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Nematode succession during composting and the potential of the nematode community as an indicator of compost maturity

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ABSTRACT

One of the key issues in compost research is to assess when the compost has reached a mature stage. The maturity status of the compost determines the quality of the final soil amendment product. The nematode community occurring in a Controlled Microbial Composting (CMC) process was analyzed with the objective of assessing whether the species composition could be used as a bio-indicator of the compost maturity status. The results obtained here describe the major shifts in species composition that occur during the composting process. Compared to terrestrial ecosystems, nematode succession in compost differs mainly in the absence of K-strategists and numerical importance of diplogastrids. At the beginning of the composting process (thermophilic phase), immediately after the heat peak, the nematode population is primarily built by bacterial feeding enrichment opportunists (cp-1) (Rhabditidae, Panagrolaimidae, Diplogastridae) followed by the bacterial-feeding general opportunists (cp-2) (Cephalobidae) and the fungal-feeding general opportunists (Aphelenchoididae). Thereafter, during the cooling and maturation stage, the bacterial-feeding-predator opportunistic nematodes (*Mononchoides* sp.) became dominant. Finally, at the most mature stage, the fungal-feeding Anguinidae (mainly *Ditylenchus filimus*) were most present. Both, the Maturity Index (MI) and the fungivorous/bacterivorous ratio (f/b ratio), increase as the compost becomes more mature (ranging, respectively, from 1 to 1.86 and from 0 to 11.90). Based on these results, both indices are suggested as potential suitable tools to assess compost maturity.

1. Introduction

Composting is an aerobic, heat-producing and controlled process by which microorganisms convert a mixed organic substrate into carbon dioxide (CO_2), water, inorganic nutrients and stabilized organic matter. Control of the environmental conditions (moisture, temperature, substrate composition and oxygenation) during the process distinguishes composting from natural rotting or decomposition (Zucconi and de Bertoldi 1987; Baldwin and Greenfield 2006). The application of compost to soil has several benefits. The stabilized organic matter in compost improves soil structure. Consequently, soil aeration, soil porosity, water holding capacity and drainage increase (Kuo et al. 2004; Cogger 2005; Baldwin and Greenfield 2006). Furthermore, compost can provide an important source of nutrients for plants (for reviews see Cogger 2005; Zvomuya et al. 2008), especially the compost nitrogen that becomes available for plants after mineralization in the soil (Hadas and Portnoy 1997). In addition, composts are known to suppress plant diseases through a combination of physiochemical and biological mechanisms (Akhtar and Malik 2000; Gamliel et al. 2000; Reuveni et al. 2002; Bailey and Lazarovits 2003; Vallad et al. 2003; Kuo et al. 2004).

Controlled Microbial Compost (commonly known as CMC or "Leubke compost") is a premium grade and well-humified compost. The CMC method was developed through on-farm and laboratory research by the Leubke family (Diver 2004). During the process, the compost is aerated by turning and is monitored to ensure high standards of quality. A microbial starter is usually added to inoculate the compost (Diver 2004). The composting is carried out in windrows, which are covered to prevent nutrient leaching, reduce gaseous emissions and reduce heat loss (Rees 2007).

During composting, organic materials are disintegrated by processes associated with several organisms. The taxa that are most important to the composting process are Bacteria, Algae,

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Fungi, Isopoda, Acari, Nematoda and Protozoa. This wide spectrum of organisms forms a complex and rapidly changing community. Up to the present, only the dynamics of the bacterial community have been thoroughly investigated in relation to composting processes (e.g. Herrmann and Shann 1997; Ishii et al. 2000; Alfreider et al. 2002; Tiquia et al. 2002; Ryckeboer et al. 2003; Tiquia 2005; Fracchia et al. 2006; Halet et al. 2006). Research concerning the role of nematodes in decomposition processes tends to focus on specific natural processes in the soil (Ingham et al. 1985; Ruess 2003; Ruess and Ferris 2004; Wang et al. 2004; Georgieva et al. 2005; Postma-Blaauw et al. 2005) or on laboratory microcosm experiments with bacterial-feeding nematodes and their influence on the decomposition rate of organic material of marine environments (De Mesel et al. 2003, 2004, 2006). Although nematodes appear to be numerically important in the composting process, and their diversity and density in mature compost are considered crucial to constructing a robust soil food web (Ingham 2001, 2006; Ingham and Slaughter 2004), knowledge of the diversity and succession of the nematode community during the composting process is completely lacking. Moreover, nematodes show several characteristics which make them ideal bio-indicators of the ecosystem quality. Nematode community analyses are very useful in assessing ecosystem status and functions since nematodes are ubiquitous and easy to sample (Bongers and Ferris 1999; Ritz and Trudgill 1999; Yeates and Bongers 1999; Neher 2001; Yeates 2003). Furthermore, the species composition of the samples reflects a wide range of abiotic parameters such as substrate texture, climate, biogeography, organic inputs and both natural and anthropogenic disturbances (Yeates 1984; Neher 2001; Yeates 2003). The use of nematodes as functional indicators relies on the allocation of nematodes to feeding groups (Yeates et al. 1993) and reproductive strategies (cp values) (Bongers 1990; Yeates 2003). Nematode genera with the same cp value are adapted to specific environmental conditions and food sources through anatomical and physiological commonalities (Ferris et al. 2001) and are similar in their responses to disturbance (Bongers 1999; Bongers and Ferris 1999).

One of the key issues in compost research is to assess when the compost has reached a mature stage. The maturity status of the compost determines ultimately the quality of the product. So far numerous tests, based on both physical and chemical parameters, have been proposed (e.g. Butler et al. 2001; Tiquia 2005; Chikae et al. 2006; Castaldi et al. 2008) but unfortunately, many of these have not been proven rigorous, reliable or consistent enough to be used in standard protocols, and those that are would required such a substantial investment in laboratory equipment and staff training that their use in regular composting laboratories is not feasible (Kuo et al. 2004; Baldwin and Greenfield 2006).

Since information on nematode populations in compost is virtually lacking, the first objective of this study was to analyze the structure and succession of the nematode community during a composting process. Secondly, we explored the possibilities of relating the observed structure of the nematode community structure to compost maturity.

2. Material and methods

2.1. Study site and sampling

The examined compost heap was located at the Institute for Agricultural and Fisheries Research in Merelbeke, Belgium (Plant Science Unit, Growth and Development research area). The heap was composed of three different feedstock materials: 43% fine wood chippings, 43% dry hay and 14% fresh grass. The C/N ratios of de the feedstock materials were respectively approximately 90/1, 30/1 and 15/1. The heap was 50 m long, 3 m wide and 1.5 m high, and consisted of 3 m^3 feedstock materials per lineal meter. The compost was prepared according to the CMC method, but no microbial starter was added.

A total of 45 composite samples on 15 different sampling moments were taken during the entire composting process. The entire monitored process lasted six months, from September 2006 to March 2007. During the first three weeks of the process, samples were taken twice a week (6 samples), after which sampling was reduced to once a week for seven weeks (7 samples). At the end of the process the heap was sampled once after one month and again after two months. By following this sampling pattern the complete process was observed and the changes in species composition throughout could be investigated. Each sample was composed of 20 randomly picked samples of 50 ml of compost each. The samples were mixed to make a total volume of 1 L, from which a subsample of 100 ml was taken for nematode extraction. This sampling procedure was repeated 3 times per sampling event.

2.2. Data collection – environmental variables

The following abiotic variables were measured at every sampling: temperature (°C), moisture content, pH and percent carbon dioxide. Temperature and CO_2 content were measured in 3 locations on the heap using specialized equipment (respectively, Digital Thermometer GTH 1150 and Brigon Messtechnik D-63110 Rodgau). For the pH measurements, extractions of 20 g compost in 100 ml distilled water were made. The extractions were shaken by hand 3 times every 2 h and pH was measured with standard electrodes (Consort P400). The moisture content was determined by weighing 50 ml of compost before and after incubation for 48 h at 120 °C.

2.3. Nematode community analyses

The existing nematodes in the subsample (100 ml) were extracted from the compost using a modified Baermann funnel method (tray 49 cm × 37.5 cm, basket 38.5 cm × 19.5 cm) (Hooper 1986). Nematodes were counted and 100 individuals were randomly picked out using a stereomicroscope (Leica MZ95). For light microscopical observations, half of the specimens were collected in a very small drop of water in an embryo dish. Formaldehyde (4% with 1% glycerol) was heated to 70 °C and an excess (4–5 ml) was quickly added to the specimens to fix and kill the nematodes (Seinhorst 1966). The fixed nematodes were processed to anhydrous glycerol following the glycerol–ethanol method (Seinhorst 1959, as modified by De Grisse 1969) and mounted on aluminium slides with double cover slips (Cobb 1917). As a supplement to this standard evaluation method, the remaining nematodes were mounted on mass slides (slide 40 mm × 76 mm; cover glass 34 mm × 60 mm). Measurements were prepared manually with a camera lucida on an Olympus BX 51 DIC microscope (Olympus Optical, Tokyo, Japan), which was equipped with an Olympus C5060WZ camera for photographs. Nematodes were identified to genus and species whenever possible. The abundance (individuals/gram dry weight compost) of each genus or species in each sample was determined. Dauer larvae were not included in the total counts and species analysis because accurate identification is often impossible and there immobility hampers a quantitative estimation using a mobility-based nematode extraction. Additional samples, especially from which nematodes could not be detected with the modified Baermann funnel method, were incubated on agar plates

(1% nutrient agar plates containing 2.7 g bacteriological agar, 1.3 g nutrient agar and 80 µl cholesterol (5 mg ml^{-1}) in 400 ml medium and 1% bacteriological agar plates containing cholesterol (80 µl 5 mg ml^{-1} in 400 ml medium)) giving survival stages the opportunity to reactivate. The resulting data were also not further incorporated in the analysis since incubation experiments impede quantitative analysis and results were not available for all replicates.

Nematode genera were assigned to the 1–5 "coloniser-persister" cp scale according to their r and K life-strategy characteristics (Bongers 1990, 1999) and were classified according to their feeding type. These allocations were, respectively, used to calculate the Maturity Index (MI) (Bongers 1990, 1999) and the Trophic Index (TI) (Heip et al. 1985). Additionally, the Structure Index (SI), Enrichment Index (EI) (Ferris et al. 2001) and the fungivorous/bacterivorous ratio (f/b ratio), also providing an indication of the ecosystem condition, were determined. The calculation of the SI and EI is based on guilds, which combine feeding type and cp value to cluster nematode taxa. The EI is based on the expected reaction of non-herbivore, opportunistic nematodes to the increase in food and gives the abundance and activity of primary detritus-feeding nematodes. The SI indicates the sensitivity to disturbances. The EI and SI can be used to construct a faunal profile, which indicates whether the nematode community is basal, enriched or structured (Ferris et al. 2001). The f/b ratio was used as an indicator of the dominant decomposition pathway (Ferris et al. 2001; Ruess 2003; Ruess and Ferris 2004). The Shannon–Wiener index (H'), with log base 2, and the Simpson index (λ) were calculated to measure diversity. The Shannon–Wiener index is more appropriate for rare taxa (Heip et al. 1998) while the Simpson index gives more weight to the predominant taxa (Neher 2001).

2.4. Statistical analyses

First, a correlation matrix was performed to unravel possible colinearity among abiotic variables. Subsequently, in order to reduce the redundancy between the different abiotic factors measured during the composting process, a Principal Component Analysis (PCA) was performed, by which the different abiotic variables were related to each other in a single principal component. Due to strong linear dependency in the data set, differences in the MI and f/b ratio during the composting process were addressed by categorizing the data into the different composting phases (thermophilic, cooling and maturing) and performing pair-wise Mann–Whitney tests using composting phase as a factor. All analyses were conducted with the statistical software Statistica 7.0.

3. Results

3.1. Environmental variables

The abiotic conditions of the compost heap changed dramatically during the composting process (Fig. 1). The temperature showed two distinct heat peaks; one on day 3 with an average temperature of 71 °C and another on day 15 with an average temperature of 65 °C. After the second peak, the temperature

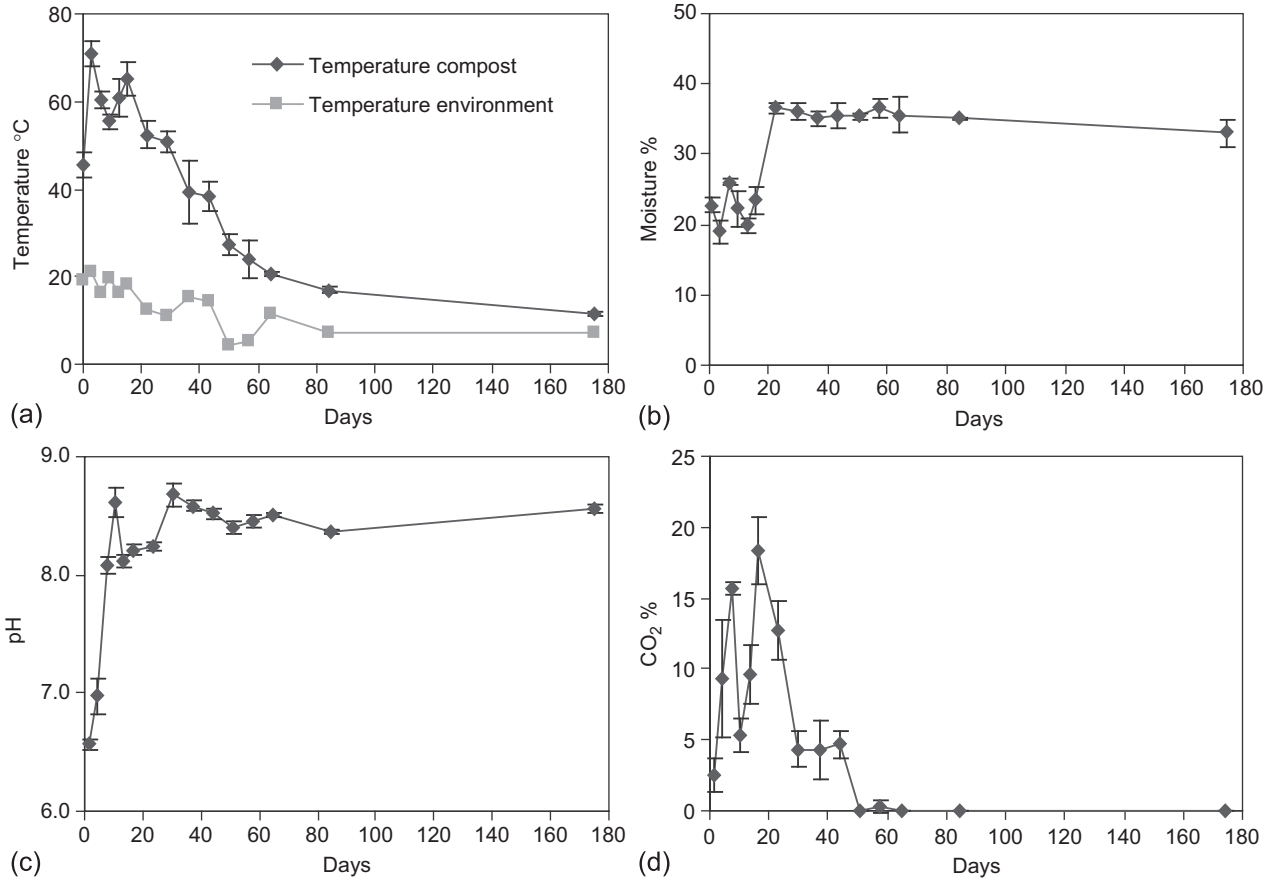

Fig. 1. Environmental variables measured during the composting process including (a) temperature of the compost (°C) and the environmental temperature (°C), (b) moisture content (%), (c) pH values and (d) CO_2 concentration (%). Error bars indicate SD.

gradually decreased until it reached approximately 10 °C (Fig. 1A). Although the moisture content and the pH of the compost heap fluctuated during the first 25 days of the process, both parameters stabilized after reaching their maxima (38% and 8.67%, respectively) (Fig. 1B and C). The CO_2 concentration (Fig. 1D) also showed two maxima during the first 29 days (15% on day 18, and 18% on day 6) and decreased afterwards in two stages (from 4.5% to 0%). Correlation analysis revealed that temperature was positively correlated with CO_2 concentration, moisture content and enviromental temperature (Table 1). Enviromental temperature also correlated positively with CO_2 concentration and negatively with both moisture content and pH. The PCA performed using heap temperature, pH, CO_2 and humidity reduced the variation to only one principal component which accounted for 67% of the variation within the data matrix and to which heap temperature and humidity contributed the most (see vector loadings, Table 1).

3.2. Nematode community analyses

3.2.1. Species composition and number of nematodes

In total 18 genera belonging to 12 families were identified from the 15 sampling occasions during the complete process. The individual samples were generally characterized by relatively few taxa (maximum 9 different species). The most common taxa were *Aphelenchoides* sp., *Diploscapter coronatus, Mononchoides* sp., *Cephalobus* sp. and *Panagrolaimus labiatus*. Other taxa, e.g. *Diplogastrellus* sp., *Diplogaster* sp., *Halicephalobus gingivalis* and *Ditylenchus filimus*, were rare and were detected only at very specific periods during the process. Table 2 provides an overview of the species detected at every sampling occasion. For more detailed information about the species observed during the composting process, see http://www.nematology.ugent.be/vce.html. Also survival stages could be isolated with the modified Baermann funnel method (Table 2). The number of nematodes

Table 1
Pearson correlation coefficients and product moment correlation coefficients among continuous environmental variables (Temperature, CO_2, Moisture, pH, Env. temperature) measured during the composting process and the vector loadings of the Principal Component Analysis (PCA).

	Temperature	CO_2	Moisture content	pH	Env. temp.	Vector loadings PCA
Temperature	1					−0.91
CO_2	0.83***	1				−0.76
Moisture content	−0.67**	−0.48	1			0.86
pH	−0.43	−0.20*	0.62*	1		0.64
Env. temp.	0.86***	0.61*	−0.73**	−0.55**	1	–

*$p < 0.05$; **$p < 0.01$; ***$p \leq 0.001$.

Table 2
Nematode species list with presence of the species during the composting process and information on the dauer larvae found during the process. The feeding type of each species is also provided (3=bacterial feeding, 2=fungal feeding, 3–5a=bacterial-feeding-predator (ingester), 8=omnivorous). All species were isolated using the modified Baermann funnel method except for the species with an asterisk, which were isolated after incubation of compost on agar plates.

Taxa	Feeding-type	Day 0	3	6	9	12	15	22	29	36	43	50	57	64	84	175
Rhabditis sp 1	3	■														
Rhabditis sp 2	3	■														
Rhabditis sp 3	3	■														
Diplogastrellus sp.	3	■														
Diplogasteritus sp.	3	■					■		■			■	■	■		■
Panagrolaimus labiatus	3	■					■	■			■	■	■			
Rhabditidae sp.	3						■	■		■	■	■		■	■	■
Cephalobidae sp.	3							■								
Cephalobus sp1	3							■	■	■	■	■	■	■	■	
New genus Ordo Rhabditina	3							■	■	■			■			
Diploscapter coronatus	3									■		■	■	■	■	■
Rhabditis (*Cephaloboides*) sp1	3													■		
Rhabditis (*Poikilolaimus*) sp1	3													■	■	■
Halicephalobus gingivalis	3														■	
Rhabditophanes cobbi	3															■
Rhabditis (*Mesorhabditis*) sp1	3															■
Aphelenchoididae sp1	2	■							■	■		■	■	■	■	
Aphelenchoides sp1	2							■	■	■	■	■	■	■	■	
Aphelenchoides sp2	2										■					
Paratylenchus sp.	2													■		
Ditylenchus filimus	2														■	■
Diplogaster sp.	3-5a	■														
Mononchoides sp.	3-5a								■	■	■	■	■	■	■	■
Qudsianematidae sp.	8													■		
SURVIVAL STAGE RECORD																
Rhabditidae dauer											■					
Diplogastridae dauer								■	■	■	■	■	■	■	■	
Unknown dauer										■						
*Halicephalobus gingivalis**			■	■	■											
*Diploscapter coronatus**			■	■	■											

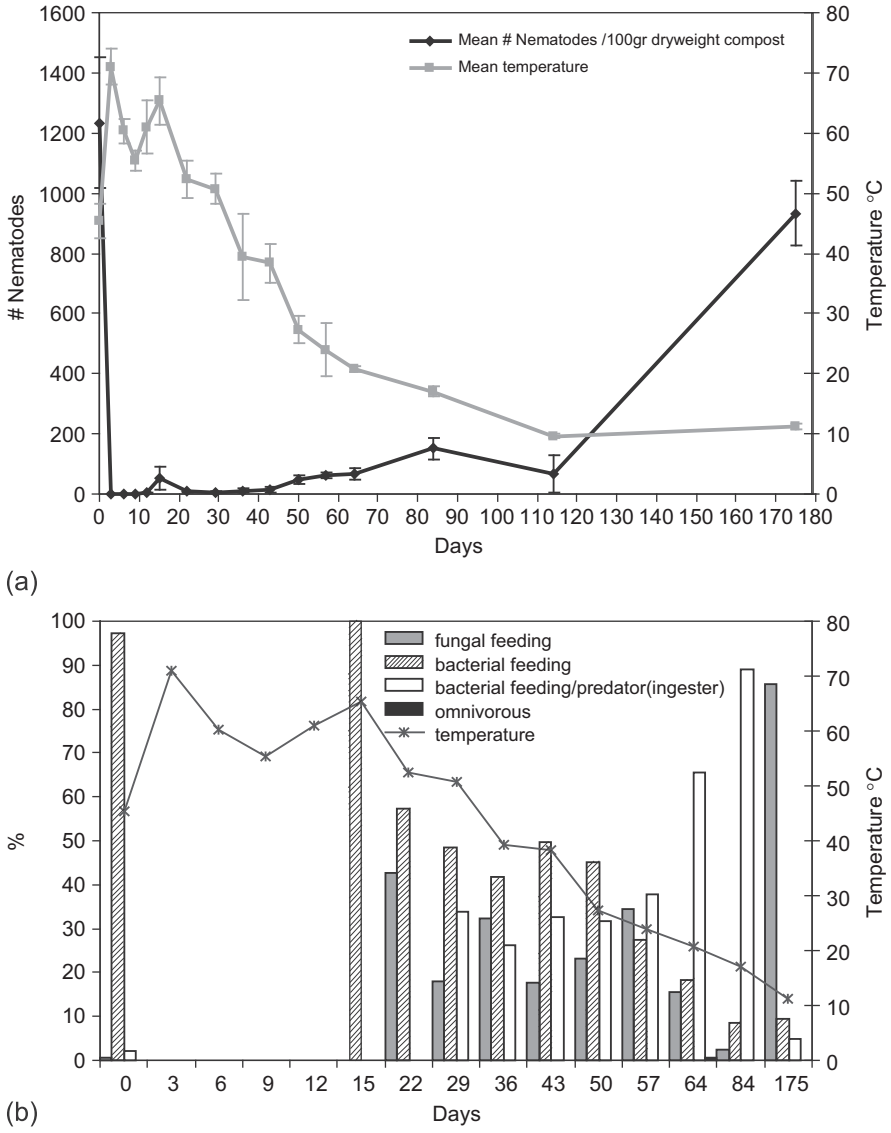

Fig. 2. (a) The number of nematodes (—◆—) and the temperature of the compost (—■—) during the process. (b) The percent contribution of each feeding type (fungal-feeding ▬, bacterial-feeding ▨, bacterial–feeding-predator (ingester) □, omnivorous nematodes ■) and the temperature of the compost (—✳—) at every sampling occasion.

gradually increased with decrease in temperature (Fig. 2A). Immediately after the heat peak, on day 3 until day 9, nematodes could not be detected, except for *H. gingivalis* and *D. coronatus*, which were detected after analyses of these compost samples incubated on agar plates (Table 2). Most likely the latter were reactivated dauer stages. Thereafter, the number of nematodes increased gradually until the final sampling event. The highest numbers of nematodes were found in the first and in the last samples (respectively, 1234 and 933 nematodes per 100 g dry weight compost).

3.2.2. *Functional groups: feeding type and cp value*

The composition of nematode feeding types showed a clear dominance of bacterial feeders (16 species or 55% of the total abundance), followed by the subdominant fungal feeders (5 species or 33.3% of the total abundance) and the bacterial-feeding and predatory (of nematodes) nematodes (2 species or 11.7% of the total abundance) (Table 3). Fig. 2B displays the feeding-type compositions per sample based on the 3 replicas. Bacterial-feeding nematodes were present in all nematode-containing samples, but most samples included fungal-feeders and bacterial-feeding-predator nematodes as well as bacterial-feeders (days 36, 43, 50, 57, 64, 84 and 175). For the first 50 days of the process, bacterial-feeding nematodes were clearly dominant. From day 22 onwards, the fungal-feeding nematodes were also detected in the samples. The density of the bacterial-feeding-predator nematodes increased gradually from day 29 onwards, and this type dominated the samples of days 64 and 84. In the most mature sample the fungal feeders were clearly dominant.

The distribution of the nematode genera from the composting process along the cp scale was uneven. The enrichment opportunists (cp-1 value) were dominant (16 species or 66.7% of the total abundance) while the general opportunists (cp-2 value) were subdominant (7 species or 33.3% of the total abundance). One genus with a cp-4 value was present on day 64 but genera with a cp-3 value were completely absent (Table 3). The most mature

Table 3
Overview of the means ± SD of the abundance of nematodes (per 100 ml compost), number of genera, percent contribution to the functional groups (trophic groups: type 2 (fungal-feeding nematodes), type 3 (bacterial-feeding nematodes), type 3-5a (bacterial-feeding- predator nematodes), type 8 (omnivorous nematodes) and cp-groups: cp-1 (enrichment opportunists), cp-2 (general opportunists), cp-4 (persisters)) and the values of the indices: TI (Trophic Index), f/b (fungivorous/bacterivorous ratio), MI (maturity index), EI (enrichment index), SI (structure index), H' (Shannon–Wiener index) and λ (Simpson Index)) at every sampling event.

	DAY														
	0	**3**	**6**	**9**	**12**	**15**	**22**	**29**	**36**	**43**	**50**	**57**	**64**	**84**	**175**
Adundance	1234 ± 217.65	0	0	0	0	53 ± 37.64	8 ± 1.04	6 ± 2.35	13 ± 7.44	25 ± 13.25	49 ± 13.43	64 ± 9.68	68 ± 18.77	151 ± 35.09	933 ± 106.78
# Genera	4 ± 1	0	0	0	0	3 ± 1	3 ± 1	3 ± 2	3 ± 1	3 ± 1	6 ± 1	6 ± 1	7 ± 2	5 ± 1	5 ± 1
Functional groups %															
Trophic groups %															
type 2	1 ± 0.8	0	0	0	0	0	43 ± 20.1	18 ± 21.7	32 ± 14.3	18 ± 17.0	23 ± 7.5	35 ± 19.1	15 ± 9.4	3 ± 1.5	86 ± 7.1
type 3	97 ± 1.7	0	0	0	0	100 ± 0.0	57 ± 20.1	48 ± 38.2	42 ± 30.3	50 ± 53.0	45 ± 12.2	28 ± 3.4	18 ± 8.6	8 ± 2.5	10 ± 5.2
type 3–5a	2 ± 2.3	0	0	0	0	0	0	34 ± 26.0	26 ± 34.7	33 ± 37.8	32 ± 19.6	38 ± 17.3	66 ± 2.5	89 ± 3.9	5 ± 1.9
type 8	0	0	0	0	0	0	0	0	0	0	0	0	1 ± 0.9	0	0
Cp-groups %															
cp-1	99 ± 0.8	0	0	0	0	100 ± 0.0	57 ± 20.1	82 ± 21.7	68 ± 14.3	82 ± 17.0	77 ± 7.5	65 ± 19.1	84 ± 9.8	97 ± 1.5	14 ± 7.1
cp-2	1 ± 0.8	0	0	0	0	0	43 ± 20.1	18 ± 21.7	32 ± 14.3	18 ± 17.0	23 ± 7.5	35 ± 19.1	15 ± 9.4	3 ± 1.5	86 ± 7.1
cp-4	0	0	0	0	0	0	0	0	0	0	0	0	1 ± 1.0	0	0
Indices															
TI	0.94 ± 0.03	0	0	0	0	1.00 ± 0.00	0.76 ± 0.21	0.61 ± 0.34	0.48 ± 0.06	0.64 ± 0.24	0.40 ± 0.07	0.39 ± 0.03	0.50 ± 0.04	0.80 ± 0.06	0.75 ± 0.11
f/b	0.00 ± 0.01	0	0	0	0	0	0.83 ± 0.63	0.50 ± 0.87	1.33 ± 1.45	2.68 ± 2.50	0.52 ± 0.04	1.24 ± 0.83	0.92 ± 0.74	0.28 ± 0.12	11.90 ± 8.15
MI	1.00 ± 0.01	0	0	0	0	1.00 ± 0.00	1.41 ± 0.20	1.13 ± 0.22	1.29 ± 0.14	1.21 ± 0.17	1.24 ± 0.08	1.33 ± 0.19	1.15 ± 0.11	1.03 ± 0.01	1.86 ± 0.07
EI	100.00 ± 0.19	0	0	0	0	100.00 ± 0.00	84.94 ± 9.58	96.00 ± 6.93	91.27 ± 4.79	93.45 ± 5.56	93.14 ± 2.52	98.41 ± 7.36	96.18 ± 2.86	99.37 ± 0.35	62.25 ± 5.39
SI	0	0	0	0	0	0	0	0	0	0	0	0	8.45 ± 14.63	0	0
H'	1.21 ± 0.34	0	0	0	0	0.85 ± 0.19	1.12 ± 0.21	0.84 ± 0.76	1.05 ± 0.19	0.69 ± 0.45	1.32 ± 0.25	1.38 ± 0.10	1.15 ± 0.17	0.48 ± 0.13	0.57 ± 0.22
λ	0.37 ± 0.16	0	0	0	0	0.47 ± 0.06	0.36 ± 0.09	0.55 ± 0.40	0.40 ± 0.09	0.63 ± 0.26	0.33 ± 0.08	0.31 ± 0.04	0.47 ± 0.04	0.79 ± 0.07	0.75 ± 0.11

Table 4
Mean Maturity Index and f/b ratio during the three different phases of the composting process.

Index	Composting phase			
	Thermophilic	Cooling	Maturing	*P*
MI	$0.81 \pm 0.59^*$	$1.24 \pm 0.12^*$	1.34 ± 0.34	0.001
f/b	0.30 ± 0.56	1.50 ± 1.72	$3.58 \pm 6.13^*$	0.05

Significant differences between phases are indicated by an asterisk after pair-wise Mann–Whitney non-parametric tests.

stage (day 175) was dominated by cp-2 genera, unlike the other samples, wherein the genera with a cp-1 value were dominant (Table 3).

3.2.3. *Indices and integration of the abiotic data*

At the beginning of the process and immediately after the heat peak, the TI, based on the defined feeding types, was relatively high, due to the dominance of a single feeding type (i.e. bacterial feeding) (Table 3). The lowest TI values, due to the more equal distribution of the feeding types in the samples, appear from day 29 onwards, in the first half of the composting process when the temperature is still relatively high (40–50 °C). At the most mature stage, when the temperature of the heap most closely approximated the environmental temperature, the TI increased again as a result of the dominance of one feeding group (i.e. fungal feeding). The f/b ratio showed a distinct change during the process (Table 3). The f/b ratio fluctuated between 0 and 2.68 with a maximal peak (11.90 ± 8.15) on day 175, in line with the enhancement of fungal-feeding nematodes (Table 3). The cp values of the genera were used to calculate the MI (Table 3). For the first 84 days of the process, the MI varied between 0.68 and 1.58 (Table 3). The pair-wise Mann–Whitney test revealed differences in the MI and f/b ratios between the different phases of the composting process (thermophilic phase: days 3–15, cooling phase: days 22–43, maturing phase: days 50–175) (Table 4). The mean MI and f/b ratio during the three composting phases are given in Table 4. The MI and the f/b ratio both showed a significant difference between the maturing and the two previous phases (*p* values, respectively, 0.001 and 0.05) (Table 4). Mark that especially the f/b ratio and maturity index trend are strongly influenced by the results of one single divergent sampling point (day 175). This limitation necessitates caution in the further interpretation of the statistical results. The diversity was highest on days 36 and 57, and slightly lower at the end of the process (Table 3). However, the observed fluctuations in diversity were not statistically significant. Neither the EI nor the SI showed a clear trend during the process, nor could they be linked to nematode succession. This could be attributed to the fact that these indices are designed for more complex, larger scale and longer lasting processes.

In summary, the taxonomic analysis of the nematode community revealed three clear successional phases after the heat peak. At the beginning of the process, just after the temperature peak observed on day 3, the nematode population was made up primarily of bacterial-feeding enrichment opportunists (cp-1) (Rhabditidae, Panagrolaimidae, Diplogastridae) followed by the bacterial-feeding general opportunists (cp-2) (Cephalobidae) and the fungal-feeding general opportunists (Aphelenchoididae). Thereafter, the opportunistic bacterial-feeding-predator nematodes (*Mononchoides* sp.) became the dominant species. Finally, at the most mature stage, the fungal-feeding Anguinidae (e.g. *D. filimus*) was the most abundant group.

4. Discussion

The nematode community in compost has hitherto never been thoroughly investigated. The results obtained in this study describe major shifts in species composition during the composting process, and moreover, link these structural community changes with the shifts in abiotic conditions that take place during the process.

Several authors have already proposed the use of nematode assemblages as powerful tools to analyze ecosystem processes and quality (e.g. Bongers and Ferris 1999; Ritz and Trudgill 1999; Ferris et al. 2001; Neher 2001; Ferris and Bongers 2009; Yeates et al. 2009). The calculation of nematode-based indices is based on the allocation to functional groups and basic insights into the successional changes within a given studied system. A composting process is most likely an outstanding example of an ecosystem in transition that can be evaluated by the succession of nematodes.

In our case, the maturity index and the f/b ratio showed a clear pattern during the process and therefore seem to be suitable indices to evaluate the composting process. The MI and the f/b ratio both increase as the compost becomes more mature. According to Bongers 1999, a rapidly changing environment with an abundance of food is typically inhabited by opportunistic nematodes, starting with enrichment opportunists (cp-1), which are gradually replaced by general opportunists (cp-2). This trophic situation results in relatively low MI values at the beginning of the process and, by contrast, significantly higher MI values at the end of the process. The f/b ratio clearly reflects the shift in prevalence of bacterial-feeding nematodes in the thermophilic and cooling phases, to fungal-feeding nematodes in the maturation phase. This ratio can also be used to indicate the dominating decomposing pathway in a decomposing environment (Bongers and Bongers 1998; Ruess 2003; Ruess and Ferris 2004). From our analysis we could see that the first 84 days of the process, during which the f/b ratio is typically relatively low, decomposition occurred mainly through the bacterial-dominating pathway. However, in the final stage of the process (day 175), when the ratio is typically highest, the decomposition mainly occurred through the fungi-dominated pathway. This pattern may be an indication of a retardation of the decomposition rate due to the fungal-associated decomposition of more complex organic materials (Ruess and Ferris 2004).

A more detailed analysis of the successional changes of the nematode community revealed that the composting process actually undergoes a meticulous succession of r-strategists. According to Wharton (1986), habitats subject to environmental extremes do not favor K-strategists. This is most likely the main reason for their absence during the composting process. The first nematodes capable of colonizing the compost during the last phase of the heat peak (= thermophilic phase, $T \geq 45$ °C) belonged to the genera *Diplogasteritus*, *Panagrolaimus* and *Rhabditis*. This first population (on day 15) of early colonizers in a nutrient-rich environment was 100% bacterial-feeding and enrichment opportunistic nematodes, as proposed by Bongers (1990) and confirmed by many others (e.g. Ettema and Bongers 1993; Bardgett et al. 1998; Wasilewska 1998). At the very beginning of the cooling phase, from days 22–29, this first population was subverted by a population dominated by the genera *Cephalobus* and *Aphelenchoides*, both general opportunists (cp-2) and respectively bacterial and fungal-feeding. The replacement of the enrichment opportunists belonging to the Rhabditidae family (cp-1) by general opportunists from the family Cephalobidae (cp-2) and the occurrence of fungal-feeding nematodes has also been observed by Ferris and Matute (2003), Wang et al. (2004) and Georgieva et al. (2005) during the decomposition of several plant residues in soil. During the cooling phase (also called mesophilic phase,

$T \leq 45$ °C), occurring from day 36 onwards, the dominance of the former nematodes started to decrease and other species started to inhabit the compost: e.g. *D. coronatus*, *Rhabditis (Cephaloboides)* sp. and *Mononchoides* sp. Since bacterial-feeding fauna mirrors previous bacterial production (Georgieva et al. 2005; Ferris and Bongers 2006), this shift in nematode species composition and increase in the number of nematodes can be linked to increase in bacterial activity in the cooling phase and to the presence of completely different bacterial populations in the thermophilic and mesophilic phases as described by Ishii et al. (2000), Ryckeboer et al. (2003) and Halet et al. (2006). The cooling phase environment (≤ 45 °C), with bacteria, fungi and various nematode species in abundance, gave *Mononchoides* sp. the opportunity to start blooming. This differs from decomposition in soil where Neodiplogastridae (including *Mononchoides*) dominate from the beginning (Georgieva et al. 2005). This retardation might possibly be explained by the relatively high and lethal temperatures in the beginning of the cooling phase (± 40 °C). During maturation at the end of the process, from days 84–175, a shift in prevalence of bacterivorous to fungivorous nematodes took place, which can be associated with the transition from mainly bacterial activity during the thermophilic and early cooling stages to an increase in activity of fungi in late cooling and maturation stages (Ryckeboer et al. 2003). Moreover, it is known that fungal energy channels predominate when the organic material is of a high C/N ratio and, conversely, bacterial decomposition channels predominate when the organic material is of a low C/N ratio (Ruess 2003; Ruess and Ferris 2004) (cfr. high C/N ratios of feedstock materials). In a study by Ferris and Matute (2003), the rate of succession from bacterivorous to fungivorous nematodes increased in plots receiving high C/N materials (Ferris and Matute 2003). Most likely, when looking at the whole process, during the thermophilic phase the extreme environmental circumstances (i.e. temperature) are the limiting factors for nematode succession, whereas during the mesophilic and maturation phases, food resources might be the most important selective force for successional events.

According to the scanty literature, remarkably similar taxa to those observed in this study have been described from compost (Gagarin 2000; http://www.soilfoodweb.com). The majority of species described from other compost heaps also belonged to the rhabditids and the diplogasterids and nearly always the same genera (i.e. *Cephalobus*, *Rhabditis*, *Diploscapter*, *Aphelenchoides* and *Ditylenchus*) (Gagarin 2000; http://www.soilfoodweb.com). More specific similarities with other observations from compost include *P. labiatus* (China; Andrassy 1984), *D. filimus* (West Canada; Anderson 1983), *H. gingivalis* (USA, Riverside; Nadler et al. 2003) and *Rhabditis (Poikilolaimus)* sp. (mushroom compost, Russia; Gagarin 2000). Remarkably, notwithstanding the nematode destructive heat peak, the geographic disparity and different feedstock materials, the same genera and even the same species were found in these studies, including this one. Where do these "compost" nematodes come from? The composting process is an "open" process and the ability to arrive in a new habitat does not necessarily mean that the nematodes also become established. As a result it makes little difference whether the species come from "contaminations" by movement of air, water and tillage machinery or from awakened dauer stages or eggs, the surrounding soil or by insect phoresy, because the typical compost environment will ultimately serve as the fundamental selective force regardless of origin (for overview on nematode dispersal see Hodda et al. 2009). Hence, the nematode indices proposed herein for assessing compost maturity might be of universal relevance, although further research is required to clarify the ways in which nematodes can arrive at a compost heap.

Unlike Manso (2004), who only found bacterial-feeding Rhabditidae in mature compost, diplogasterids appeared to be numerically important (4 different genera were found). In particular, *Mononchoides* sp. was numerically important from days 29–84. According to Yeates et al. (1993), 2 of the recorded diplogasterid genera (*Diplogastrellus* and *Diplogasteritus*) are strictly bacterial-feeding nematodes (feeding type 3). The 2 other genera (*Mononchoides* and *Diplogaster*) could belong to the bacterial-feeding nematodes as well as to the predator (ingester) nematodes (feeding type 5a) and to the omnivorous nematodes (feeding type 8) (Yeates et al. 1993). Because species within the same feeding group may vary in their food resources and some species can feed on several food resources, the allocation of nematodes to a specific feeding type is often uncertain (Yeates et al. 1993; Yeates 2003). The herein numerically very important *Mononchoides* sp. appeared to have a biphasic feeding ability (as described earlier by Yeates 1969, 1970), namely on bacteria and other nematode species (Steel, unpublished data). The neodiplogasterids *Mononchoides* sp. and the diplogasterid *Diplogaster* sp. were therefore allocated to a combined feeding group "bacterivorous–predator (ingester)" (feeding type 3–5a) (see also Georgieva et al. 2005). However, most terrestrial nematode indices (e.g. EI, CI and TI) do not incorporate this new feeding type and thus are not usable for compost. Diplogasterids are known to be prey-selective to plant-parasitic nematodes (Khan and Kim 2007), and therefore, are very promising biological control agents (Bilgrami and Jairajpuri 1988; Bilgrami et al. 2005; Bilgrami 2008). This study shows that a composting process can provide a great range of potential predator nematodes. This is particularly an important factor in the suppressive capacity of compost against plant diseases.

In conclusion, this study produced some promising results. The successional changes of the nematode community during the process demonstrated opportunities to describe and evaluate the condition of the composting process. Although further research needs to be performed in order to strengthen these findings, the nematode-based indices maturity index and fungivorous/bacterivorous ratio are probably the most suitable tools to assess compost maturity. Thus, the next step should be to analyze different composting processes and more time frames in order to correlate particular maturity index and fungivorous/bacterivorous ranges to the state and maturity of the compost process. Finally, further work is required to asses the effectiveness and importance of the remarkably high number of bacterial-feeding-predator nematodes during certain compost stages on the potential suppressive effect of compost.

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