and treatment effects were evaluated by ANOVA followed by post-hoc Tukey tests (Chambers et al., 1992). Community patterns (feeding types, c-p groups and family-level communities) were analysed in relation to treatment, sampling day and environmental variables (pH, NH_4^+,NO_3^-, P and N) using partial redundancy analysis (RDA) calculated on Bray-Curtis distance. Factors and variables were selected using stepwise forward selection (ordistep function: vegan package 2.3–0). Significance of the ordination axes were assessed using permutation tests (1000 permutations, p-value threshold = 0.05).

All statistical analyses were performed with R statistical software (version 3.1.0) (R Development Core Team, 2013) and the vegan package (2.3–0).

3. Results

3.1. Temporal patterns of decomposition stages

Over the course of the experiment, four out of five ground pigs went through all six decomposition stages by day 367 and had reached the remains stage, whereas one cadaver was still in the dry stage (Fig. 2). The hanging pigs had at least reached the dry stage (4 cadavers), with one cadaver already in the remains stage (Fig. 2). Decomposition was at first slower for the ground pigs where the bloated stage lasted on average twice as long as in the hanging cadavers (i.e. eight vs. four days; $p < 0.05$, *t*-test, adjusted p-value according to Holm). However, the active decay stage was significantly longer in the hanging cadavers ($p < 0.01$, *t*-test, adjusted p-value according to Holm).

3.2. Nematode density

Nematode density (100 g^{-1} dry soil) sharply increased under the ground pigs from D0 (933 ± 260) to D15 (13,780 ± 13,755) (ANOVA, Tukey HSD, $p < 0.01$, Fig. 3, Table S1). Under the hanging pigs the trend was similar, not as strong but also significantly different (D0: 874 ± 274, D15: 8261 ± 10,531, ANOVA, Tukey HSD, $p < 0.05$, Fig. 3, Table S1). In contrast there was no significant temporal variation in nematode density in the control and fake pig plots (Fig. 3).

3.3. Feeding groups

Bacterivorous nematodes were the most abundant feeding group in all treatments, followed by herbivores and predators (Table 1). Fungivorous nematodes reached somewhat lower densities, and omnivores were least abundant (Table 1). Density of bacterivorous nematodes under the ground pigs was significantly higher than in all other treatments (ANOVA, Tukey HSD, $p < 0.05$).

In the RDAs (calculated on raw nematode densities in 100 g^{-1} dry soil, Fig. 4 a,b,c) a nematode group/family is correlated to/influenced by an environmental/explanatory variable if its orthogonal projection on the vector of the environmental variable is far from zero. The length of the arrow and its angle to an axis gives the strength of the impact (maximum: length = 1, angle = 0°).

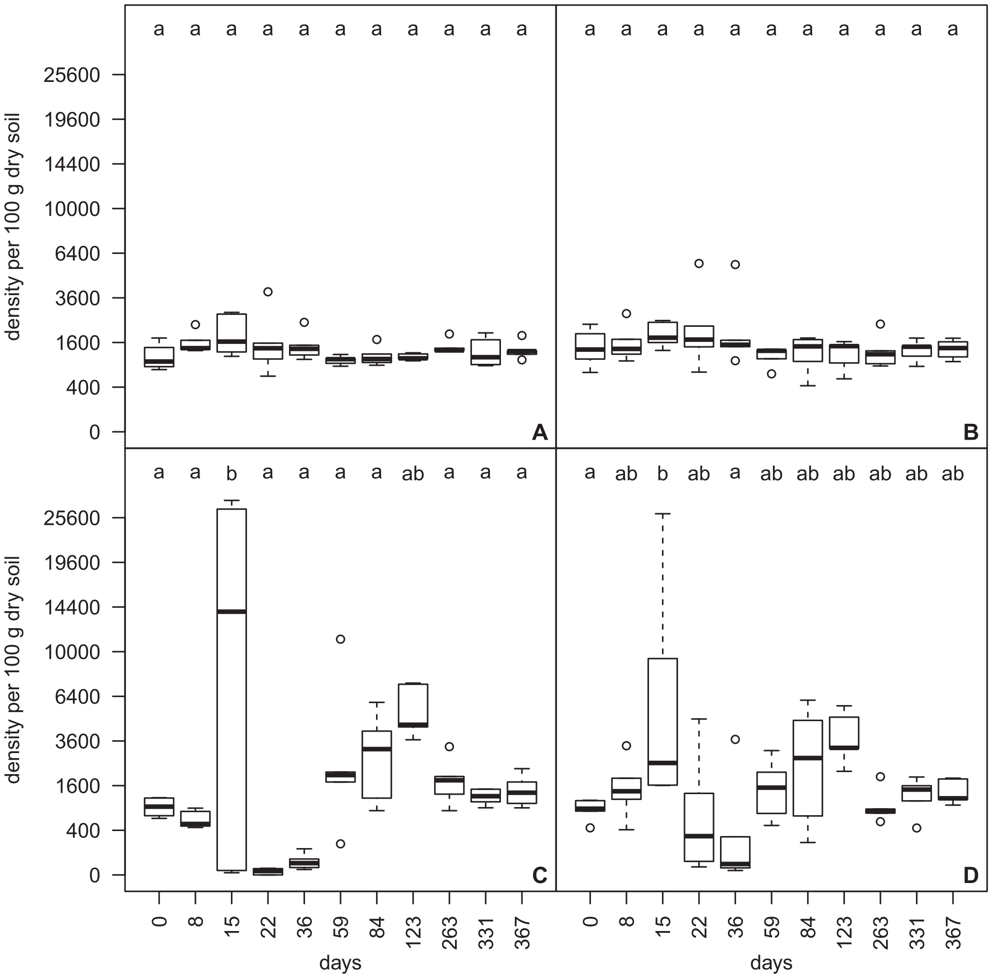

Fig. 3. Box plots showing temporal patterns of soil nematode density in 100 g^{-1} dry soil in the four treatments (A) control, (B) fake pig, (C) ground pig and (D) hanging pig in a spruce forest at the Bois-du-Clos experimental site (Neuchâtel, Switzerland). Different letters (a and b) indicate significant differences among sampling days (ANOVA, Tukey HSD). White box = interquartile range (IQR); Solid black bar = median; Error bar = maximum (top)/minimum (bottom) value excluding outliers; Open circle = outliers.

Table 1
Overall density of nematode feeding groups in 100 g^{-1} dry soil at the Bois-du-Clos experimental site (Neuchâtel, Switzerland) in the control, fake pig, ground pig and hanging pig treatments: average (ave), minimum (min), maximum (max) density and standard deviation (SD).

Feeding groups	Control			Fake			Ground			Hanging		
	Min ± sd	Max ± sd	Ave ± sd	Min ± sd	Max ± sd	Ave ± sd	Min ± sd	Max ± sd	Ave ± sd	Min ± sd	Max ± sd	Ave ± sd
bacterivores	272.26 ± 122.97	525.41 ± 192.37	398.06 ± 73.60	378.36 ± 266.31	1934.46 ± 1924.96	751.16 ± 499.55	0.48 ± 0.43	22,824.84 ± 7863.33	3755.58 ± 6635.44	94.4 ± 158.49	2828.40 ± 606.05	1185.65 ± 831.43
fungivores	27.12 ± 23.56	188.19 ± 83.60	116.28 ± 45.39	34.77 ± 39.14	691.65 ± 830.21	187.54 ± 176.83	0 ± 0	103.15 ± 85.06	25.87 ± 35.76	0 ± 0	99.09 ± 77.34	37.94 ± 36.88
herbivores	226.33 ± 72.19	472.03 ± 192.36	364.80 ± 81.25	329.92 ± 133.20	723.72 ± 520.53	523.09 ± 134.53	0 ± 0	437.90 ± 187.88	116.40 ± 152.07	0 ± 0	378.96 ± 308.33	117.65 ± 154.09
omnivores	17,47 ± 19.89	46.35 ± 35.97	26.69 ± 7.85	0 ± 0	66.24 ± 72.00	18.13 ± 17.89	0 ± 0	18.14 ± 7.73	3.77 ± 6.02	0 ± 0	9.37 ± 16.22	1.10 ± 2.86
predators	144.60 ± 83.49	356.71 ± 10.41	242.63 ± 58.04	153.76 ± 56.07	713.99 ± 521.51	284.48 ± 184.73	0 ± 0	265.63 ± 90.05	47.92 ± 80.38	0 ± 0	222.73 ± 115.71	41.48 ± 70.52

The further away a point is located in the direction of an axis, the more it is influenced by the variable pointing in the same direction. The closer the coordinates of nematode groups/families are to a sample centroid, the more abundant they are in the sample group. Sample centroids that are close together in an ordination space are more similar in their community structure than those that are far away from each other. Thus, a strong dominance of bacterivores in the ground and hanging cadaver samples was correlated with changes in soil pH and phosphorous content (permutation test, $p < 0.05$; Fig. 4a, Table S2).

3.4. *Colonizer-persister (c-p) groups*

In the control samples c-p 4, c-p 2 and c-p 3 co-dominated, while in the fake pig treatment c-p 2 was clearly dominant, followed by c-p 1 and c-p 4 (Table 2). In both pig treatments c-p 1 was the most abundant group, followed by c-p 2, then c-p 4 for the ground pig treatment and c-p 3 for the hanging pig treatment (Table 2). Overall the density of c-p 1 in the ground pig treatments differed significantly from the other treatments (ANOVA, Tukey HSD, $p < 0.05$). In the fake pig treatment c-p 2 differed significantly from all others (ANOVA, Tukey HSD, $p < 0.01$), and c-p 3 to c-p 5 in the fake pig and control treatments differed from both cadaver treatments (ANOVA, Tukey HSD, $p < 0.001$). The RDA showed that the samples from the two cadaver treatments diverged due to the strong dominance of c-p 1 associated with increases in soil pH and ammonium content (permutation test, $p < 0.05$; Fig. 4b, Table S2).

3.5. *Families*

In total 28 nematode families were identified (Table 3). The three most abundant families were Tylenchidae, Plectidae and Rhabditidae in the controls, Tylenchidae, Cephalobidae and Rhabditidae in the fake pig samples, Rhabditidae, Diplogasteroididae and Neodiplogasteridae in ground pig samples, and Rhabditidae, Neodiplogasteridae and Diplogasteroididae in the hanging pigs samples (Table 3); the latter two families were exclusively found in the ground and hanging pig treatments.

The RDA showed that the divergence of nematode communities in both pig treatments as compared to the control and fake pig treatments was correlated, first to an increase in soil nitrate and then to increases in pH and phosphorous and ammonium content (permutation test, $p < 0.05$; Fig. 4c, Table S2). Most nematode families responded negatively to cadavers with the notable exceptions of Rhabditidae, Neodiplogasteridae and Diplogasteroididae (Fig. 4c). The position of samples in the ordination space showed that, although by D263-D367 communities from both cadaver treatments were clearly converging towards the control and fake pig communities, they still remained different.

3.6. *Nematode diversity, richness, evenness and maturity indices*

Overall Simpson diversity (Fig. 5a) was significantly highest in the control, lower in the fake pig samples, and lowest in the two cadaver treatments (ground and hanging) (ANOVA, Tukey HSD, $p < 0.001$). In the ground and hanging pig samples diversity decreased at D8 and stayed fairly low until D263, being significantly different from D0 (ground pigs: $p < 0.001$, hanging pigs: $p < 0.05$; ANOVA, Tukey HSD). After that it increased again in the ground pig treatment at D331, with significant differences to the preceding time points from D8 to D263 (ANOVA, Tukey HSD, $p < 0.05$).

Family richness overall was significantly highest in the controls, lower in the fake pig samples (ANOVA, Tukey HSD, $p < 0.01$), and lowest in the ground and hanging pig samples (ANOVA, Tukey HSD, $p < 0.001$; Fig. 5b). In the control samples family richness remained

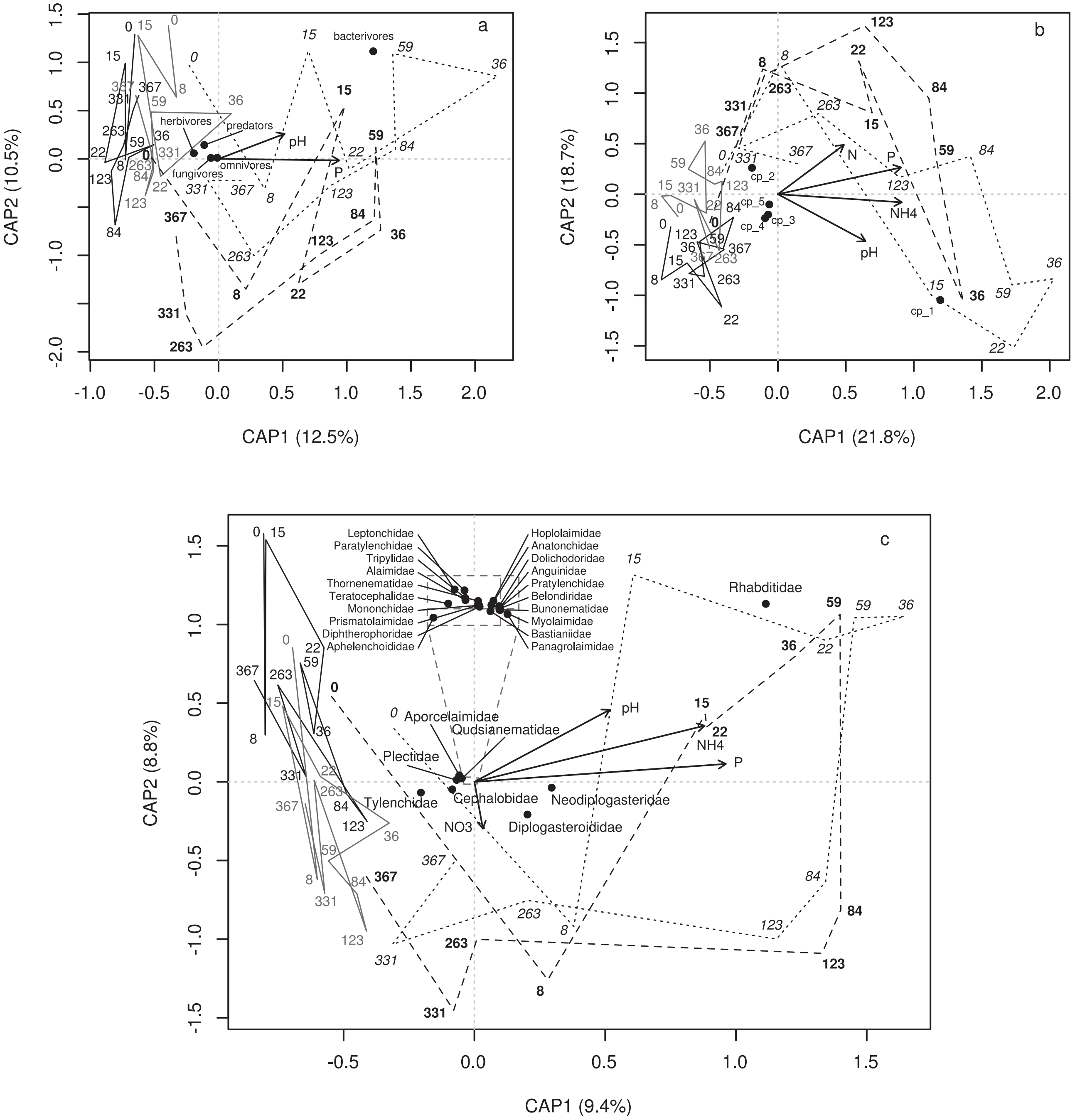

Fig. 4. Redundancy analysis (RDA) ordination diagram showing the temporal patterns of soil nematode (a) feeding groups, (b) c-p groups and (c) families in control, fake pig, ground pig and hanging pig treatments in a spruce forest at the Bois-du-Clos experimental site (Neuchâtel, Switzerland). The lines (solid black: control; solid grey: fake; dotted: ground pig; dashed: hanging pig) join the centroids of replicates from each sampling day (numbers indicating the time since death in days). Arrows represent the environmental/explanatory variables selected by stepwise selection to discriminate the above-mentioned nematode groups (response variables). Stepwise selection alternated between forward selection and backward elimination. This overcame the problem of using either forward selection or backward elimination where all variables that are included/eliminated at a previous step are kept in the model/removed from the model (even though they might not contribute much after other variables are incorporated) (Legendre and Legendre, 1998).

constant throughout the experiment. In contrast it decreased in the ground pig samples significantly from 15 ± 2 at D0 to 5 ± 3 at D8 and 1 ± 1 at D22, remaining low until D263 (ANOVA, Tukey HSD, $p < 0.001$). Family richness recovered completely by D331 and D367 with no significant differences compared to D0. Hanging pig samples showed the same pattern, but the effect was less pronounced. Richness dropped from 13 ± 2 at D0 to 7 ± 3 at D8, reached a minimum of 2 ± 1 at D59, but did not drop to 0, with D0 being significantly different from the subsequent time points D15 to D123 (ANOVA, Tukey HSD, $p < 0.05$), but not from D263-D367 where it had increased again reaching 12 ± 2 at D367.

Family richness declined from an average of 14.7 ± 2.1 at D0 (i.e., before the cadavers were placed) to 1.3 ± 1.0 (ground pigs), and from 12.6 ± 2.3 (D0) to 5.1 ± 2.8 (hanging pigs) during the active decay stage (ANOVA, Tukey HSD, $p < 0.05$, Fig. 6). By the end of the experiment, in the dry and remains stage, family richness was on average about half of that of D0 (but no longer significantly different) under both treatments (7.7 ± 4.7 in the ground pigs and

Table 2
Overall density of nematode functional c-p groups in 100 g^{-1} dry soil at the Bois-du-Clos experimental site (Neuchâtel, Switzerland) in the control, fake, ground and hanging pig treatments: average (ave), minimum (min), maximum (max) density and standard deviation (SD).

c-p groups	Control			Fake			Ground			Hanging		
	Min ± sd	Max ± sd	Ave ± sd	Min ± sd	Max ± sd	Ave ± sd	Min ± sd	Max ± sd	Ave ± sd	Min ± sd	Max ± sd	Ave ± sd
c-p 1	18.80 ± 18.94	368.47 ± 169.85	137.01 ± 100.90	12.43 ± 21.53	1503.30 ± 1907.44	294.93 ± 425.28	0.48 ± 0.43	22,871.19 ± 7783.23	3665.92 ± 6694.42	25.53 ± 35.46	2846.27 ± 601.41	1046.82 ± 833.08
c-p 2	226.18 ± 67.48	443.26 ± 207.67	310.74 ± 76.25	297.07 ± 296.99	2095.58 ± 2537.70	748.40 ± 508.23	0 ± 0	493.29 ± 159.76	174.21 ± 206.95	0 ± 0	644.83 ± 344.43	223.87 ± 229.95
c-p 3	131.03 ± 42.13	302.29 ± 34.53	211.47 ± 49.90	152.51 ± 49.50.	355.45 ± 402.00	243.35 ± 63.68	0 ± 0	133.21 ± 95.17	29.20 ± 45.45	0 ± 0	227.82 ± 145.26	44.91 ± 68.29
c-p 4	207.85 ± 95.46	442.49 ± 100.98	320.50 ± 79.86	142.38 ± 67.53	493.26 ± 159.26	294.93 ± 425.28	0 ± 0	277.21 ± 57.25	45.16 ± 85.00	0 ± 0	227.74 ± 66.66	41.76 ± 76.93
c-p 5	94.17 ± 40.65	277.12 ± 61.83	168.84 ± 51.58	81.87 ± 31.79	670.81 ± 583.23	216.20 ± 165.88	0 ± 0	174.12 ± 138.43	33.24 ± 55.10	0 ± 0	156.14 ± 117.83	26.64 ± 46.36

7.7 ± 3.8 in the hanging pigs).

Overall, Hill's evenness in the hanging and fake pig treatments differed significantly from the control and ground pig treatments (ANOVA, Tukey HSD, $p < 0.05$). Hill's evenness did not show significant differences over time regardless of the treatment (Fig. 5c).

The maturity index (MI) in the control and fake pig treatments was overall significantly higher compared to the ground and hanging pig treatments (ANOVA, Tukey HSD, $p < 0.001$). The MI remained stable (mostly 2.5–3.5) in the control and the fake pig treatments throughout the experiment (Fig. 5d), with no significant differences over time. By contrast, in both the ground and hanging pig treatments it dropped sharply to ca. 1 at D8 and D36 in the ground pig and hanging pig treatments, respectively, and remained low until D123 in both, with significant differences between D0 and all other time points (ANOVA, Tukey HSD, $p < 0.001$). Higher values were recorded on the last three sampling dates (D263-D367), but still significantly lower compared to D0 (ANOVA, Tukey HSD, $p < 0.001$).

4. Discussion

4.1. Shifts in nematode density and community structure in response to cadaver decomposition

Nematode density, diversity and community structure are known to vary among ecosystems in relation to differences in soil type, climate and vegetation (Boag and Yeates, 1998), and we therefore hypothesised that we would observe clear changes in response to decomposing cadavers. In the control and fake pig samples nematode density was somewhat lower than the values reported in a similar habitat by Bongers and Bongers (1998), i.e., ca. 1400 vs. ca. 3000 ind. 100 g^{-1} soil, and did not change during the course of the experiment. The communities in the control and fake pig samples were dominated by bacterial-feeding nematodes (Cephalobidae, Plectidae and Rhabditidae) and herbivores (Tylenchidae) which are frequently dominant in soils (Yeates, 2003). A similar community structure from a study of spruce stands in south-west Germany was reported by Ruess (1995). Other studies have shown that, amongst bacterial feeders, Cephalobidae were the most abundant group in soils, and Plectidae were indicative of stressed natural environments (Yeates, 2003).

In contrast to the stability of nematode density observed in the control plots, we observed a clear peak in density in both cadaver treatments on D15 which corresponded to the active decay phase. Bacterial feeding nematodes, primarily Rhabditidae, are known to respond positively to nutrient enrichment (e.g., water or organic matter) compared to other bacterivores such as the Cephalobidae (Bongers, 1990; Ferris and Matute, 2003; Georgieva et al., 2005; Blanc et al., 2006; Steel et al., 2010). The increase in Rhabditidae abundance, which we observed in the later stages of decomposition in response to the nutrient pulse and associated enhanced bacterial density, is in line with several recent studies (Metcalf et al., 2013; Carter et al., 2015; Weiss et al., 2016). Rhabditidae (c-p 1 nematodes) are typically r-strategists, with rapid population increases typically recorded two to three weeks after manure addition to soil (Bongers and Ferris, 1999). This rapid increase may also partly be explained by the fact that the Rhabditidae can be transported to new food sources by phoresy on scavenger insects (Bongers and Ferris, 1999). For example, *Rhabditis stammeri* is known to live exclusively on cadavers and is transported by insects, especially the burying beetle *Nicrophorus vespilloides* (Richter, 1993).

Overall, hanging pigs had less impact on soil communities than ground pigs during the active decay phase. Furthermore, the first density peak at D15 was somewhat lower as compared to the

Table 3

Overall density of nematode families in 100 g^{-1} dry soil at the Bois-du-Clos experimental site (Neuchâtel, Switzerland) in the control, fake, ground and hanging pig treatments: average (ave), minimum (min), maximum (max) density and standard deviation (SD). Highest average densities (first three) in each treatment are given in bold.

No.	Families	Control			Fake			Ground			Hanging		
		Min ± sd	Max ± sd	Ave ± sd	Min ± sd	Max ± sd	Ave ± sd	Min ± sd	Max ± sd	Ave ± sd	Min ± sd	Max ± sd	Ave ± sd
1	Alaimidae	20.03 ± 12.39	70.80 ± 20.25	44.90 ± 16.57	7.12 ± 12.34	43.89 ± 43.42	22.02 ± 14.34	0 ± 0	18.88 ± 16.39	5.73 ± 8.08	0 ± 0	29.71 ± 7.06	4.47 ± 8.83
2	Anatonchidae	0 ± 0	27.11 ± 20.79	11.24 ± 9.25	0 ± 0	24.52 ± 23.31	7.65 ± 8.74	0 ± 0	10.16 ± 10.58	1.82 ± 3.50	0 ± 0	25.32 ± 36.49	6.15 ± 9.40
3	Anguinidae	0 ± 0	11.88 ± 11.46	1.53 ± 3.75	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
4	Aphelenchoididae	0 ± 0	81.81 ± 36.92	40.56 ± 24.01	12.86 ± 22.27	628.95 ± 885.93	121.19 ± 175.06	0 ± 0	103.15 ± 85.06	22.32 ± 34.75	0 ± 0	89.67 ± 68.48	31.41 ± 36.11
5	Aporcelaimidae	36.73 ± 24.75	157.44 ± 34.83	85.71 ± 34.57	41.33 ± 42.24	503.89 ± 535.76	129.82 ± 132.20	0 ± 0	95.77 ± 73.48	21.47 ± 36.98	0 ± 0	111.72 ± 78.21	18.34 ± 33.30
6	Bastianiidae	0 ± 0	27.21 ± 29.62	9.54 ± 8.29	0 ± 0	56.16 ± 97.27	11.46 ± 18.01	0 ± 0	10.96 ± 9.64	1.31 ± 3.36	0 ± 0	15.86 ± 16.52	2.48 ± 5.61
7	Belondiridae	0 ± 0	4.67 ± 8.09	0.68 ± 1.57	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
8	Bunonematidae	0 ± 0	3.72 ± 6.44	0.34 ± 1.12	0 ± 0	15.47 ± 26.79	2.76 ± 5.34	0 ± 0	10.56 ± 11.41	1.75 ± 3.92	0 ± 0	6.53 ± 11.30	0.84 ± 2.05
9	Cephalobidae	0 ± 0	189.99 ± 122.02	53.98 ± 48.42	82.12 ± 39.93	984.90 ± 1610.07	**316.28 ± 281.76**	0 ± 0	233.08 ± 145.70	68.14 ± 90.49	0 ± 0	435.03 ± 384.75	119.32 ± 152.76
10	Diphtherophoridae	6.42 ± 11.13	28.44 ± 4.19	16.58 ± 6.96	4.53 ± 7.84	105.42 ± 182.59	27.73 ± 4.53	0 ± 0	56.02 ± 60.27	7.11 ± 16.74	0 ± 0	13.23 ± 19.19	4.33 ± 6.08
11	Diplogasteroididae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3120.98 ± 1101.67	**313.78 ± 933.26**	0 ± 0	659.23 ± 1141.81	**125.64 ± 219.62**
12	Dolichodoridae	0 ± 0	4.06 ± 7.03	0.37 ± 1.22	0 ± 0	40.74 ± 70.56	3.70 ± 12.28	0 ± 0	11.03 ± 10.59	1.00 ± 3.32	0 ± 0	16.26 ± 28.27	1.48 ± 4.90
13	Hoplolaimidae	0 ± 0	61.86 ± 35.80	8.65 ± 19.69	0 ± 0	38.68 ± 27.06	3.52 ± 11.66	0 ± 0	21.43 ± 22.94	1.95 ± 6.46	0 ± 0	10.33 ± 9.20	0.94 ± 3.11
14	Leptonchidae	5.42 ± 4.71	100.49 ± 71.35	57.61 ± 30.40	0 ± 0	60.99 ± 56.64	27.47 ± 24.19	0 ± 0	12.58 ± 5.86	1.83 ± 4.22	0 ± 0	36.18 ± 25.24	3.35 ± 10.89
15	Mononchidae	13.97 ± 12.95	51.01 ± 51.55	26.60 ± 13.67	0 ± 0	40.59 ± 28.06	17.40 ± 13.84	0 ± 0	54.81 ± 49.85	8.16 ± 16.62	0 ± 0	10.33 ± 9.20	1.24 ± 3.17
16	Myolaimidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	6.85 ± 11.86	0.62 ± 2.06	0 ± 0	17.58 ± 23.19	1.60 ± 5.30
17	Neodiplogasteridae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1185.55 ± 1183.52	**255.27 ± 422.61**	0 ± 0	1524.55 ± 1366.20	**239.23 ± 490.39**
18	Panagrolaimidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	89.39 ± 154.82	8.13 ± 26.95
19	Paratylenchidae	34.04 ± 58.96	122.49 ± 212.16	62.73 ± 25.40	0 ± 0	13.58 ± 23.52	1.77 ± 4.30	0 ± 0	0 ± 0	0 ± 0	0 ± 0	23.49 ± 40.69	4.49 ± 7.82
20	Plectidae	78.34 ± 6.26	157.83 ± 58.51	**119.01 ± 28.19**	66.11 ± 5.78	215.48 ± 142.29	124.64 ± 48.37	0 ± 0	198.16 ± 33.02	44.94 ± 71.12	0 ± 0	74.71 ± 35.67	24.42 ± 29.33
21	Pratylenchidae	0 ± 0	0 ± 0	0 ± 0	0 ± 0	18.11 ± 31.36	1.65 ± 5.46	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
22	Prismatolaimidae	7.09 ± 12.27	34.55 ± 32.81	23.61 ± 9.17	0 ± 0	43.05 ± 60.58	19.22 ± 12.13	0 ± 0	29.51±±39.02	6.04 ± 9.95	0 ± 0	49.72 ± 12.58	8.57 ± 15.07
23	Qudsianematidae	30.58 ± 34.18	144.87 ± 70.13	81.14 ± 32.85	35.97 ± 34.25	218.23 ± 184.68	90.43 ± 51.12	0 ± 0	102.55 ± 37.43	15.36 ± 31.08	0 ± 0	69.45 ± 39.10	14.18 ± 25.45
24	Rhabditidae	13.76 ± 14.04	256.02 ± 105.68	**91.52 ± 68.39**	6.72 ± 11.64	1255.77 ± 1694.54	**206.95 ± 358.58**	0.48 ± 0.43	22,593.33 ± 8263.91	**3041.63 ± 6597.45**	12.68 ± 18.23	1664.86 ± 2659.89	**635.40 ± 506.46**
25	Teratocephalidae	25.18 ± 8.82	121.81 ± 37.29	54.25 ± 26.12	25.28 ± 9.37	77.52 ± 80.77	50.07 ± 17.95	0 ± 0	39.36 ± 29.51	10.51 ± 15.09	0 ± 0	55.86 ± 59.75	14.40 ± 19.18
26	Thornenematidae	17.47 ± 19.89	41.68 ± 28.82	26.01 ± 6.68	0 ± 0	66.24 ± 72.00	18.13 ± 17.98	0 ± 0	18.14 ± 7.73	3.77 ± 6.02	0 ± 0	9.37 ± 16.22	1.10 ± 2.86
27	Tripylidae	14.03 ± 24.30	78.91 ± 86.53	37.95 ± 18.13	3.36 ± 5.82	96.04 ± 97.66	36.92 ± 26.15	0 ± 0	9.86 ± 17.08	1.11 ± 2.99	0 ± 0	11.42 ± 19.78	1.57 ± 3.71
28	Tylenchidae	153.88 ± 81.94	370.02 ± 96.04	**288.07 ± 68.32**	329.92 ± 133.20	712.90 ± 490.46	**509.90 ± 120.69**	0 ± 0	437.90 ± 187.88	111.86 ± 146.83	0 ± 0	364.89 ± 183.40	

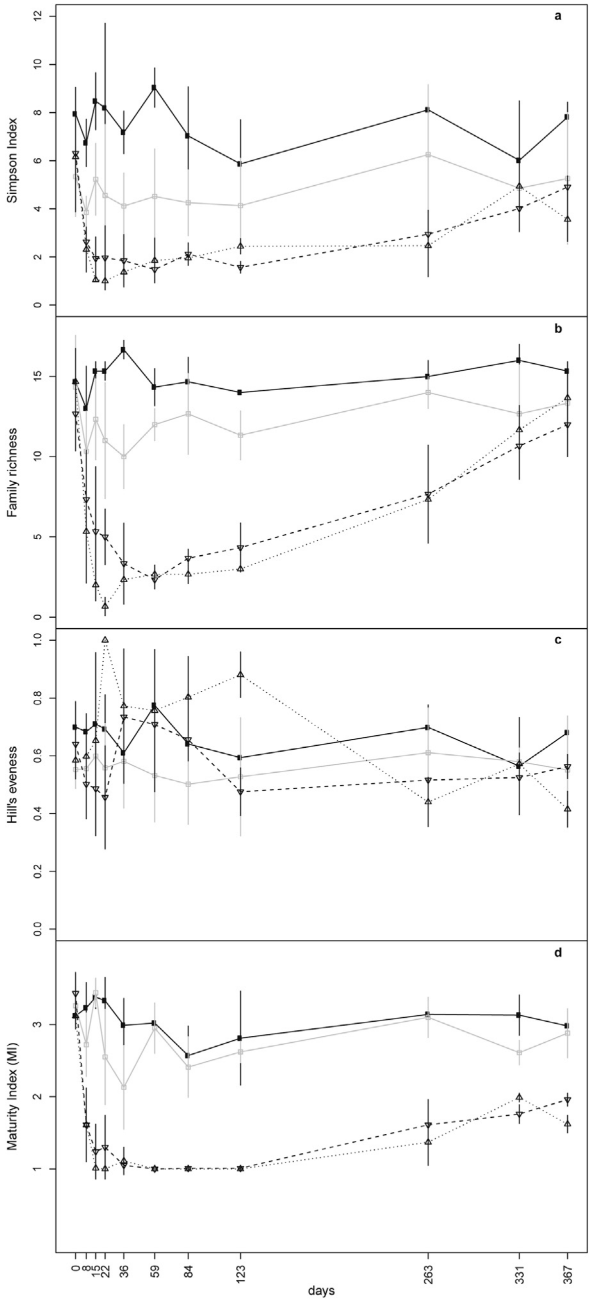

Fig. 5. Temporal patterns of soil nematodes (family level) in the four treatments (control, fake pig, ground pig and hanging pig) in a spruce forest at the Bois-du-Clos experimental site (Neuchâtel, Switzerland) (a) Simpson diversity index, (b) family richness, (c) Hill's evenness, (d) Maturity index (MI). Treatments are indicated by line type: solid/circles: control; grey/squares: fake; dotted/triangle up: ground pig; dashed/triangle down: hanging pig.

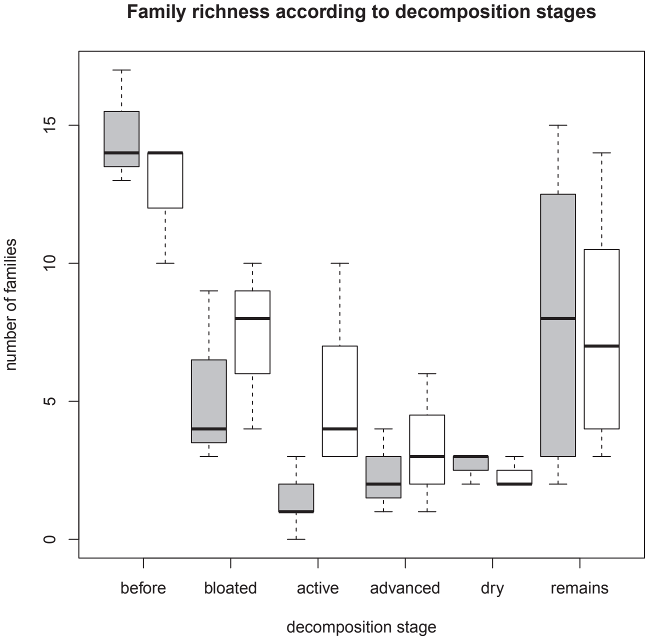

Fig. 6. Boxplot showing the number of nematode families according to the decomposition stages in the ground pig treatment (grey boxes) and in the hanging pig treatment (white boxes) at the Bois-du-Clos experimental site (Neuchâtel, Switzerland). White box = interquartile range (IQR); Solid black bar = median; Error bar = maximum (top)/minimum (bottom) value excluding outliers.

ground pigs. The impact of hanging pigs was due to the so-called drip zone, a secondary site of activity after the cadaver itself (Shalaby et al., 2000), which is not in direct contact with the soil.

The decline of nematode density (notably to almost zero in the ground pig treatments) towards the end of the active decay stage (D22) was most likely due to a hostile environment caused by cadaveric fluids and the associated change in microclimatic conditions (i.e., higher temperature). Rhabditidae are known to be vulnerable to thermal stress (Venette and Ferris, 1997), and cadavers with associated insect larval masses can generate temperatures up to 50 °C, with the difference between ambient and cadaver temperatures exceeding 20 °C (Charabidze et al., 2011). When microbial activity decreases, Rhabditidae stop feeding and form survival stages, i.e., dauer larvae (Bongers and Bongers, 1998). Although the decrease on D22 was observed in all plots of the ground pig treatment, in two of the five plots the peak in nematode abundance was not apparent on D15, explaining the large error bar in Fig. 3. Since an increase in nematode abundance was not observed at later time points, it might have occurred before D15, but would then not have been recorded given our sampling intervals of one week.

In the hanging pig treatment the active decay stage lasted significantly longer, probably mainly because the larvae that fell to the ground were unable to regain the carcass, which slowed down the removal of biomass (Shalaby et al., 2000). This is in accordance with the delayed density decrease to almost zero under the hanging pig treatment on D36. Shalaby et al. (2000) also observed a similar delay in the progression of decomposition of hanging cadavers compared to ground cadavers due to cooling effects of the air and the inability to form large heat-generating maggot masses, resulting in reduced numbers of Diptera larvae and the inability of ground-dwelling arthropods to access the carcass. This reduced micro-environmental impact of the hanging cadavers has likely also contributed to the weaker responses of nematode communities in our study.

By D36 the density of Rhabditidae had slowly started to increase again in both cadaver treatments. As the active decay stage terminated, Diptera larvae had partly migrated from the carcass, and the impact from the cadavers was clearly declining. Increased rainfall at the end of July and beginning of August 2013 (Fig. 1) further contributed to improved conditions for Rhabditidae (Sohlenius, 1985). A second, though not significant peak in nematode density at D123 in the cadaver treatments corresponded to the remains stage which was dominated by three families Rhabditidae, Neodiplogasteridae and Diplogasteroididae, the latter two were only observed in the cadaver treatments. Like Rhabditidae, the Diplogasteroididae and Neodiplogasteridae may disperse over relatively long distances by phoresy (Steel et al., 2013). Whereas the Rhabditidae are bacterial feeders (Yeates et al., 1993), Neodiplogasteridae and Diplogasteroididae are also known to prey on other nematodes (Von Lieven and Sudhaus, 2000; Steel et al. 2011) which may have hindered a re-occurring dominance of Rhabditidae at D123. In both cadaver treatments nematode density decreased after the second peak (D263) and thereafter was more or less stable until the end of the experiment.

4.2. Feeding groups

Apart from bacterial feeders the other trophic groups disappeared completely in the ground pig treatment (omnivores at D8, fungivores at D15, and herbivores and predators at D22) and remained absent until D123. Higher-trophic level nematodes such as predators and omnivores are considered more sensitive to environmental changes than lower-trophic level nematodes such as bacterial and plant-feeders (Bongers and Bongers, 1998; Šalamún et al., 2012; Thakur et al., 2014). By D263 all trophic groups were again present, indicating that the communities were recovering from the stressed environment.

4.3. Colonizer-persister (c-p) groups

The above-mentioned findings were reflected in the c-p groups, i.e., in the ground pig treatment c-p groups 2–5 were only present at the beginning (D0 and D8) and the end of the experiment (D263-D367), and were completely absent in between (i.e. D15-D123 for c-p 2–4 and D22-D123 for c-p 5). Steel et al. (2010) found a shift in dominance from c-p 1 to c-p 2 in compost succession between 22 and 29 days. In our study the initial highly enriched and then unfavourable conditions probably made it difficult for c-p 2 nematodes to become established, even after the collapse of the c-p 1 group. The comparatively longer generation time of c-p 2 taxa likely also prevented them from reaching high abundance. The absence of c-p 3–5 (persisters) is unsurprising given their known sensitivity to disturbance, e.g., the release of cadaveric fluids and increase in temperature (Ferris and Bongers, 2009).

4.4. Nematode diversity and maturity indices

Whereas diversity, richness and maturity indices did not change over time in the control and fake pig samples, they were all clearly affected by the presence of the cadavers. Nematode diversity, family richness and maturity index (MI) were significantly reduced in the cadaver treatments. Though caution should be exercised in the use of univariate statistics to describe nematode communities (Wall et al., 2002), high nematode diversity is considered to be indicative of relatively stable conditions (Bongers and Bongers, 1998), while stress causes a decrease in nematode family richness and diversity resulting in the dominance of a few taxa (Georgieva et al., 2002). Previous studies have observed a decrease in MI under disturbed conditions (Bongers, 1999; Ettema and Bongers, 1993; Georgieva et al., 2002). In the cadaver treatments, MI was significantly reduced until the end of the experiment, in contrast to the other nematode indices (family, trophic group and c-p group) which showed signs of recovery.

4.5. Composts as analogues to cadaver impacts?

To our knowledge this is the first study exclusively focusing on cadaver impacts on soil nematodes, which makes it difficult to compare our results to previous studies. However, shifts in nematode communities have been well studied in composts and plant litter decomposition (Georgieva et al., 2005; Steel et al., 2010, 2012; 2013). Decomposing cadavers and composts are similar in that they both release considerable amounts of nutrients and are characterized by well-defined phases in the decomposition process. We would thus expect some similarities between temporal patterns of nematode community changes in response to cadavers and compost. However, the higher nutrient content of cadavers as compared to wood and plant litter, and the difference in the stoichiometry of the released fluids, can be expected to drive contrasting patterns of community changes.

At the beginning of the composting process there is a clear dominance of bacterivorous enrichment opportunists (Rhabditidae, Panagrolaimidae) and bacterivorous/predacious Diplogasteridae, followed by bacterivorous (Cephalobidae) and fungivorous general opportunists (Aphelenchoididae, Anguinidae) in the subsequent stages (Steel et al., 2010, 2013). The dominance of Rhabditidae at the beginning of the decomposition process, and the later occurrence of diplogasterids, was also observed in our study. In the ground pig treatment Neodiplogasteridae were first observed on D15, then disappeared and reappeared on D59 after the end of the active decay phase. Delayed occurrence of Neodiplogasteridae in composts, compared to soil where they are abundant from the beginning of the decomposition processes (Georgieva et al., 2005), is due to the relatively high and lethal temperatures (ca. 40 °C) at initiation of the composting process (Steel et al., 2010).

Thus, despite similarities in the community dynamics there are also clear differences. In our study there was no increase or replacement of Rhabditidae by Cephalobidae beneath the decomposing cadavers. Cephalobidae are, apart from soil, rather common in litter and rotting plant tissues and might not favour the altered soil conditions caused by cadaveric fluids. Additionally, the increase in abundance of fungal feeders during the maturation phase of the composting process (Steel et al., 2010, 2013) was not documented in our study where no increase in fungal feeders was observed, be it in the ground or hanging pig treatment over the course of the experiment. This comparison shows that the patterns of change in nematode communities are only partly similar between composts and cadaver-impacted soils.

4.6. Conclusions

We expected to observe very clear responses of soil nematodes to decomposing cadavers, and this was indeed the case. Decomposing cadavers modified the soil environment and allowed previously absent or rare taxa to reach high densities, thus clearly altering the communities of soil nematodes. Interestingly, such changes were already obvious at the relatively crude taxonomic resolution we used (i.e. family level), but may be even clearer if a higher resolution were used (e.g. using molecular approaches). The clear contrast in all metrics used suggests that nematodes could be used as a tool to document the presence of cadavers and the time since death. Further studies in different climatic conditions, seasons, vegetation and soil types will, however, be necessary before such a tool can be validated. It would also be useful to assess if a higher taxonomic resolution could give more precise results. Also, the impact of different nutrient sources (e.g. faeces, urine) and perturbation (e.g. fire, physical disturbance) should be compared more systematically to determine if the indicators we identified are indeed specific to decomposing cadavers.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2016.09.011.

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