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Factors influencing the nematode community during composting and nematode-based criteria for compost maturity

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ABSTRACT

Pilot studies indicate that shifts in the nematode species composition, life strategies and feeding behavior during composting appear to be fairly consistent and, therefore, promising as a potential tool to assess compost maturity. However, this has been only based on a limited number of, mainly, non-replicated observations. In this study, we tested whether the nematode community succession patterns are recurrent for parallel processes and assessed the relationship between the changes in the nematode community and potential important variables (i.e., temperature, duration of composting and the microbial community). The nematode and microbial community of three simultaneously running Controlled Farm Composting and a reference Green Waste composting process were analyzed through time. Bacterial-feeding enrichment opportunists were most numerous during and directly after the heat peaks. Subsequently, the bacterial-feeding/predator community dominated and the fungal-feeding nematodes became more dominant during maturation, confirming general community patterns from previous experiments. Nematode abundances significantly fluctuated with temperature and the relative abundance of fungal-feeding nematodes increased as the duration of the curing process increased. The amount of fungal-feeding nematodes was associated significantly with both duration of composting and temperature, and the F/(F + B) ratio was only significantly associated with duration of composting. Based on these results, and additional data from an industrial reference compost process and on available literature, a Nematode-based Index of Compost Maturity (NICM) is proposed, combining four nematode-based criteria (i.e., nematode abundance, F/(F + B) ratio, the presence of more than one fungal-feeding taxon and the presence of diplogasterids). Nevertheless, the NICM should be considered as work in progress which should be tested for a wider range of composts from diverse feedstock mixtures, locations (sites) and composting techniques, to validate the use of the index and allow more reliable interpretation of particular values of this index.

1. Introduction

Composting is an aerobic, heat-producing and controlled process in which microorganisms convert a mixed organic substrate into CO_2, water, inorganic nutrients and stabilized organic matter. The final compost must be of high quality, i.e., stable, mature and free of health and environmental risks (Cesaro et al., 2015; Wichuk and McCartney, 2010), to be considered beneficial for the soil or to be responsible for associated advantages like improved nutrient capacity of the soil (Tognetti et al., 2008) and disease suppressive activity (Mehta et al., 2014; Oka, 2010). The quality of the organic matter and hence the value as fertilizer, the physical characteristics and the biology (i.e. inhabiting organisms) are responsible for these beneficial effects. Next to sufficiently high temperature and thus, adequate sanitization as a prerequisite, key issues in compost research and crucial for compost quality assessment are the maturity and stability measures used to evaluate the composting process. Maturity is a general term describing the suitability of the compost for a particular end use, while stability can be defined as the extent to which readily biodegradable material has decomposed (Gomez et al., 2006). Compost stability is usually assessed using a measure for the activity of the microbial community (Neher et al., 2017; Wichuk and McCartney, 2010). Nevertheless, maturity is often informally defined as the state in which compost is dominated by humic substances (Dinel et al., 1996) or when the

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temperature reaches a near-ambient level (Cooperland, 2000). For the past decade, researchers have proposed multiple chemical, physical (Sellami et al., 2008; Zmora-Nahum et al., 2005) and biological parameters (Gomez et al., 2006) to assess compost maturity. To the best of our knowledge, the hitherto proposed tests are imprecise, unsuitable for a wide range of input materials, and incapable of quantifying both compost maturity and stability (Wichuk and McCartney, 2010).

The taxa most essential to the composting process are bacteria, algae, fungi, Isopoda, Acari, Nematoda and protozoans (Cooperland, 2000; Young et al., 2005). This wide spectrum of organisms makes up a complex and rapidly changing community. Of all these taxa, only nematodes (Steel et al., 2013a; Steel et al., 2010) and microbial communities (i.e., bacteria, actinobacteria and fungi) (Ryckeboer et al., 2003; Steel et al., 2013a) are ubiquitous in all stages of the composting process, making them the key groups to monitor. A significant advantage of using nematodes to assess compost maturity is their established status as environmental indicators (Bongers and Ferris, 1999; Neher, 2001; Yeates, 2003) of ecosystem processes such as organic enrichment (Ferris and Bongers, 2006); moreover, changes in the food web are mirrored in shifts in nematode feeding group and taxonomic composition (Yeates et al., 2009). According to pilot studies based on large-scale farm composting systems and small-scale processes in compost barrels (Steel et al., 2013a; Steel et al., 2010; Steel et al., 2013b), shifts in nematode species composition, life-history strategies and feeding behavior occur during the process of composting. At the beginning of the process, during the thermophilic phase, the nematode community is primarily comprised of bacterial-feeding enrichment opportunists (cp-1) (Rhabditidae, Panagrolaimidae, Diplogasteridae), followed by the bacterial-feeding general opportunists (cp-2) (Cephalobidae) and the fungal-feeding general opportunists (Aphelenchoididae), and finally, after a transient dominance of bacterial-feeders/predators (Neodiplogasteridae) in the cooling phase, fungal-feeding general opportunists (Anguinidae and Aphelenchoididae) become more dominant during the maturation phase. This increasing proportion of fungal-feeding nematodes during the composting process has been proposed as a potential indicator of compost maturity (Steel et al., 2013a; Steel et al., 2010). Compared to the nematode community, the shifts in the microbial community structure, as revealed by phospholipid fatty acids (PLFA), were less pronounced and mostly restricted to the first month of composting (Steel et al., 2013a).

Although nematode community succession appears to be consistent and promising as a tool to assess compost maturity, these patterns have hitherto been based on only a limited number of observations. A better insight into the underlying factors that cause these remarkable shifts in composition of nematode communities, such as processing time, compost temperature and/or microbial community structure, requires parallel controlled composting experiments (Steel et al., 2010; Steel et al., 2013a). In this study, the nematode and microbial community of three simultaneously running controlled farm composting processes, with different proportions of feedstock materials, were monitored through time to assess a) whether the nematode community succession patterns were consistent across different composting processes; and b) the relationship of nematode community changes with variables such as temperature, duration of composting, and the microbial community. Our second main goal was to translate the obtained process-based insights together with literature data into criteria for biological compost maturity. A single industrial green waste composting process was also sampled as a reference of industrial scale composting for comparison with the smaller-scale experimental farm composts.

2. Materials and methods

2.1. Composting sites and sampling

Three composts were produced simultaneously according to the on-farm Controlled Microbial Composting (CMC)-method (Diver, 2004) in open-air windrows covered with semipermeable fabric when needed on a concrete floor at the experimental farm of the Institute for Agricultural and Fisheries Research (ILVO at Merelbeke, Belgium). These composts will be referred to as Farm 1, 2 and 3. Three compost windrows (each 15 m long, 3 m wide and 1.5 m high with 3 m^3 feedstock materials per meter) were established with different ratios of hay and ground poplar bark, i.e., 25/75%, 50/50% and 75/25% (vol/vol), respectively. The hay was a mixture of grass and clover hay in which the amount of grass hay in the three compost piles was 0%, 23% and 46% (vol/vol), respectively. Other than the feedstock material (not part of current research question), the experimental conditions of the three composts are identical so that the variability associated with the studied patterns can be estimated. Other than the feedstock material, which was not part of current research question, the experimental conditions of the three composts are identical and therefore treated as replicates to study the temporal patterns in nematode community composition. Each composting process was managed individually, based on monitored temperature, moisture content and CO_2 levels. Urea was added at the start in all three composts to decrease the C/N ratio of the feedstock towards 30:1, which is considered an ideal starting ratio for composting (Zorpas et al., 2009), and cane molasses plus spoiled ensilaged maize were mixed in the feedstock as a compost starter. The windrows were turned on days three and ten to avoid excessive CO_2 concentrations. On day 83 of the composting process, the windrows were moved and stored in three piles for further maturation. The water content of the composting piles was controlled by opening or closing the semipermeable fabric covers depending on the precipitation and temperature forecast, and by manually adding water (2000 L added to Farm 1 on day 10). Samples were taken from the feedstock mixture (day 0) and on days 3, 7, 10, 17, 24, 35, 49, 63, 77, 105, 119, 133, 147, 175, 203. On each of these 16 consecutive sampling events, three composite samples were taken for each of the three compost processes as further detailed below. Positive effects on crop performance (D'Hose et al., 2012) and soil quality (D'Hose et al., 2014; Willekens et al., 2014) were found for farm composts that were produced at the same site as the composts in this study, which is used as a basis to assign them a high quality status.

The reference industrial green waste compost was produced by the Inter-municipal Society of Public Health in Moen, Belgium. The composting process consisted of five phases. During the first phase a mixture of available feedstock materials was made (i.e., 35% grass, 15% mixed green waste, 40% wood chips, 10% roots of trees). These materials (± 700 m^3, 450 kg/m^3) were then placed into a long windrow (50 m long, 8 m wide and 3 m high) and covered with a semipermeable fabric cover for four weeks. Afterwards, the cover was removed, water was added (25,000 L) and the windrow was turned mechanically (phase 2). Then the windrow was covered again, turned after two weeks (phase 3) and subsequently kept uncovered and turned at three-week intervals (phase 4) to mature. Finally, the compost was sieved and the fraction < 15 mm was sold as compost (phase 5). Sampling took place from the freshly mixed materials (day 0 = phase 1) and during every turning event in each phase (on days 33, 39, 61 and 83 in phase 2,3,4 and 5 respectively).Three composite samples were taken per sampling event.

Each composite sample consisted of 20 thoroughly-mixed and randomly-chosen samples (50 mL each in the farm composts and 1 L each in the reference green waste compost), and of this total volume (respectively 1 L and 20 L), a subsample of 400 mL was taken for nematode extraction (Been et al., 2006). Another portion of each composite sample (± 600 mL) was freeze dried (Christ, Gamma 1–20, Osterode am Harz, Germany), ground and stored frozen for carbon (C), nitrogen (N) and Phospholipid Fatty Acids (PLFA) analyses.

2.2. Abiotic variables

Temperature and CO_2 content of the farm composts were measured at three random locations in the windrow using specialized equipment (Digital Thermometer GTH 1150 and Brigon Messtechnik D-63110

Rodgau respectively). Temperature of the green-waste compost was measured continuously at a depth of 50 cm using five thermocouple sensors (Thermibel, Belgium). Moisture content (%), pH and C/N ratio were measured in three replicates at every sampling time. Extractions of 20 g compost in 100 mL distilled water were shaken manually three times every two hours and the pH was measured with standard electrodes (Consort P400, Turnhout, Belgium). The moisture content was calculated by determining the weight loss of 50 mL compost after drying for 48 h at 102 °C. Total C and N contents were measured with a Variomax CNS element analyzer (Elementar GmbH, Hanau, Germany), applying the Dumas method (EN[1] 13654-2). Oxygen uptake rate (OUR) and NO_3-N/NH_4-N ratio were quantified on days 91 and 203 for the farm compost processes according to Grigatti et al. (2011). Based on neutral detergent fiber (NDF), acid detergent fiber (ADF) and acid detergent lignin (ADL) according to Vansoest et al. (1991), the biodegradation potential of the feedstock mixtures and the finished composts in the farm and green waste compost was calculated as the holocellulose/lignin ratio: (%hemicellulose +%cellulose)/%lignin, with%hemicellulose =%NDF − %ADF, and%cellulose =%ADF − %ADL, Vandecasteele et al. (2016).

2.3. Nematode community analyses

The nematode communities of all samples of the farm composts and the industrial green waste compost were analyzed. Methods for sample processing, nematode extraction, fixation and slide preparation followed those of Steel et al. (2013a). Nematode genera were assigned to the "coloniser-persister" cp-scale according to their r and K life history characteristics (Bongers, 1990) to calculate the Maturity Index (MI), which is the weighted mean cp-score of the in our case only free-living nematodes in the assemblage (Bongers, 1990); they were also assigned to feeding types according to (Yeates et al., 1993), extended with empirical evidence (e.g. Okada et al., 2002; Steel et al., 2011) to calculate the fungivores/bacterivores ratio (F/(F + B) ratio) (Yeates et al., 1993). In the F/(F + B) ratio, only the fungivorous and bacterivorous nematodes *sensu stricto* were included, i.e., bacterivores/predators such as some diplogasterid nematodes were excluded because their feeding habit can be either bacterial-feeding or predatory (Steel et al., 2011) or even fungal-feeding (Serobyan et al., 2013) and most likely changes as a function of the availability of different food resources (Bilgrami et al., 2008).

2.4. Microbial community analyses

PLFAs were analyzed from all sampling days (except days 119, 133 and 147) of the farm composts and of the industrial green waste compost. PLFAs of all these samples were extracted using a modified Bligh & Dyer technique (Bligh and Dyer, 1959; Moeskops et al., 2010). 18:1ω9c and 18:2ω6,9 were used as markers for fungal biomass, 10*Me*16:0 and 10*Me*18:0 were regarded as indicator PLFAs for Actinobacteria. The sum of the marker PLFAs for Gram-negative (16:1ω7c, 18:1ω7c, *cy*17:0 and *cy*19:0) and Gram-positive (*i*14:0, *i*15:0, *a*15:0, *i*16:0, *a*16:0, *i*17:0 and *a*17:0) bacteria was used as an estimate of the total bacterial biomass and the PLFAs 15:0 + 17:0 and 16:1ω5 were used for Arbuscular Mycorhizal Fungi (AMF). See Steel et al. (2013a) for more details.

2.5. Data analysis

Shifts in nematode community composition during the farm compost processes were assessed using non-metric Multi-Dimensional Scaling (nMDS in Primer 6 (Clarke and Warwick, 2001)) based on Bray-Curtis similarity matrices of square-root transformed abundance data (numbers/100 g compost dry weight). Indicative delineation of composting phases was based on the shifts in the nematode community because delineation based on temperature alone was impossible. Delineated compost phases were: days 0–10, 17–49, 63–133 and 147–203 (see Results for more details).

Changes in the concentrations of the marker fatty acids (mol%) in farm composts were analyzed using Principal Component Analysis (PCA) in Primer 6 (Clarke and Warwick, 2001). Because assumptions for one-way ANOVA of normality and homogeneity of variances could not be fulfilled, the functional group concentrations of Gram-positive and Gram-negative bacteria, fungi, and Actinobacteria, and the nematode-based indices MI and F/(F + B) of the different composting phases were compared using non-parametric Kruskal-Wallis ANOVA followed, in case of a significant factor effect, by Mann-Whitney U pairwise tests with Bonferroni correction ($\alpha = 0.01$) in Statistica 6.0 (Statsoft Inc.).

A stepwise BIOENV (Primer 6 (Clarke and Warwick, 2001)) procedure was performed to identify the set of abiotic variables (duration of composting, temperature, C/N ratio, pH, moisture content, CO_2) that best explained the variation in the nematode community composition. The relationship between the explanatory variables (temperature, the amount of fungal PLFA, day and a quadratic day effect to account for a possible non-linear relationship between the dependent variable and time) and nematode abundance, absolute number of fungal-feeding nematodes and the F/(F + B) were modeled by means of a generalized linear mixed model with a normal, Poisson and binomial error distribution, respectively. Analyses were performed separately for absolute (GLIMMIX procedure in SAS v.9.3. (SAS Institute Inc., Cary, NC, USA)) and proportional nematode abundances (MIXED procedure in SAS v.9.3.). Given that the time intervals at which nematode numbers were assessed were shorter at the beginning of the experiment, the variable day was log transformed before analysis. As nematode densities were measured repeatedly on each of the three farm compost windrows, we also accounted for temporal autocorrelation in all models by fitting a first-order autoregressive variance structure to the residual errors. Compost windrow was further included as a random effect. Degrees of freedom were adjusted by means of the Kenward-Roger approximation (Verbeke and Molenberghs, 2009).

Nematode density, total PLFA concentration, total bacterial and fungal abundance, and relative concentrations of microbial functional groups of the green waste reference compost (i.e., Gram-positive, Gram-negative, and Actinobacteria) were compared between sampling days using one-way ANOVA and subsequent post hoc Tukey HSD tests (double square root transformed data for nematode densities) in Statistica 6.0 (Statsoft Inc.).

2.6. Design of the nematode-based index of compost maturity (NICM)

The Nematode-based Index of Compost Maturity (NICM) is calculated based on the value of four criteria of the nematode community: nematode density, the F/(F + B) ratio, the diversity of fungal feeding-taxa and the presence of diplogasterids. More explanation and justification for this selection of criteria is provided in the discussion (4.4).

To give equal weight to each criterion, the scores for each criterion are scaled between 0 and 1 (with 0.75 as target value, see below), except for the 'presence of diplogasterids' criterion where only 2 values are possible (presence = 0.75 and absence = 0). Both nematode abundance and F/(F + B) ratio enter our index with the "S" shape of a logistic curve as changes in very low values or very high values of the variable should not significantly influence the index; it is rather the intermediate values that provide the most information. Given the family of generalized logistic functions is parameterized by Γ and Ω, $y = 1/(1 + 10^{\wedge}(- \Gamma (x\text{-}\Omega)))$, we selected a logistic function for each variable by specifying the value Ω at which the maximum rate of change of the criterion occurs and the amount x at which y = 75% of the criteria component should be obtained (Fig. 1). For nematode

[1] EN: European Standard. European Standards are developed by CEN, the European Commission for Standardization. Numbers refer to the specific protocols.

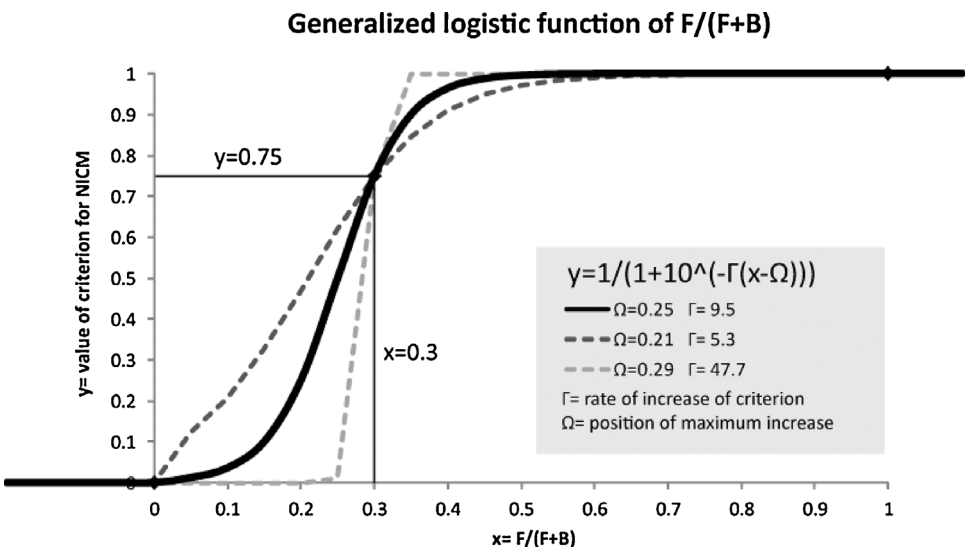

Fig. 1. The Nematode-based Index of Compost Maturity (NICM) is the result of the sum of four criteria. Illustrated is a generalized logistic function of one of these criteria, i.e. the F/(F + B) ratio. The values for each criterion are scaled between 0 and 1 and we specified the amount Ω at which the maximum rate of change of the criterion occurs and the amount x at which y = 75% of the criteria component should be obtained. For our example, the F/(F + B) ratio, we assigned Ω = 0.25 and assumed [x = 0.3, y = 0.75] to find Γ. X was set here at 0.3 because this was the smallest F/(F + B) ratio for mature compost, based on all available data (this study and Steel et al., 2013b). In this figure, we also demonstrate the influence of the parameters Γ and Ω on the shape of the logistic curve, i.e. with Ω = 0.25 and Γ = 9. Changes in very low or very high values contribute comparatively less to the resulting NICM value.

abundance we selected Ω = 475 and solved for Γ assuming [x = 600, y = 0.75]. X was set to 600 based on the lowest recorded value of nematode abundance for finished compost in which the nematode succession, temperature and C/N profile together with OUR, NO_3/NH_4 ratio and biodegradation potential indicated compost stability and maturity (i.e. in Farm2). For the F/(F + B) ratio, we chose Ω = 0.25 and assumed [x = 0.3, y = 0.75] to find Γ. X was set here at 0.3 because this was the average value for the F/(F + B) ratio in the small scale barrel composts (Steel et al., 2013b) which had, of all available data of monitored compost processes, the lowest value for F/(F + B) while still being considered mature based on the nematode succession (biological data) and the temperature, C/N, moisture and pH profile (abiotic data). For the number of fungal feeding taxa only a limited number of values, i.e. 0, 1, 2, 3, or 4, were possible and these were given the following scores: [x = 0, y = 0], [x = 1, y = 0.3], [x = 2, y = 0.75] and [x = 3 or 4, y = 1] using a linear function. For the diplogasterid criterion, only two index scores are possible, i.e. the presence = 0.75 or absence = 0 of diplogasterids. The target value for biologically rich mature compost to be reached for each criterion is 0.75 (see above, value set in logistic function). Therefore, a compost index starting from 3 is considered mature (i.e. 4*0.75). Summing the scores for each criterion results in an index with a minimum value of 0 and a maximum value of 3.75 (i.e. 3*1 + 0.75 for the presence of diplogasterids).

3. Results

3.1. Abiotic variables

The abiotic variables of Farm 1, 2 and 3 exhibited very similar trends through time (Fig. 2). Given the considerable temperature fluctuations, the compost process cannot be categorized in the typical temperature related compost phases, i.e., thermophilic, cooling and maturation (Steel et al., 2013a; Steel et al., 2010). The processes started with characteristic heat peaks (Fig. 2A). The turning of the compost windrows on days three and ten caused a temporary temperature drop (arrows in Fig. 2A). Afterwards, the temperature fluctuated till day 91, after which a distinct gradual increase of temperatures was observed, with secondary maxima on days 119–133. These increased temperatures coincided with a period of increased CO_2 production, probably caused by moving and storing the compost for maturation on day 83 (Fig. 2B). From day 133–203 the temperatures gradually decreased to near ambient levels. The pH fluctuated during the first month with maximum levels (8.8–9.0) on day 28. Afterwards, the pH first decreased and then increased again to remain more or less constant (Fig. 2C). The C/N ratio gradually decreased through time from 35 to 40 to a stable value of approximately 20 from day 105 onwards (Fig. 2D). The moisture content was always higher than 30% (Fig. 2E). The OUR decreased from 4, 5.5, and 8 on day 91–3.8, 3.5, and 3.5 on day 203 in Farm 1, 2 and 3 respectively. A low OUR (< 5 mmol O_2 kg/OM/h) is typical of very stable composts. The NO_3/NH_4 ratio, which was > 1 in all samples, indicated a substantial release of mineral N and thus also a high compost stability. The biodegradation potential decreased from 1.9 ± 0.04, 2.2 ± 0.05 and 3.1 ± 0.03 in the feedstock mixtures to 1.1 ± 0.05, 1.2 ± 0.06 and 1.2 ± 0.05 in the finished compost in farm 1, 2 and 3, respectively, indicating ongoing biochemical stabilization during the composting process.

In the reference green waste composting on an industrial scale (Fig. S1), temperatures were always very high, between 50 and 80 °C without distinct heat peaks, except immediately after the windrow was turned. The pH increased from 5.3 ± 0.24 to levels between 7 and 8. The C/N ratio gradually decreased from 22.5 ± 0.27 to 13.1 ± 0.56 and the moisture content hardly exceeded 10%, except for day 33 when water was added. The biodegradation potential decreased from 2.7 ± 0.19 in the feedstock mixture to 1.4 ± 0.06 in the finished compost indicating stabilization of the compost during composting.

3.2. Microbial community

The composition of the microbial community of the farm composts changed primarily during the first weeks of composting. From day 24 onward, the PLFA based patterns were remarkably stable (Table 1). This is visualized by a PCA of the relative biomarker concentrations, which shows a clear discrimination mainly along the first axis, between early (until day 17) and later compost stages (Fig. 3A), independent of the compost process (i.e., Farm 1, Farm 2 and Farm 3). The increasing 10Me16:0 (Actinobacteria) and decreasing 18:1ω7 (Gram-negative) biomarkers contributed most to the first axis (which explains 56% of the variation), while the second axis (26% of the variation) was defined mostly by decreasing fungal and AMF (18:2ω6,9 and 16:1ω5C respectively) biomarkers and the increasing Gram-negative biomarker i16:0 (Fig. 3B). The total PLFA was highest after the heat peaks on day 35 and/or day 49 and afterwards decreased again (Table 1). All samples showed a distinct dominance of Gram-positive bacteria except for day 0 in all farm processes and days 7 and 17 in Farm 3. Comparison of the relative abundance of the functional microbial groups between composting phases (indicatively delineated based on the changes in the nematode community) revealed differences between the first phase (day 0–10) and the other phases (day 17–49, day 63–133, day 147–203). Gram-negative bacteria were most abundant during the first

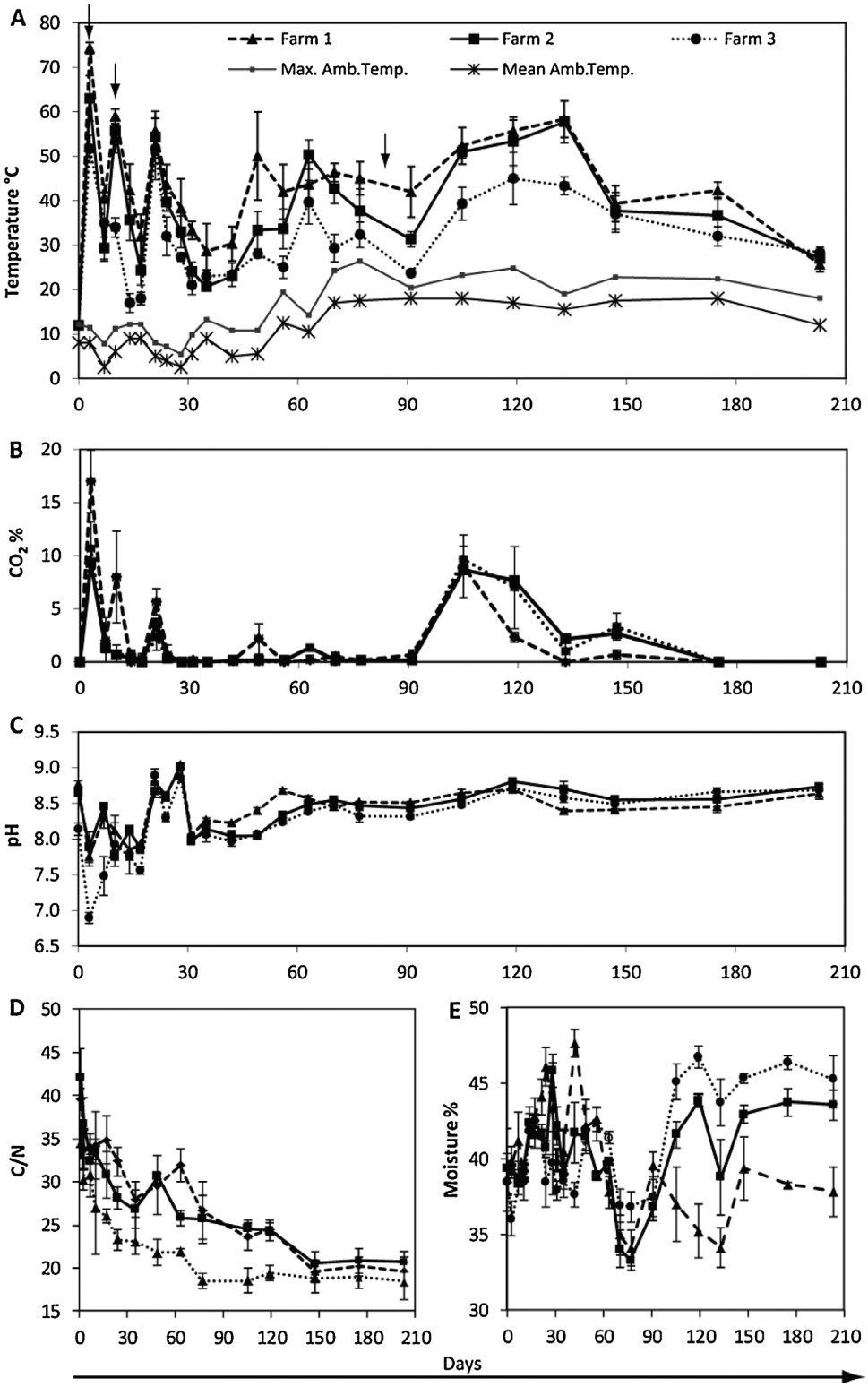

Fig. 2. Abiotic variables measured during the three farm composting processes (Farm 1, Farm 2 and Farm 3) including: (A) Temperature of the compost (°C) and mean and maximum ambient temperatures (°C) per day (24 h), (B) CO_2 content (%), (C) pH values, (D) C/N ratio, (E) moisture content (%). Error bars indicate SD based on three replicates. Arrows indicate turning events of the windrows.

ten days of composting and their concentrations declined during days 17–49 and days 63–133. Actinobacteria increased gradually during the process, with greater abundances at days 63–133 and days 147–203 compared to days 0–10. The fungal PLFA decreased in the beginning of the process as temperatures increased, but peaked on day 35 in Farm 1 and on days 35 and 49 in Farm 2 and 3, and afterwards decreased again with significantly lower concentrations during days 147–203 compared to days 17–49. Accordingly, the F/(F + B) ratio initially decreased with increasing temperatures and peaked on days 35–49, with significantly greater values on day 35 (Farm 1 & 3; $p < 0.04$, < 0.001) and day 49 (Farm 2 $p < 0.05$) compared to all later stages, except between days 35 and 77 in Farm 3. Unlike the steadily increasing proportions of fungal-feeding nematodes, the fungal PLFA remained remarkably stable and relatively low after day 63, even when temperatures were near ambient levels. The amount of fungal PLFA had no significant effect ($p \geq 0.05$) on the absolute number of fungal-feeding nematodes and thus no additional information was explained by adding this variable in the model.

Table 1
Total PLFA (nmol/g dry compost), F/(F + B) ratio and main biomarker concentrations (mol%) ± standard deviation, during the on-farm processes. *The used biomarker for AMF is questionable in a compost environment (see Steel et al., 2013a), hence the concentrations of this group are provided but not used in further community analyses.

Day	Gram +	Gram −	Total Bact	Actinobacteria	Fungi	AMF*	Total PLFA	F/(F + B)
	Farm 1							
0	30 ± 0.69	40.1 ± 0.88	72.6 ± 1.58	2.1 ± 0.05	22 ± 1.57	3.31 ± 0.05	1287 ± 95.9	0.2 ± 0.02
3	61.5 ± 1.79	22.9 ± 1.38	87.9 ± 0.43	1.1 ± 0.01	10.3 ± 0.39	0.63 ± 0.06	2103 ± 152.6	0.1 ± 0
7	53.2 ± 3.95	28.6 ± 3.8	85 ± 0.55	1.4 ± 0.08	12 ± 0.38	1.58 ± 0.25	1767 ± 238.4	0.1 ± 0
10	55.4 ± 0.86	21.5 ± 2.01	83.4 ± 0.42	5.4 ± 2.09	8.5 ± 1.89	2.77 ± 0.19	1921 ± 250.7	0.1 ± 0.02
17	51.7 ± 1.95	17.7 ± 1.01	73.2 ± 2.11	7.1 ± 0.13	11.8 ± 1.58	7.92 ± 0.42	1724 ± 110.4	0.1 ± 0.02
24	54 ± 2.98	16.8 ± 1.98	75 ± 1.62	6.7 ± 0.74	10.4 ± 1.48	7.86 ± 1.53	1674 ± 527.6	0.1 ± 0.02
35	42.1 ± 1.64	20 ± 0.26	64.4 ± 1.9	7.6 ± 0.16	18.6 ± 1.67	9.31 ± 0.23	3182 ± 126.9	0.2 ± 0.02
49	47.4 ± 0.57	18 ± 0.5	69 ± 0.74	8.3 ± 0.15	15.1 ± 1.04	7.6 ± 0.32	2452 ± 112.1	0.2 ± 0.01
63	50.6 ± 1.63	15.9 ± 2.7	70.5 ± 0.87	13.5 ± 0.68	8.8 ± 0.64	7.3 ± 1.23	1906 ± 173.4	0.1 ± 0.01
77	48.9 ± 8.68	15.3 ± 4.61	68.1 ± 4.65	10.6 ± 0.85	12 ± 3.19	9.32 ± 2.29	2208 ± 337.4	0.2 ± 0.04
105	47.5 ± 0.58	19.1 ± 0.32	70.1 ± 0.61	10.1 ± 0.2	11.3 ± 0.62	8.47 ± 0.1	2204 ± 158.1	0.1 ± 0.01
175	49.4 ± 3.18	17.9 ± 3.88	70.5 ± 2.05	11.2 ± 0.63	10.4 ± 1.48	7.87 ± 1.24	1667 ± 231.7	0.1 ± 0.02
203	49.1 ± 0.4	20.2 ± 0.32	72.3 ± 0.29	11.8 ± 0.21	8.7 ± 0.42	7.15 ± 0.19	1985 ± 140	0.1 ± 0
	Farm 2							
0	27.9 ± 1.49	39.7 ± 0.56	70.2 ± 1.4	1.7 ± 0.03	25.2 ± 1.28	2.88 ± 0.12	1297 ± 60.7	0.3 ± 0.01
3	52.5 ± 1.19	29.1 ± 0.92	85.1 ± 0.71	1.5 ± 0.17	12.3 ± 0.71	1.17 ± 0.12	1811 ± 310.2	0.1 ± 0.01
7	49.8 ± 1.73	31.8 ± 1.74	84.6 ± 0.62	1.5 ± 0.19	12.4 ± 0.43	1.47 ± 0.17	2056 ± 199.2	0.1 ± 0
10	46.6 ± 1.24	28.9 ± 0.6	78.7 ± 1.16	3.2 ± 0.13	14.4 ± 1.14	3.6 ± 0.15	2136 ± 286.1	0.2 ± 0.01
17	39.9 ± 1.07	22.8 ± 0.86	65.8 ± 1.85	6 ± 0.23	16.4 ± 0.44	11.83 ± 1.19	2342 ± 133.7	0.2 ± 0.01
24	50.9 ± 2.75	17.7 ± 2.65	72.2 ± 0.74	7.8 ± 0.06	13 ± 1.26	7.02 ± 0.64	2841 ± 259.4	0.2 ± 0.01
35	38.1 ± 0.69	19.2 ± 0.33	59.7 ± 0.94	7.1 ± 0.25	22 ± 1.42	11.16 ± 0.72	3581 ± 86.4	0.3 ± 0.02
49	36.8 ± 0.71	20 ± 0.29	59.4 ± 0.89	6.2 ± 0.27	24.8 ± 0.92	9.62 ± 0.25	3128 ± 257	0.3 ± 0.01
63	46.9 ± 1.27	16.3 ± 1.89	66.8 ± 0.59	9.6 ± 0.32	13 ± 0.69	10.52 ± 1.46	2641 ± 346.1	0.2 ± 0.01
77	51.4 ± 3.94	15.5 ± 2.07	71.3 ± 5.99	12.3 ± 2	9.5 ± 3.64	6.96 ± 4.35	1855 ± 296.6	0.1 ± 0.05
105	44.2 ± 1.23	21.4 ± 1.25	68.8 ± 1.29	8 ± 0.46	13.8 ± 1.2	9.34 ± 0.45	2494 ± 751.5	0.2 ± 0.01
175	45.2 ± 0.61	18.4 ± 2.88	67.1 ± 2.88	12.2 ± 0.84	11.9 ± 1.44	8.81 ± 2.44	2105 ± 227.6	0.2 ± 0.02
203	41.9 ± 2.13	20.7 ± 0.48	65.6 ± 1.61	12.4 ± 0.35	12.8 ± 1.61	9.24 ± 0.33	2265 ± 17.1	0.2 ± 0.02
	Farm 3							
0	26.2 ± 0.29	41.9 ± 0.15	70.4 ± 0.23	1.2 ± 0.06	25.9 ± 0.21	2.48 ± 0.13	2055 ± 178.8	0.3 ± 0
3	52.6 ± 1.78	26.8 ± 1.2	82.5 ± 0.58	1 ± 0.18	15.1 ± 0.5	1.47 ± 0.71	2698 ± 84	0.2 ± 0
7	39.7 ± 0.27	40.6 ± 0.97	83 ± 0.7	1.1 ± 0.11	14.2 ± 0.84	1.73 ± 0.04	2986 ± 707.1	0.1 ± 0.01
10	43.7 ± 2.41	29.6 ± 1.43	76.8 ± 1.41	2.9 ± 0.18	17 ± 1.35	3.25 ± 0.53	2625 ± 137.7	0.2 ± 0.01
17	30.5 ± 0.95	32.1 ± 0.37	65.1 ± 0.66	2.5 ± 0.18	24.5 ± 0.85	7.88 ± 0.07	3108 ± 487.9	0.3 ± 0.01
24	44.1 ± 0.38	21.1 ± 0.74	68.1 ± 0.77	5.4 ± 0.31	20.9 ± 0.26	5.68 ± 0.3	4123 ± 66	0.2 ± 0
35	35.5 ± 0.24	20.8 ± 0.48	58.6 ± 0.59	5.3 ± 0.33	24.5 ± 0.76	11.57 ± 0.31	4773 ± 324.1	0.3 ± 0.01
49	37.5 ± 0.42	21.7 ± 0.49	61.7 ± 0.6	4.8 ± 0.23	23.3 ± 0.46	10.27 ± 0.6	4689 ± 68.9	0.3 ± 0
63	39.8 ± 1.72	20.3 ± 0.59	62.8 ± 1.82	6.9 ± 0.53	18.6 ± 1.69	11.81 ± 0.21	3713 ± 171.5	0.2 ± 0.02
77	38.4 ± 0.4	18.7 ± 0.3	59.9 ± 0.15	7 ± 0.18	19.8 ± 0.43	13.31 ± 0.45	3107 ± 75.1	0.2 ± 0
105	39.5 ± 0.8	23.2 ± 0.4	65.7 ± 1.01	5.6 ± 0.27	18.1 ± 1.35	10.62 ± 1.25	3178 ± 362	0.2 ± 0.01
175	42.1 ± 0.71	21.9 ± 1.44	67 ± 0.9	8.7 ± 0.45	14 ± 0.86	10.32 ± 1.98	2294 ± 381.5	0.2 ± 0.01
203	39.4 ± 0.49	22.8 ± 0.2	64.8 ± 0.55	8.9 ± 0.16	15.5 ± 0.48	10.74 ± 0.48	2427 ± 53.6	0.2 ± 0.01

In the reference green waste composting process, the total PLFA on day 0 and day 33 was higher ($p < 0.001$) compared to days 39, 61 and 83. During the process, the fungal PLFA significantly ($p < 0.001$ between all samples) decreased with time, while the share of the Gram-positive bacteria increased with time ($p < 0.03$ between all samples). According to the decreasing fungal PLFA, the F/(F + B) ratio also sharply decreased from 2.2 ± 0.19 on day 0–0.2 ± 0.01 on day 83 (Table S1, and Fig. S5).

3.3. Nematode community

Nematode numbers rapidly increased on day 17, shortly after turning the windrows, i.e., when the temperature dropped (i.e., 7920 ± 1603, 3792 ± 1137 and 9575 ± 2407 nematodes/100 g compost DW in Farm 1, Farm 2 and Farm 3, respectively). In the subsequent composting phases, nematode densities were also inversely related with temperature ($p < 0.001$) (Table 2, Fig. S2) but not related with duration of composting (day) (MIXED procedure). 40 °C appeared to be more or less the threshold temperature for nematode densities to decrease or increase. Nematode densities were significantly lower for all sampling events at temperatures higher than 40 °C.

Independently of the feedstock material ratios, patterns of the nematode community assembly were remarkably similar for all three farm compost processes (Farm 1 in Fig. 4A, Farm 2 & Fig. S3 and S4). This was confirmed by a nMDS: the nematode communities were grouped primarily according to duration of composting rather than to the original compost feedstock composition- i.e., Farm 1, Farm 2 and Farm 3 (results not shown). Species composition in the compost was best explained by duration of composting ($r = 0.58$, stepwise BIOENV) which was correlated negatively with C/N ratio ($r = -0.77$). Bacterial-feeding enrichment opportunists (cp-1) dominated the nematode community from days 0–10. The most prominent species in this phase were *Rhabditella axei*, *Pelodera teres*, *Pelodera cylindrica* and *Poikilolaimus* sp., including a high number of Rhabditidae in dauer phase (i.e. an alternative developmental stage without feeding or defecation). Afterwards, from day 17–49, the bacterial-feeding/predators (*Mononchoides composticola*) became dominant, although this dominance was less pronounced for Farm 3, especially for day 24 where they accounted for only 7.3 ± 4.1%. The proportion of fungal-feeding nematodes, especially *Aphelenchoides* sp., increased from day 49 but decreased again with persistently high temperatures. Around day 119, the nematode community in Farm 1 and 2 again changed towards a dominance of bacterial-feeding enrichment opportunists (mainly *Poikilolaimus* sp.). The proportion of fungal-feeding nematodes again increased, including other taxa than *Aphelenchoides* sp., such as *Ditylenchus* sp., Neotylenchidae spp. and Tylenchidae spp. (cp-2), from day 147 to day 203. Other general opportunists, such as *Eucephalobus* sp. (bacterial-feeding) and *Seinura* sp. (predator) (in Farm 1 and 2), also became more

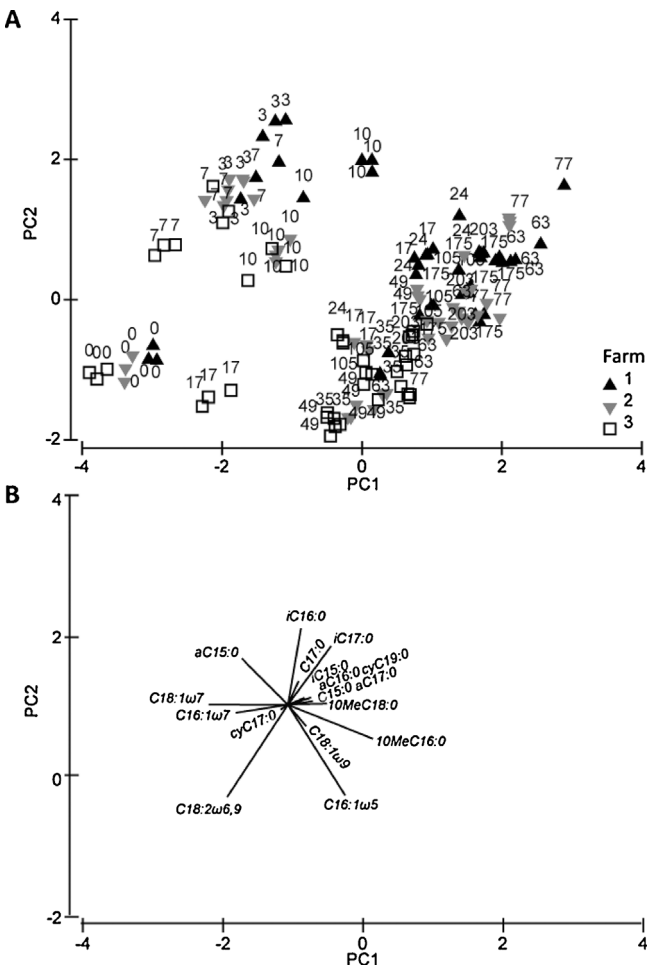

Fig. 3. (A) Two-dimensional PCA ordination of biomarker fatty acids (mol%) of the three farm composting processes (Farm 1, Farm 2, Farm 3). (B) Vector loading plot with all individual marker fatty acids.

abundant during this phase. The F/(F + B) ratio (Fig. 4B; Table 2) and the MI (Table 2) generally increased during the process but with considerable fluctuations (significant differences between day 63–133 and 147–203 compared to day 0–10 and 17–49).

The absolute number of fungal-feeding nematodes correlated negatively with temperature ($p = 0.001$) and positively with duration of composting (day) (quadratic effect of time, GLIMMIX procedure, $p = 0.029$). Based on the estimated model parameters, a positive linear fit ($r = 0.75$) was observed between the predicted and observed fungal-feeding nematode abundances (Fig. 5A). Only in the samples that were dominated by the bacterial-feeding/predators (day 17–35), none or very few fungal-feeding nematodes were found while the model (based on temperature, amount of fungal PLFA, day and a quadratic day effect as explanatory variables) predicted higher numbers. The ratio F/(F + B) was also positively correlated ($r = 0.70$) with duration of composting (quadratic day effect $p < 0.001$, day effect $p = 0.029$) but not with temperature (GLIMMIX procedure). There was a positive linear fit ($r = 0.62$) between the observed and the predicted F/(F + B) ratio based on the estimated model parameters (Fig. 5B). The model predicted the F/(F + B) ratio relatively well except for the data points in the upper left corner.

Abundances and assemblages of the nematode communities in the reference green waste composting contrasted those on an industrial scale (Table S5). Nematode densities were sparse, from completely absent or nearly so (3 ± 5 nematodes/100 g DW) to maximum 400 nematodes/100 g DW. The bacterial-feeding enrichment opportunists, such as *Procephalobus* sp., were omnipresent and comprised more than

Table 2
Overview at every sampling moment during on-farm compost processes of the means ± SD (based on three replicates) of the abundance of nematodes (per 100 g dry weight compost), number of genera and the values of the indices: F/(F + B) (fungal-feeding/fungal-feeding + bacterial-feeding), MI (Maturity Index).

Day	Farm 1					Farm 2					Farm 3				
	Abundance	# Genera	F/(F + B)	MI	Index	Abundance	# Genera	F/(F + B)	MI	Index	Abundance	# Genera	F/(F + B)	MI	Index
0	2203 ± 531	9 ± 2	0 ± 0.01	1.1 ± 0.07	2.8	3628 ± 2034	8 ± 1	0 ± 0.02	1.2 ± 0.06	2.3	6266 ± 1604	9 ± 1	0 ± 0.01	1 ± 0	2.3
3	6 ± 5	3 ± 1	0.1 ± 0.06	1.1 ± 0.06	0.3	10 ± 2	9 ± 2	0 ± 0.01	1 ± 0.01	1.3	282 ± 27	12 ± 3	0 ± 0.01	1 ± 0.02	1.5
7	28 ± 3	4 ± 1	0 ± 0	1 ± 0	0.0	469 ± 170	5 ± 2	0 ± 0.01	1 ± 0.02	1.8	1170 ± 287	13 ± 1	0 ± 0.01	1 ± 0.01	2.3
10	1784 ± 485	5 ± 1	0 ± 0	1 ± 0	2.0	141 ± 41	6 ± 1	0 ± 0.01	1 ± 0.01	1.4	292 ± 52	11 ± 2	0 ± 0.01	1 ± 0.01	1.5
17	7920 ± 1603	7 ± 2	0 ± 0	1 ± 0	2.0	3792 ± 1137	4 ± 0	0 ± 0	1 ± 0	2.0	9575 ± 2407	8 ± 1	0 ± 0	1 ± 0.01	2.0
24	214 ± 114	4 ± 2	0 ± 0	1 ± 0	1.1	47 ± 10	4 ± 2	0 ± 0	1 ± 0	1.0	33 ± 20	5 ± 2	0 ± 0	1 ± 0	1.0
35	1199 ± 176	4 ± 1	0 ± 0	1 ± 0	2.0	933 ± 153	4 ± 2	0 ± 0.06	1 ± 0.01	2.3	1470 ± 408	5 ± 1	0 ± 0	1 ± 0	2.0
49	140 ± 35	8 ± 3	0.2 ± 0.13	1.1 ± 0.07	2.1	951 ± 78	7 ± 3	0.1 ± 0.06	1 ± 0.02	2.7	1650 ± 193	6 ± 2	0 ± 0.04	1.1 ± 0.01	2.3
63	54 ± 14	5 ± 5	0.4 ± 0.01	1.3 ± 0.01	2.7	137 ± 20	6 ± 1	0.7 ± 0.05	1.6 ± 0.03	2.8	957 ± 195	7 ± 1	0.2 ± 0.11	1.1 ± 0.08	3.2
77	17 ± 3	5 ± 1	0.6 ± 0.18	1.5 ± 0.17	2.3	203 ± 19	4 ± 1	0.8 ± 0.11	1.9 ± 0.01	1.4	2446 ± 509	6 ± 0	0.3 ± 0.13	1.2 ± 0.07	3.1
105	26 ± 16	6 ± 1	0.7 ± 0.18	1.8 ± 0.15	2.8	80 ± 67	5 ± 1	0.6 ± 0.08	1.7 ± 0.13	2.3	1797 ± 130	7 ± 1	0.1 ± 0.04	1.1 ± 0.04	2.3
119	73 ± 34	8 ± 1	0.6 ± 0.04	1.7 ± 0.05	3.0	15 ± 8	8 ± 1	0.4 ± 0.04	1.5 ± 0.03	3.0	278 ± 144	6 ± 1	0.2 ± 0.06	1.1 ± 0.05	2.2
133	206 ± 80	10 ± 1	0.3 ± 0.08	1.2 ± 0.07	2.7	302 ± 81	6 ± 2	0.3 ± 0.15	1.3 ± 0.14	2.8	479 ± 71	6 ± 2	0.3 ± 0.12	1.2 ± 0.09	3.2
147	229 ± 191	6 ± 1	0.6 ± 0.1	1.9 ± 0.01	2.1	268 ± 53	8 ± 2	0.5 ± 0.2	1.7 ± 0.04	3.1	734 ± 138	7 ± 2	0.2 ± 0.08	1.2 ± 0.1	3.2
175	537 ± 80	9 ± 0	0.5 ± 0.12	1.8 ± 0.06	3.6	538 ± 68	8 ± 0	0.4 ± 0	1.5 ± 0.1	3.6	740 ± 45	8 ± 2	0.4 ± 0.12	1.4 ± 0.08	3.9
203	1662 ± 157	7 ± 1	0.8 ± 0.17	1.8 ± 0.15	4.0	596 ± 52	9 ± 1	0.7 ± 0.09	1.5 ± 0.15	3.7	768 ± 113	8 ± 1	0.4 ± 0.19	1.3 ± 0.2	3.9

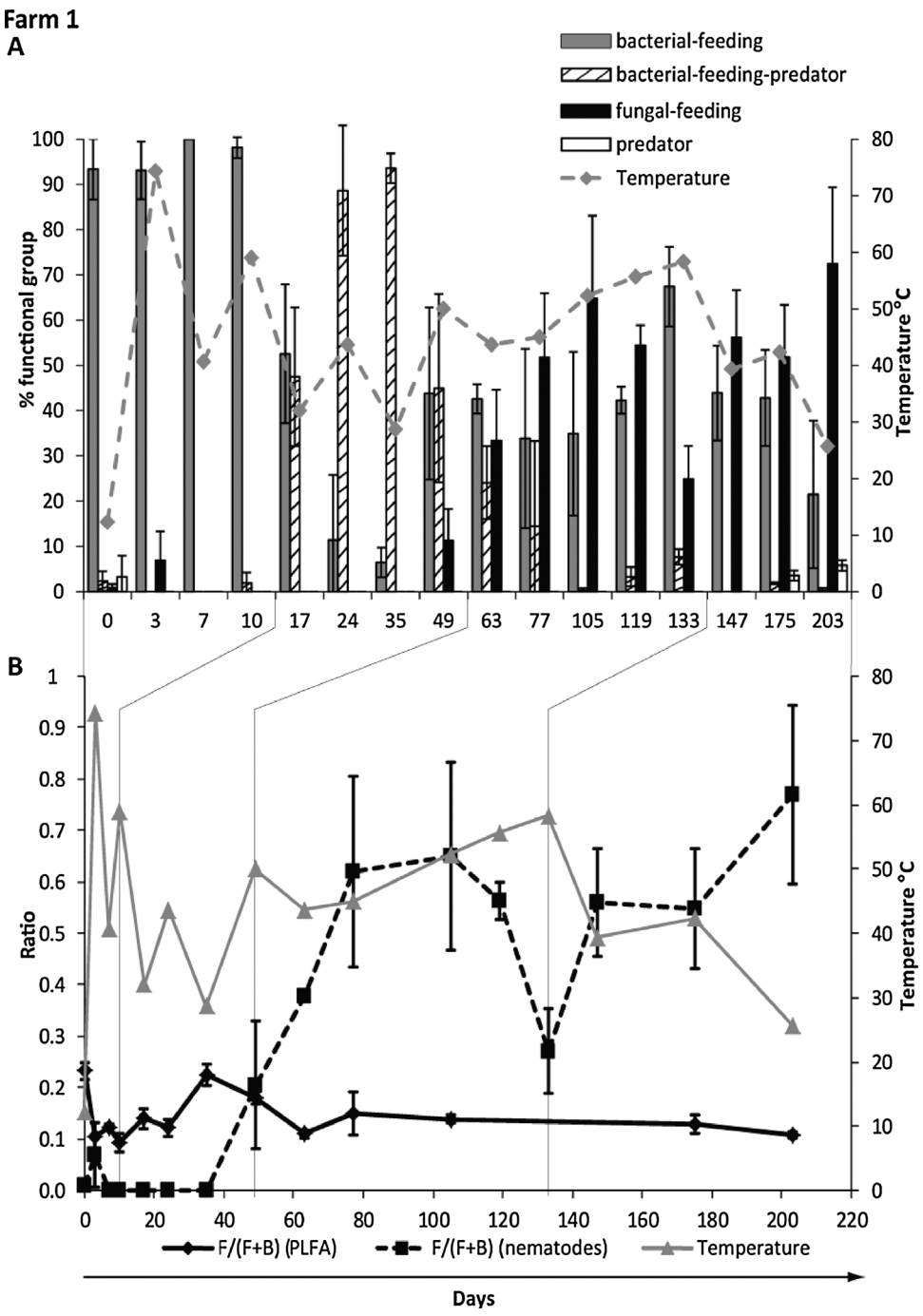

Fig. 4. Farm 1. (A) The percent contribution of each feeding type (fungal-feeding, bacterial-feeding, bacterial-feeding/predator at every sampling moment. Omnivores *s.s.* (Yeates et al., 1993) (low in abundance) are not represented in the graph. (B) F/(F + B) ratio based on fungal and bacterial PLFAs and F/(F + B) ratio based on the fungal- and bacterial-feeding nematode densities. Standard deviations are indicated as error bars. Vertical lines represent phases delineated by key-point changes in the nematode community.

80% of the community in all samples except at day 61, but were not found in the farm compost processes. *Aphelenchoides* was the only fungal-feeding nematode genus in the industrial scale green-waste compost; it was present on all days, except day 39, but never reached proportions greater than 8%. The bacterial-feeding/predator *Mononchoides composticola* occurred solely on day 33 and at that time made up only 7% of the community. In contrast with the farm compost processes, the Nematode-based indices (F/(F + B) and MI) were always low and remained more or less constant.

See Tables S2-S4 for further detail on the nematode species composition during the composting processes.

4. Discussion

4.1. Microbial succession

Gram-positive bacteria were most prominent during the heat peaks, while the proportion of the Gram-negative bacteria peaked during the intermediate temperature drop (day 7). This sequence agrees with previous reports (Steel et al., 2013a; Steger et al., 2003). Increased proportions of Actinobacteria at the later stages of farm compost reflect their relatively slow rate of growth and copiotrophic life style (Bolta et al., 2003; Hellmann et al., 1997; Steger et al., 2003). In contrast to several other studies, the proportion of fungi decreased with increasing temperature. Specifically, the proportions of fungal PLFA in all three farm compost processes studied here and in Bolta et al. (2003) continued to decrease, rather than increase, during the cooling phase, even

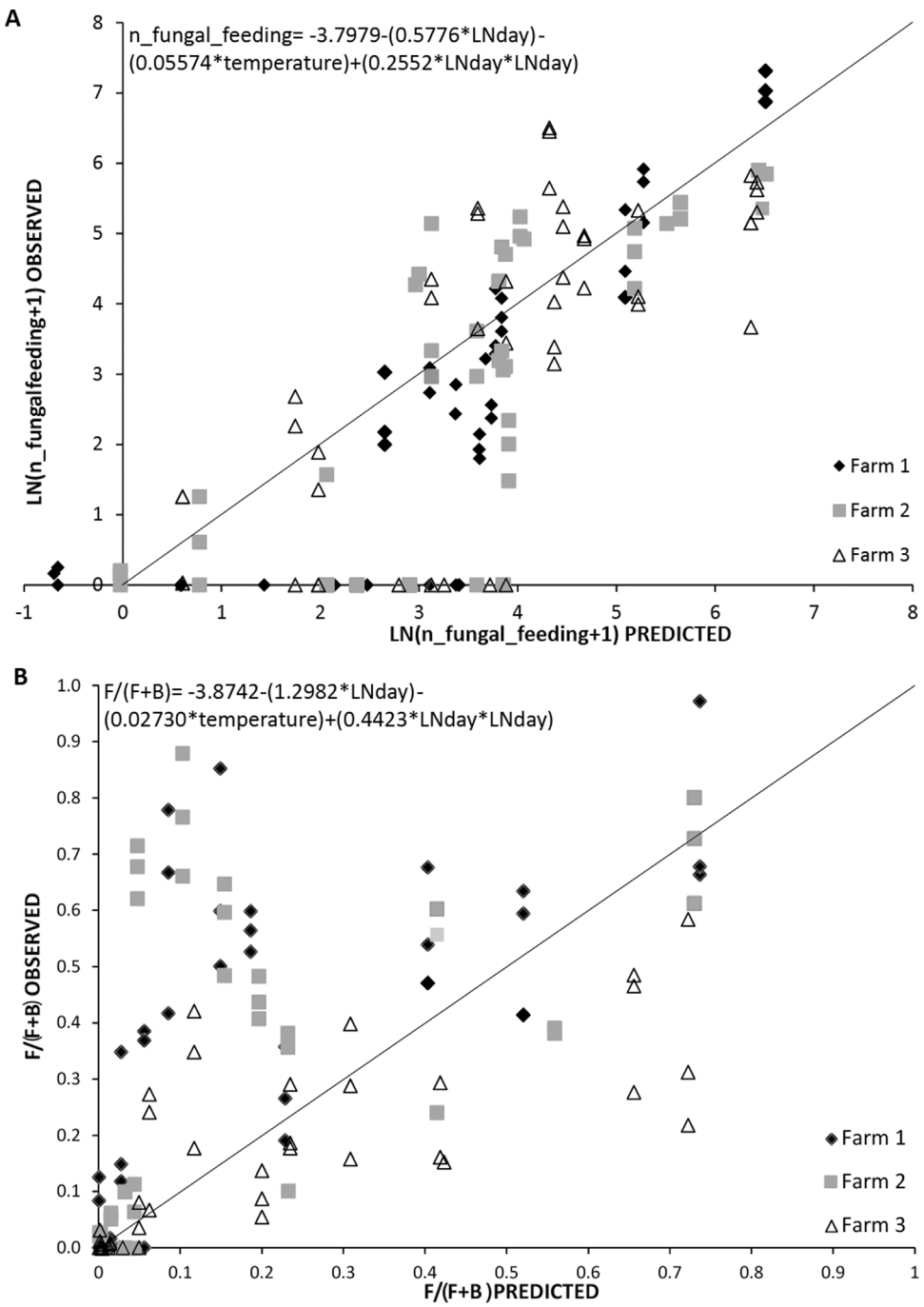

Fig. 5. (A) The predicted against the observed numbers of fungal-feeding nematodes for Farm 1, 2 and 3. (B) The predicted against the observed F/(F + B) ratio for Farm 1, 2 and 3.

near ambient temperatures (Ryckeboer et al., 2003; Steel et al., 2013a; Steger et al., 2003). It is unlikely that this could be completely attributed to the possible delay of fungal growth by previously elevated temperatures or suppressive (top-down) control of the abundant fungal-feeding nematodes. Alternatively, specificity issues related to the limited number of fungal biomarkers (i.e., 18:1ω9c and 18:2ω6,9) could have influenced our results. Although these fungal biomarkers were positively correlated to each other, it is known that they also occur in plant cells (Frostegard et al., 2011), of which the concentration in our composts was very high compared to soils. Fungal diversity is known to increase with duration of composting (Ryckeboer et al., 2003) and it is possible that some fungi appearing more at the end of the composting process were not detected. This might also explain why the increased levels of fungal-feeding nematodes did not coincide with increased levels of fungal PLFA. Conversely, Sánchez-Moreno et al. (2006) reported that the fungal-feeding nematodes in soil were not related as strongly with ergosterol as expected. This might also indicate that proxies for fungal biomass are not well correlated with the actual size of the fungal feeder populations (Sánchez-Moreno et al., 2006). Although, PLFA analyses are generally regarded as a sensitive and reliable method to quantitatively assess the changes in biomass in the major groups of microorganisms (Frostegard et al., 2011), microbial ecoenzymes are recently proposed as potential biological compost maturity indicators (Neher et al., 2017).

Compared to the nematode community succession, the changes in the microbial community based on PLFA analyses were mostly concentrated in the first month of composting and were less pronounced and not unequivocal among examined processes (this study vs. Steel et al. (2013a)). Especially the absence of a clear pattern in the later compost stages hampers the use of the microbial community as a bio-

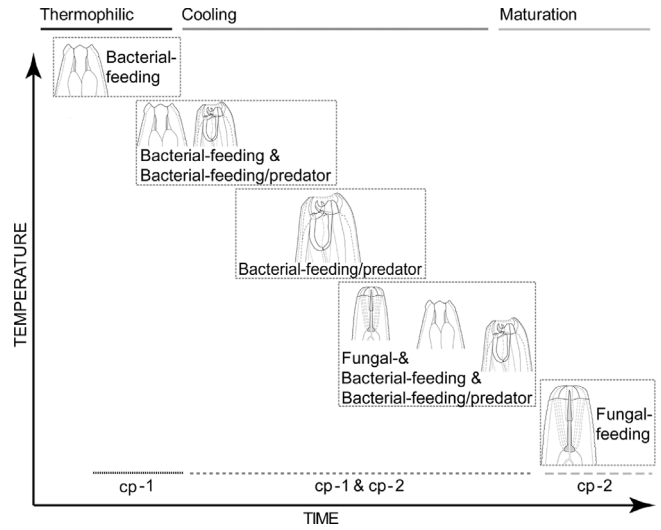

Fig. 6. General succession of nematodes during composting. Nematodes with cp-1 and cp-2 are enrichment opportunists and general opportunists, respectively. Nematode feeding types are presented schematically by nematode heads of *Panagrolaimus* sp. (bacterial-feeding), *Ditylenchus* sp. (fungal-feeding), and *Mononchoides composticola* (bacterial-feeding/predator).

indicator of compost maturity. Only the abundance of Actinobacteria generally increases during the process and the change of their assemblage composition may be a possible indicator of maturity (Steger et al., 2007).

4.2. Nematode succession

Although the timing of the nematode succession in the farm composts varies and the shifts are not as clearly delineated according to the three temperature related composting phases (thermophilic, cooling and maturation phase) compared to previous studies, the typical shifts in nematode assemblages are still present and are remarkably similar (Steel et al., 2013a; Steel et al., 2010; Steel et al., 2013b). Only the industrial scale reference process did not show such patterns. This typical succession of nematodes is associated with major shifts in life strategies and feeding group composition (Fig. 6). At the beginning of the process (thermophilic phase), immediately after the heat peak, the nematode population primarily consisted of bacterial-feeding enrichment opportunists (cp-1) (Rhabditidae, Panagrolaimidae and Diplogasteridae), supplemented with fewer bacterial-feeding (Cephalobidae) and/or fungal-feeding (Aphelenchoididae) general opportunists (cp 2). Thereafter, during the cooling and maturation stages, first the bacterial-feeding/predator enrichment opportunistic nematodes (mainly *Mononchoides composticola*) became dominant and finally, during the most mature stages, the relative importance of fungal-feeding general opportunists other than Aphelenchoididae, such as Anguinidae (mainly *Ditylenchus filimus*), Neotylenchidae and Tylenchidae increased. Hence, the nematode community undergoes a succession of r-strategists, from enrichment opportunists (cp-1) to general opportunists (cp-2), and based on feeding type, from mainly bacterial-feeders via a dominance of bacterial-feeding/predators to a proportional increase of fungal-feeders (Fig. 6). Except for the absence of K-strategists and a pronounced dominance of the Neodiplogasteridae, this process is largely similar to that observed during decomposition of plant residues in the soil (Ferris and Matute, 2003; Georgieva et al., 2005; Wang et al., 2004).

Studies on the suppressive effects of compost have largely ignored nematodes in composts even though there is ample evidence that adding compost to the soil causes changes to the whole soil nematode community, hereby affecting the presence and abundance of different nematode groups (overview in Thoden et al. (2011)). Nevertheless, short-term incubations with nematode-rich composts pointed to a possible persistence in soil of some compost nematodes (Steel et al., 2012). As abundance, activity and (functional) diversity of nematode communities are important for the continuity of their ecosystem services (Ferris, 2010), the nematodes in compost might contribute directly to the resilience of the soil food web. Further experiments will have to reveal whether the nematodes in compost directly contribute to the nematode assemblage in soil or whether, alternatively, the observed effects are due to the overall stimulation of the resident soil fauna by compost addition.

4.3. Nematodes vs. known parameters as indicators of compost maturity

Importantly, the absence of a linear relationship of temperature and time in the current study facilitated the distinction between the effect of temperature and duration of composting. The density of fungal-feeding nematodes is, like the total density of nematodes, significantly related to temperature, but also to duration of composting. The model only overestimates fungal-feeding nematodes when the bacterial-feeding/predators (i.e., *Mononchoides composticola*) were dominant and possibly affected fungal-feeding nematode abundances due to predation (Steel et al., 2011). In addition they can most likely also exhibit fungal-feeding behavior which has also been reported for *Pristionchus pacificus* of the same nematode family (Furst von Lieven and Sudhaus, 2000). In contrast, the F/(F + B) ratio appeared to be less affected by temperature and was only significantly positively related with duration of composting, confirming its potential as an indicator of compost maturity (Steel et al., 2013a; Steel et al., 2010).

Although temperature decline during composting correlated well with a number of commonly used maturity parameters (e.g., C/N ratio, dehydrogenase activity, ATP content) (Tiquia et al., 2002), compost maturity assessment solely based on compost temperature may give misleading information (Wichuk and McCartney, 2010), i.e., when compost process temperature is inhibited by suboptimal conditions. In our study, for example, stable temperature values were found from day 35 onwards. A NO_3-N/NH_4 −N ratio > 1 (Bernal et al., 1998) and an oxygen uptake ratio (OUR) between 5 and 10 mmol O_2/kg OM/h (Grigatti et al., 2011), both measures of chemically mature composts, were already reached after 91 days in this study. The C/N ratio also remained stable (± 20) from day 150 onwards. In contrast, the nematode community underwent some significant changes, including a relative increase of fungal-feeding nematodes. The initial in fungivorous nematodes coincides with decreasing C/N ratios during the composting process and indicates decomposition of more recalcitrant material. It is well known that fungal energy channels predominate when the organic input, like the feedstock materials in the farm compost processes, is characterized by a high C/N ratio (between 30 and 60), and conversely, bacterial decomposition channels predominate when the organic material has a low C/N ratio (Ruess, 2003). This also explains the lower proportion of fungal-feeding nematodes in Farm 3, as the feedstock C/N was lower than Farm 1 and 2 (i.e. 40 compared to 66 and 53; Fig. 1). Biochemical composition, expressed as the biodegradation potential (i.e. the holocellulose to lignin ratio), is another indicator that reflects greater degradation potential of feedstock mixture in Farm 3 (3.1) than for Farm 1 and 2 (1.9 and 2.2 respectively) (Vandecasteele et al., 2016). Also, bacteria and fungi have different and more complex communities in the post-thermophilic phases, which importantly offer a suitable substrate and environment for organisms that possibly promote bio-control, fertility and/or plant growth (Neher et al., 2013). This indicates that chemical maturity does not necessarily coincide with biological maturity and that maturation or curing is critical for the biological compost component and its benefits.

4.4. Nematode-based index of compost maturity (NICM)

Applications of biologically mature compost have a positive effect on soil quality. The absence of clear criteria to assess the biological

Table 3
Overview of the proposed nematological criteria to assess biological compost maturity applied on composts at the end of the composting process. Index scores based on the proposed criteria for biological maturity of all examined composts in this study and available literature data; FC stands for Farm Compost. When values are highlighted in grey the respective criterion had very low values.

CRITERIA	Abundance */100 g DW*	F/(F + B)	Fungal-feeding taxa	Diplogasterids	Index *score/3.75*	Duration of composting *days*	References
FC 75% poplar bark	1662 ± 157	0.77 ± 0.17	3	+	**3.7**	203	this study (Farm 1)
FC 50% poplar bark	596 ± 52	0.71 ± 0.09	4	+	**3.5**	203	this study (Farm 2)
FC 25% poplar bark	768 ± 113	0.37 ± 0.12	3	+	**3.6**	203	this study (Farm 3)
reference green waste	177 ± 57	0.003 ± 0.005	1	absence	**0.4**	83	this study
FC poplar bark 1	933 ± 107	0.9 ± 0.06	1	+	**3.0**	175	Steel et al. (2010)
FC oak bark[a]	1700 ± 300	0.52 ± 0.05	2	+	**3.5**	364	Steel et al. (2012)
FC poplar bark 3[a]	3100 ± 520	0.67 ± 0.04	2	+	**3.5**	364	Steel et al. (2012)
FC Norway spruce[a]	2000 ± 400	0.56 ± 0.06	2	+	**3.5**	364	Steel et al. (2012)
FC Willow wood chips[a]	4000 ± 720	0.86 ± 0.02	3	+	**3.7**	168	Steel et al. (2012)
FC poplar wood chips[a]	4400 ± 669	0.73 ± 0.07	2	absence	**2.7**	168	Steel et al. (2012)
FC poplar bark 4[a]	900 ± 190	0.83 ± 0.08	2	+	**3.5**	168	Steel et al. (2012)
green waste[a]	300 ± 40	0.4 ± 0.11	2	+	**2.6**	unknown	Steel et al. (2012)
FC poplar bark 2	722 ± 158	0.5 ± 0.26	2	+	**3.4**	162	Steel et al. (2013a)
barrel control treatment	3573 ± 2170	0.42 ± 0.35	1	+	**3.0**	112	Steel et al. (2013b)
barrel soil treatment	2575 ± 506	0.12 ± 0.03	2	+	**2.6**	112	Steel et al. (2013b)
barrel net treatment	2056 ± 1281	0.24 ± 0.17	1	+	**2.5**	112	Steel et al. (2013b)
FC leek + wood chips[a]	10359 ± 1295	0.42 ± 0.16	4	+	**3.75**	unknown	Joos et al., in prep
Vermicompost[a]	1503 ± 627	0.65 ± 0.12	2	+	**3.50**	unknown	Joos et al., in prep
green waste 2[a]	2063 ± 296	0.05 ± 0.04	2	+	**2.51**	unknown	Joos et al., in prep
green waste 3[a]	6966 ± 3575	0.65 ± 0.12	3	+	**3.75**	unknown	Herren et al., in prep
green waste 4[a]	1212 ± 118	0.21 ± 0.06	3	+	**3.04**	unknown	Herren et al., in prep
green waste 5[a]	154 ± 51	0.28 ± 0.14	2	absence	**1.47**	unknown	Herren et al., in prep

[a]only final stage compost available and samples were sieved prior to nematode extraction.

maturity, however, forms a considerable gap. Based on current results in combination with literature data, we propose biological maturity is an indicator of high quality composts. We propose a Nematode-based Index of Compost Maturity (NICM) based on the following specific lines of evidence that the nematode community can serve as a tool to assess biological compost maturity: (1) repeatable and predictable pattern of nematode succession during composting (this study and Steel et al., 2010, 2013a, 2013b), which is not significantly influenced by time of year, used feedstock materials or differences in accessibility; (2) selected nematode parameters have a relatively well understood relationship with certain informative abiotic compost parameters such as temperature and duration of composting (this study); (3) distinct nematode pattern differences between carefully managed compost (used as models of biological maturity) and a biologically poor industrial scale green waste process (this study and Steel et al., 2012). Following on these evident advantages to use nematodes as an indicator of compost biological maturity, the proposed nematode-based index is based on four criteria which are discussed below, based on all available evidence.

Nematode density. High numbers of nematodes are potentially beneficial for maintenance of a solid, balanced and healthy soil food web through ecosystem services, and indicate biologically mature compost. In the controlled and well-balanced compost processes (this study and Steel et al., 2013a, 2013b), nematode abundance was never below 600 ind/100 g DW at near-ambient temperatures. In contrast, the biologically poor green waste composts contained far fewer nematodes, i.e., maximum 300 ind/100 g DW.

F/(F + B) ratio. This ratio reflects the characteristic increase of fungal-feeding nematodes during maturation and is therefore a suitable ratio to assess maturity and decomposition pathways. There is a large difference in the lowest levels obtained for this ratio between the industrial green waste and the farm composts (*i.e.,* 0.003 ± 0.005 in the green waste compared to between 0.37 ± 0.12 and 0.9 ± 0.06 in all other composts).

The diversity of fungal-feeding taxa. Immediately after the heat peak, usually only one fungal-feeding taxon (mostly Aphelenchoididae) was present, while later, during maturation, other fungal-feeding taxa appeared. Hence, mature compost can be characterized by, next to the early appearing Aphelenchoididae, at least one additional fungal-feeding taxon, such as species from the Tylenchidae, Neotylenchidae and/or Anguinidae.

The presence of diplogasterids (Diplogasteridae *sensu lato*). The presence of bacterivorous-predatory diplogasterids, in addition to taxa feeding solely on bacteria or fungi, provides an easy indication of more trophic diversity as well as presence of higher trophic levels. These diplogasterids may essentially be considered omnivores *s.l.* to which ecological theory and modeling often attribute a key role in determining food web stability, principally because they increase connectance (Bascompte et al., 2005; Moens et al., 2004) and/or diversity (Gravel et al., 2011).

These four criteria were translated in four scores, of which the sum makes up the NICM. The quantitative data are expressed, via a "S"-shaped logistic function, into a score from 0 to 1 with 0.75 as the indicative score of being mature (see material and methods). This function was designed as "S"-shaped, to decrease the relative contribution of variations at very low or very high level. Qualitative data, i.e., the presence or absence of diplogasterids, is translated into a score of 0.75 vs. 0. Summing the scores results in the NICM with a minimum value of 0 and a maximum value of 3.75 ((3*1) + 0.75). A NICM starting from 3 is considered mature (i.e., 4*0.75) and can be used as the maturity threshold.

As an example, we calculated the index for all nematode-characterized composts in this and previous studies at the end of the composting process (Table 3) and the development of the index during the composting process of this study (for farm composts Table 2 and for the reference green waste compost Table S1). All farm and barrel composts, with careful selection of the feedstock materials and precise monitoring of the process, have a high NCIM index (i.e., 2.7–3.75). Except for the FC poplar wood chips, which was not completely chemically stable at the time of sampling (Steel et al., 2012), and some composts from colonization experiments (barrel soil and net treatment from Steel et al., 2013b), all these composts have index scores equal to or higher than 3, indicating mature compost. In contrast, the industrial produced reference green waste compost has a very low score (0.4) and is indicated as biologically very poor and thus immature.

As this index is only based on easily identifiable feeding types or the

presence or absence of taxa, it can be applied by a non-expert after limited training and easily calculated online (http://spark.rstudio.com/bsierieb/ninja/, Sieriebriennikov et al., 2014). However, current index should be considered as work in progress and has some limitations. The criteria are based on several datasets but with an imbalance of used compost methods, *i.e.,* a dominance of Controlled Microbial farm Composting, green waste feedstock and only in one geographical region. Therefore, the index should be tested for a wide range of composts from diverse feedstock mixtures (including biowastes, sludges, and manures), locations (sites) and composting techniques, to allow more reliable interpretation of particular values of this index. Most importantly, the relation between the proposed index and the soil quality after compost applications has not yet been verified. It remains to be tested whether a putatively mature compost is effectively more beneficial. Hence, we recommend the proposed criteria to be tested, validated and fine-tuned as more data become available.

5. Conclusions

During the composting process of three composts, changes in composition of nematodes were thoroughly monitored and analyzed. This revealed a repeatable and predictable pattern of nematode succession in all examined processes, except for the industrial green waste compost. This pattern was independent of scale, season of composting, and/or composition of the feedstock mixture. In contrast to the microbial community pattern (based on PLFA data), the observed nematode succession was clearly related to changes during the composting process (i.e., composting phases, temperature and duration of composting) and is thus a promising tool to evaluate compost maturity. An index including four criteria to assess biological compost maturity based on characteristics of the nematode community is proposed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2017.10.039.

References

Bascompte, J., Melian, C.J., Sala, E., 2005. Interaction strength combinations and the overfishing of a marine food web. Proc. Natl. Acad. Sci. U. S. A. 102, 5443–5447.
Been, T.H., Schomaker, C.H., Perry, R.N., Moens, M., 2006. Distribution Patterns and Sampling, Plant Nematology. CABI publishing, Wallingford, pp. 302–326.
Bernal, M.P., Paredes, C., Sanchez-Monedero, M.A., Cegarra, J., 1998. Maturity and stability parameters of composts prepared with a wide range of organic wastes. Bioresour. Technol. 63, 91–99.
Bilgrami, A.L., Ciancio, A., Mukerji, K.G., 2008. Biological Control Potentials Of Predatory Nematodes, Integrated Management and Biocontrol of Vegetable and Grain Crops Nematodes. Springer, pp. 3–28.
Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37, 911–917.
Bolta, S.V., Mihelic, R., Lobnik, F., Lestan, D., 2003. Microbial community structure during composting with and without mass inocula. Compost Sci. Util. 11, 6–15.
Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends Ecol. Evol. 14, 224–228.
Bongers, T., 1990. The maturity index – an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19.
Cesaro, A., Belgiorno, V., Guida, M., 2015. Compost from organic solid waste: quality assessment and European regulations for its sustainable use. Res. Conserv. Recycl. 94, 72–79.
Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation, 2nd edition. PRIMER-E, Plymouth.
Cooperland, L.R., 2000. Composting: art and science of organic waste conservation to a valuable soil resource. Lab. Med. 31, 283–290.
D'Hose, T., Cougnon, M., De Vliegher, A., Willekens, K., Van Bockstaele, E., Reheul, D., 2012. Farm compost application: effects on crop performance. Compost Sci. Util. 20, 49–56.
D'Hose, T., Cougnon, M., De Vliegher, A., Vandecasteele, B., Viaene, N., Cornelis, W., Van Bockstaele, E., Reheul, D., 2014. The positive relationship between soil quality and crop production: a case study on the effect of farm compost application. Appl. Soil Ecol. 75, 189–198.
Dinel, H., Schnitzer, M., Dumontet, S., 1996. Compost maturity: chemical characteristics of extractable lipids. Compost Sci. Util. 4, 16–25.
Diver, S., 2004. Controlled Microbial Composting and Humus Management: Leubke Compost. ATTRA- National Sustainable Agriculture Information Service.
Ferris, H., Bongers, T., 2006. Nematode indicators of organic enrichment. J. Nematol. 38, 3–12.
Ferris, H., Matute, M.M., 2003. Structural and functional succession in the nematode fauna of a soil food web. Appl. Soil Ecol. 23, 93–110.
Ferris, H., 2010. Contribution of nematodes to the structure and function of the soil food web. J. Nematol. 42, 63–67.
Frostegard, A., Tunlid, A., Baath, E., 2011. Use and misuse of PLFA measurements in soils. Soil Biol. Biochem. 43, 1621–1625.
Furst von Lieven, A., Sudhaus, W., 2000. Comparative and functional morphology of the buccal cavity of Diplogastrina (Nematoda) and a first outline of the phylogeny of this taxon. J. Zool. Syst. Evol. Res. 38, 37–63.
Georgieva, S., Christensen, S., Petersen, H., Gjelstrup, P., Thorup-Kristensen, K., 2005. Early decomposer assemblages of soil organisms in litterbags with vetch and rye roots. Soil Biol. Biochem. 37, 1145–1155.
Gomez, R.B., Lima, F.V., Ferrer, A.S., 2006. The use of respiration indices in the composting process: a review. Waste Manage. Res. 24, 37–47.
Gravel, D., Canard, E., Guichard, F., Mouquet, N., 2011. Persistence increases with diversity and connectance in trophic metacommunities. PLoS One 6.
Grigatti, M., Cavani, L., Ciavatta, C., 2011. The evaluation of stability during the composting of different starting materials: comparison of chemical and biological parameters. Chemosphere 83, 41–48.
Hellmann, B., Zelles, L., Palojarvi, A., Bai, Q.Y., 1997. Emission of climate-relevant trace gases and succession of microbial communities during open-window composting. Appl. Environ. Microbiol. 63, 1011–1018.
Mehta, C.M., Palni, U., Franke-Whittle, I.H., Sharma, A.K., 2014. Compost: its role, mechanism and impact on reducing soil-borne plant diseases. Waste Manage. 34, 607–622.
Moens, T., Yeates, G.W., De Ley, P., 2004. Use of carbon an energy sources by nematodes. In: Cook, R.C., Hunt, D.J. (Eds.), Proceeding of the Fourth International Congress of Nematology, 2002. Tenerife, Spain. pp. 529–545.
Moeskops, B., Sukristiyonubowo Buchan, D., Sleutel, S., Herawaty, L., Husen, E., Saraswati, R., Setyorini, D., De Neve, S., 2010. Soil microbial communities and activities under intensive organic and conventional vegetable farming in West Java, Indonesia. Appl. Soil Ecol. 45, 112–120.
Neher, D.A., Weicht, T.R., Bates, S.T., Leff, J.W., Fierer, N., 2013. Changes in bacterial and fungal communities across compost recipes, preparation methods, and composting times. PLoS One 8.
Neher, D.A., Fang, L., Weicht, T.R., 2017. Ecoenzymes as indicators of compost to suppress rhizoctonia solani. Compost Sci. Util. 1–11.
Neher, D.A., 2001. Role of nematodes in soil health and their use as indicators. J. Nematol. 33, 161–168.
Oka, Y., 2010. Mechanisms of nematode suppression by organic soil amendments–A review. Appl. Soil Ecol. 44, 101–115.
Okada, H., Tsukiboshi, T., Kadota, I., 2002. Mycetophagy in filenchus misellus (Andrassy, 1958) lownsbery & lownsbery, 1985 (Nematoda: tylenchidae), with notes on its morphology. Nematology 4, 795–801.
Ruess, L., 2003. Nematode soil faunal analysis of decomposition pathways in different ecosystems. Nematology 5, 179–181.
Ryckeboer, J., Mergaert, J., Coosemans, J., Deprins, K., Swings, J., 2003. Microbiological aspects of biowaste during composting in a monitored compost bin. J. Appl. Microbiol. 94, 127–137.
Sánchez-Moreno, S., Minoshima, H., Ferris, H., Jackson, L.E., 2006. Linking soil properties and nematode community composition: effects of soil management on soil food webs. Nematology 8, 703–715.
Sellami, F., Hachicha, S., Chtourou, M., Medhioub, K., Ammar, E., 2008. Maturity assessment of composted olive mill wastes using UV spectra and humification parameters. Bioresour. Technol. 99, 6900–6907.
Serobyan, V., Ragsdale, E.J., Mueller, M.R., Sommer, R.J., 2013. Feeding plasticity in the nematode Pristionchus pacificus is influenced by sex and social context and is linked to developmental speed. Evol. Dev. 15, 161–170.
Sieriebriennikov, B., Ferris, H., de Goede, R.G.M., 2014. NINJA: An automated calculation system for nematode-based biological monitoring. Eur. J. Soil Biol. 61, 90–93.
Steel, H., de la Pe¤a, E., Fonderie, P., Willekens, K., Borgonie, G., Bert, W., 2010. Nematode succession during composting and the potential fo the nematode community as an indicator of compost maturity. Pedobiologia 53, 181–190.
Steel, H., Moens, T., Scholaert, A., Boshoff, M., Houthoofd, W., Bert, W., 2011. Mononchoides composticola n. sp. (Nematoda: diplogastridae) associated with composting processes: morphological, molecular and autecological characterisation. Nematology 13, 347–363.
Steel, H., Vandecasteele, B., Willekens, K., Sabbe, K., Moens, T., Bert, W., 2012. Nematode

communities and macronutrients in composts and compost-amended soils as affected by feedstock composition. Appl. Soil Ecol. 61, 100–112.
Steel, H., Buchan, D., De Neve, S., Couvreur, M., Moens, T., Bert, W., 2013a. Nematode and microbial communities in a rapidly changing compost environment: how nematode assemblages reflect composting phases. Eur. J. Soil Biol. 56, 1–10.
Steel, H., Verdoodt, F., Cerevkova, A., Couvreur, M., Fonderie, P., Moens, T., Bert, W., 2013b. Survival and colonization of nematodes in a composting process. Invertebr. Biol. 132, 108–119.
Steger, K., Jarvis, A., Smars, S., Sundh, I., 2003. Comparison of signature lipid methods to determine microbial community structure in compost. J. Microbiol. Methods 55, 371–382.
Steger, K., Sjogren, A.M., Jarvis, A., Jansson, J.K., Sundh, I., 2007. Development of compost maturity and Actinobacteria populations during full-scale composting of organic household waste. J. Appl. Microbiol. 103, 487–498.
Thoden, T.C., Korthals, G.W., Termorshuizen, A.J., 2011. Organic amendments and their influences on plant-parasitic and free-living nematodes: a promising method for nematode management? Nematology 13, 133–153.
Tiquia, S.M., Wan, J.H.C., Tam, N.F.Y., 2002. Microbial population dynamics and enzyme activities during composting. Compost Sci. Util. 10, 150–161.
Tognetti, C., Mazzarino, M.J., Laos, F., 2008. Compost of municipal organic waste: effects of different management practices on degradability and nutrient release capacity. Soil Biol. Biochem. 40, 2290–2296.
Vandecasteele, B., Willekens, K., Steel, H., D'Hose, T., Van Waes, C., Bert, W., 2016. Feedstock mixture composition as key factor for C/P ratio and phosphorus availability in composts: role of biodegradation potential, biochar amendment and calcium content. Waste Biomass Valorization 1–15.
Vansoest, P.J., Robertson, J.B., Lewis, B.A., 1991. Methods for dietary fiber, neutral detergent fiber, and nonstrach polysaccharides in relation to animal nutrition. J. Dairy Sci. 74, 3583–3597.
Verbeke, G., Molenberghs, G., 2009. Fitting linear mixed models with SAS. In: Verbeke, G.G.M. (Ed.), Linear Mixed Models for Longitudinal Data. Springer, Verlag, New York, pp. 93–119.
Wang, K.H., McSorley, R., Marshall, A.J., Gallaher, R.N., 2004. Nematode community changes associated with decomposition of Crotalaria juncea amendment in litterbags. Appl. Soil Ecol. 27, 31–45.
Wichuk, K.M., McCartney, D., 2010. Compost stability and maturity evaluation – a literature review. Can. J. Civ. Eng. 37, 1505–1523.
Willekens, K., Vandecasteele, B., Buchan, D., De Neve, S., 2014. Soil quality is positively affected by reduced tillage and compost in an intensive vegetable cropping system. Appl. Soil Ecol. 82, 61–71.
Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding-habits in soil nematode families and genera − an outline for soil ecologists. J. Nematol. 25, 315–331.
Yeates, G.W., Ferris, H., Moens, T., Van der Putten, W.H., Wilson, M.J., Kakouli-Duarte, T., 2009. The Role of Nematodes in Ecosystems Nematodes as Environmental Indicators. CAB International, Oxfordshire, pp. 1–44.
Yeates, G.W., 2003. Nematodes as soil indicators: functional and biodiversity aspects. Biol. Fertil. Soils 37, 199–210.
Young, C.C., Rekha, P.D., Arun, A.B., 2005. What Happens During Composting. Food & Fertilize Technology Center.
Zmora-Nahum, S., Markovitch, O., Tarchitzky, J., Chen, Y.N., 2005. Dissolved organic carbon (DOC) as a parameter of compost maturity. Soil Biol. Biochem. 37, 2109–2116.
Zorpas, A.A., Pereira, J.C., Bolin, J.L., 2009. Compost Evaluation and Utilization, Composting: Processing, Materials and Approaches. Nova Science Publishers, Inc, New York, pp. 31–68.