Using the biomasses of soil nematode taxa as weighting factors for assessing soil food web conditions

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Using the biomasses of soil nematode taxa as weighting factors for assessing soil food web conditions

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ABSTRACT

We propose the use of nematode generic biomasses as weighting factors for calculation of nematode community indices. Three data sets were used to calculate the indices using guild-based weighting (i.e., fixed weighting of nematode guilds) and genus-based weighting (i.e., weighting based on the nematode generic biomasses). The genus-based weighting factors were quadratically correlated with guild-based weighting factors, but the genus-based weighting factors were highly variable within each nematode guild, indicating that important information was likely missing when guild-based weighting was used. Although variation patterns of in the indices in response to management practices and land use were often similar for the two weighting systems, they sometimes differed substantially, and the specific index values frequently differed depending on which weighting system was used. In addition, the absolute values of the indices were frequently found to be different between the two weighting systems. Based on the comparison of indices from the two systems, we found that the genus-based system was complementary rather than superior to the guild-based system. It was suggested that both weighting systems should be used for the calculation of the nematode community indices in a study in order to better distinguish the treatment effects.

1. Introduction

Soil nematodes are one of the most commonly used indicators of soil food web conditions (Bongers and Ferris, 1999; Neher, 2001). This use of nematodes is based on the fact that soil nematodes exhibit differences in food sources and life history strategies and therefore occupy several trophic levels in food webs. Although Yeates et al. (1993) proposed eight trophic groups for soil nematodes, soil nematode taxa are usually assigned to five trophic groups: bacterivores (Ba), fungivores (Fu), plant feeders (Pl), omnivores (Om), and predators (Pr). Another characteristic that makes soil nematodes excellent indicators of soil conditions is that nematode life history strategies might be described with a colonizer–persister (*cp*) scale, with range from 1 (typical *r*-selected taxa) to 5 (typical *K*-selected taxa). Based on their well-documented feeding types and inferred life history strategies (or *cp* scales) (Bongers and Bongers, 1998; Ferris et al., 2001; Yeates et al., 1993), soil nematodes can be grouped into 16 functional guilds (i.e., Ba_{1-4}, Fu_{2-4}, Pl_{2-5}, Om_{4-5}, and Pr_{3-5}). They are considered as basal component (Fu_2, Ba_2), enrichment component (Ba_1) and structure component (Ba_{3-4}, Fu_{3-4}, Om_{4-5} and Pr_{3-5}) depending on what qualitative conditions in food web each guild indicates.

By weighting these functional guilds, soil nematode community indices (such as enrichment, structure, channel, and bacterivore indices) have been considered useful for assessing soil food web conditions (Ferris et al., 2001). In the formulas used to calculate these four indices, nematode guilds are assigned with different weighting factors. However, these weighting factors for nematode guilds are somewhat arbitrary and require refinement (Ferris et al., 2001). In addition, the responses of many nematode genera to resource enrichment or disturbance did not match their *cp* scale values (Fiscus and Neher, 2002; Korthals et al., 1996; Zhao and Neher, 2013). So far, however, no methodology has been developed to re-assess the *cp* scale and weighting system of nematodes.

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Table 1
Guild-based weighting factors and average fresh biomasses per individual of the genera of non-plant-feeding nematodes in three studies in southwest and southern China.

Genus	Guild[d]	Weighting factor[e]	Biomass per individual (μg)	Genus	Guild	Weighting factor	Biomass per individual (μg)
Diploscapter[c]	Ba1	3.2	0.3	*Alaimus*	Ba4	3.2	0.87
Distolabrellus[b]	Ba1	3.2	0.75	*Aphelenchoides*	Fu2	0.8	0.17
Macrolaimus[b]	Ba1	3.2	1.13	*Aphelenchus*	Fu2	0.8	0.26
Panagrolaimus	Ba1	3.2	0.84	*Ditylenchus*	Fu2	0.8	0.47
Protorhabditis	Ba1	3.2	0.41	*Filenchus*	Fu2	0.8	0.09
Pseudodiplogasteroides[b]	Ba1	3.2	0.84	*Psilenchus*	Fu2	0.8	0.45
Rhabditis[b]	Ba1	3.2	8.72	*Seinura*[c]	Fu2	0.8	0.17
Rhabditoides[b]	Ba1	3.2	7.33	*Diphtherophora*	Fu3	1.8	0.6
Rhabditonema	Ba1	3.2	0.2	*Dorylaimellus*	Fu4	3.2	0.3
Acrobeles[a]	Ba2	0.8	0.49	*Leptotylencholaimus*[b]	Fu4	3.2	0.54
Acrobeloides	Ba2	0.8	0.2	*Loncharionema*[b]	Fu4	3.2	1.07
Acrolobus[b]	Ba2	0.8	0.14	*Nimigula*[a]	Fu4	3.2	2.62
Acroukrainicus[b]	Ba2	0.8	0.37	*Tylencholaimellus*	Fu4	3.2	1.09
Cephalobus	Ba2	0.8	0.36	*Tylencholaimus*	Fu4	3.2	0.54
Cervidellus[a]	Ba2	0.8	0.15	*Dorylaimoides*	Fu4	3.2	1.13
Chronogaster[a]	Ba2	0.8	0.23	*Epidorylaimus*	Om4	3.2	1.51
Drilocephalobus	Ba2	0.8	0.1	*Eudorylaimus*	Om4	3.2	3.96
Eucephalobus	Ba2	0.8	0.29	*Microdorylaimus*	Om4	3.2	0.5
Heterocephalobus	Ba2	0.8	0.4	*Prodorylaimus*	Om4	3.2	4.09
Leptolaimus[a]	Ba2	0.8	0.17	*Pungentus*	Om4	3.2	1.75
Paraplectonema[a]	Ba2	0.8	0.51	*Thonus*	Om4	3.2	1.94
Placodira[b]	Ba2	0.8	0.45	*Thornia*	Om4	3.2	0.96
Plectus	Ba2	0.8	0.98	*Chrysonemoides*	Om5	5	0.98
Pseudacrobeles[b]	Ba2	0.8	0.49	*Mesodorylaimus*	Om5	5	5
Steratocephalus[b]	Ba2	0.8	0.08	*Amphibelondira*	Om5	5	2.62
Teratocephalus[b]	Ba2	0.8	0.09	*Tripyla*	Pr3	1.8	3.26
Tylocephalus[a]	Ba2	0.8	0.23	*Trischistoma*	Pr3	1.8	0.75
Wilsonema	Ba2	0.8	0.05	*Tobrilus*[a]	Pr3	1.8	8.38
Eumonhystera[b]	Ba2	0.8	0.22	*Stenonchulus*	Pr3	1.8	0.61
Aphanolaimus[b]	Ba3	1.8	0.43	*Anatonchus*[b]	Pr4	3.2	6.27
Bastiania[b]	Ba3	1.8	0.1	*Coomansus*	Pr4	3.2	4
Cylindrolaimus[b]	Ba3	1.8	0.77	*Iotonchus*	Pr4	3.2	3.99
Metateratocephalus	Ba3	1.8	0.08	*Miconchus*	Pr4	3.2	4
Odontolaimus	Ba3	1.8	0.19	*Clarkus*[b]	Pr4	3.2	1.47
Paraphanolaimus[b]	Ba3	1.8	0.88	*Monochus*	Pr4	3.2	4
Prismatolaimus	Ba3	1.8	0.64	*Mylonchulus*	Pr4	3.2	3.99
Rhabdolaimus	Ba3	1.8	0.09	*Aporcelaimellus*	Pr5	5	10.88
Achromadora	Ba3	1.8	0.31	*Discolaimus*[b]	Pr5	5	0.65
Microlaimus	Ba3	1.8	0.15	*Paractinolaimus*[b]	Pr5	5	10.82

[a] Nematode genus only retrieved from study 1 (data set 1) (Zhao et al., 2014b).
[b] Nematode genus only retrieved from study 2 (data set 2) (Zhao et al., 2014a).
[c] Nematode genus only retrieved from study 3 (data set 3) (Zhao et al., 2011).
[d] Guild designation is the composite of trophic group and cp value: Ba, bacterivore; Fu, fungivore; Pr, predator; Om, omnivore. Trophic group and *cp* value assignment mainly according to Yeates et al. (1993) and Bongers and Bongers (1998), respectively.
[e] Weighting factor of each nematode guild according to Ferris et al. (2001).

The individual biomass, generation time, and fecundity are important aspects of nematode life history strategies and could be useful for developing or improving a weighting system. Among these variables, nematode biomass is perhaps the easiest to determine because it can be calculated based on body length and the greatest body diameter (Andrassy, 1956; Ferris, 2010).

The objectives of the current study were to: (1) develop a new weighting system for nematodes on a fine taxonomic level (i.e., genus level) based on nematode generic biomass, and (2) use existing nematode community data to determine whether the biomasses of soil nematode genera can be used as weighting factors for the calculation of nematode community indices. We calculated soil nematode community indices using two contrasting weighting systems. In one system (designated the guild-based weighting system), weighting was based on nematode guilds according to Ferris et al. (2001). In the other system (designated the genus-based weighting system), weighting was based on the biomasses of nematode genera. We explored how the community indices differed depending on which weighting system was used. We also compared how the indices derived from the two weighting systems responded to specific disturbances and land uses. We hypothesized that the nematode community indices calculated with the genus-based and guild-based systems would be complementary in distinguishing the treatment effects.

2. Materials and methods

2.1. Data collection

Three raw data sets used in this research were obtained from three studies. In study 1, soil nematodes under different management practices (fertilization, cutting frequency and intensity, and irrigation) in hybrid napiergrass (*Pennisetum hydridum*) field were studied (Zhao et al., 2014b). In study 2, the impact of different land use (grassland, shrubland, and forest) on nematode communities was examined (Zhao et al., 2014a). In study 3, soil nematodes under the forest management practices included understory removal and all plants removal were studied (Zhao et al., 2011, 2013); the forest management practices included understory removal and all plants removal. The data from study 1, 2, and 3 are hereafter referred to as data set 1, 2, and 3, respectively.

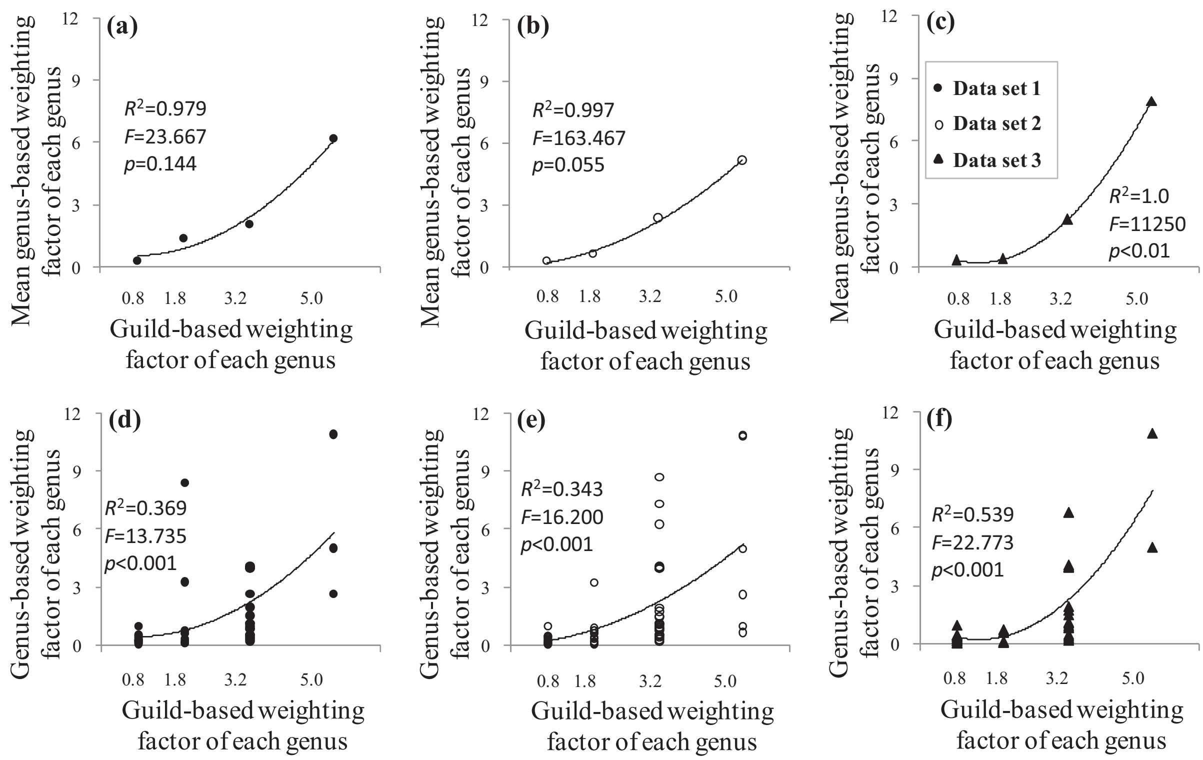

Fig. 1. Quadratic relationships between genus-based and guild-based weighting factors for soil nematodes from data set 1 (a and d), data set 2 (b and e), and data set 3 (c and f). Genus-based weighting factors in (a–c) have been averaged for each guild.

2.2. Index calculation

Nematode community indices were calculated using previously published formulas (Ferris et al., 2001; Wilson and Khakouli-Duarte, 2009):

$$\text{Enrichment index(EI)} = 100 \times \left(\frac{e}{e+b}\right) \quad (1)$$

$$\text{Structure index(SI)} = 100 \times \left(\frac{s}{s+b}\right) \quad (2)$$

$$\text{Channel index(CI)} = 100 \times \frac{\sum(\omega_{\text{Fu2}ij} \times N_{\text{Fu2}ij})}{e} \quad (3)$$

$$\text{Bacterivore index(BaI)} = 100 \times \frac{\sum(\omega_{\text{Ba2}ij} \times N_{\text{Ba2}ij})}{\sum(\omega_{\text{Ba1}ij} \times N_{\text{Ba1}ij}) + \sum(2\omega_{\text{Ba2}ij} \times \text{NBa2}_{ij})} \quad (4)$$

where 'ω' is the weighting factor of each nematode taxon, 'ij' is the number of nematode taxa in each guild and 'N' is the abundance of each nematode taxon. The values of b, e, and s are calculated as follows:

$$b = \sum(\omega_{\text{Fu2}ij} \times N_{\text{Fu2}ij}) + \sum(\omega_{\text{Ba2}ij} \times N_{\text{Ba2}ij}) \quad (5)$$

$$e = \sum(\omega_{\text{Fu2}ij} \times N_{\text{Fu2}ij}) + \sum(\omega_{\text{Ba1}ij} \times N_{\text{Ba1}ij}) \quad (6)$$

$$\begin{aligned} s = {} & \sum(\omega_{\text{Ba3}ij} \times N_{\text{Ba3}ij}) + \sum(\omega_{\text{Ba4}ij} \times N_{\text{Ba4}ij}) \\ & + \sum(\omega_{\text{Fu3}ij} \times N_{\text{Fu3}ij}) + \sum(\omega_{\text{Fu4}ij} \times N_{\text{Fu4}ij}) \\ & + \sum(\omega_{\text{Om4}ij} \times N_{\text{Om4}ij}) + \sum(\omega_{\text{Om5}ij} \times N_{\text{Om5}ij}) \\ & + \sum(\omega_{Pr3ij} \times N_{Pr3ij}) + \sum(\omega_{Pr4ij} \times N_{Pr4ij}) \\ & + \sum(\omega_{Pr5ij} \times N_{Pr5ij}) \end{aligned} \quad (7)$$

As noted above, weighting factors were determined in two ways and we refer to these as the guild-based weighting system and the genus-based weighting system, respectively. In the guild-based weighting system, weighting factors are assigned based on life strategy (primarily the trophic connectance in food webs) of each nematode guild (Ferris et al., 2001; Wilson and Khakouli-Duarte, 2009): ω_1 is 3.2, ω_2 is 0.8; ω_3 is 1.8; ω_4 is 3.2; and ω_5 is 5. In the genus-based weighting system proposed in this paper, weighting factors are assigned based on the mean fresh biomass in μg per individual nematode in each genus. The mean biomass per nematode (fresh weight, μg) of each genus was calculated as follows:

$$B = \frac{D^2 \times L}{1.6 \times 10^6} \quad (8)$$

where 'B' is the mean biomass per individual, 'D' is the greatest body diameter (μm), and 'L' is the body length (μm) (Andrassy, 1956). The biomass of each nematode genus was the average biomass of the known species of that genus. The data for 'D' and 'L' of each species were mainly obtained from Bongers (1988). When the information for 'D' or 'L' was inadequate or unavailable in Bongers (1988), the biomass of this genus was replaced with the mean biomass of the family it belongs to (Ferris, 2010). The biomasses of nematode genera in data set 1, 2, and 3 are shown in Table 1. For convenience, indices calculated for each data set using different weighting systems were distinguish as follows: (1) EI, SI, CI, and BaI for guild-based system, and (2) EI′, SI′, CI′, and BaI′ for genus-based system, respectively.

2.3. Data analysis

Quadratic regression analyses were used to examine the relationship between genus-based weighting factors and guild-based

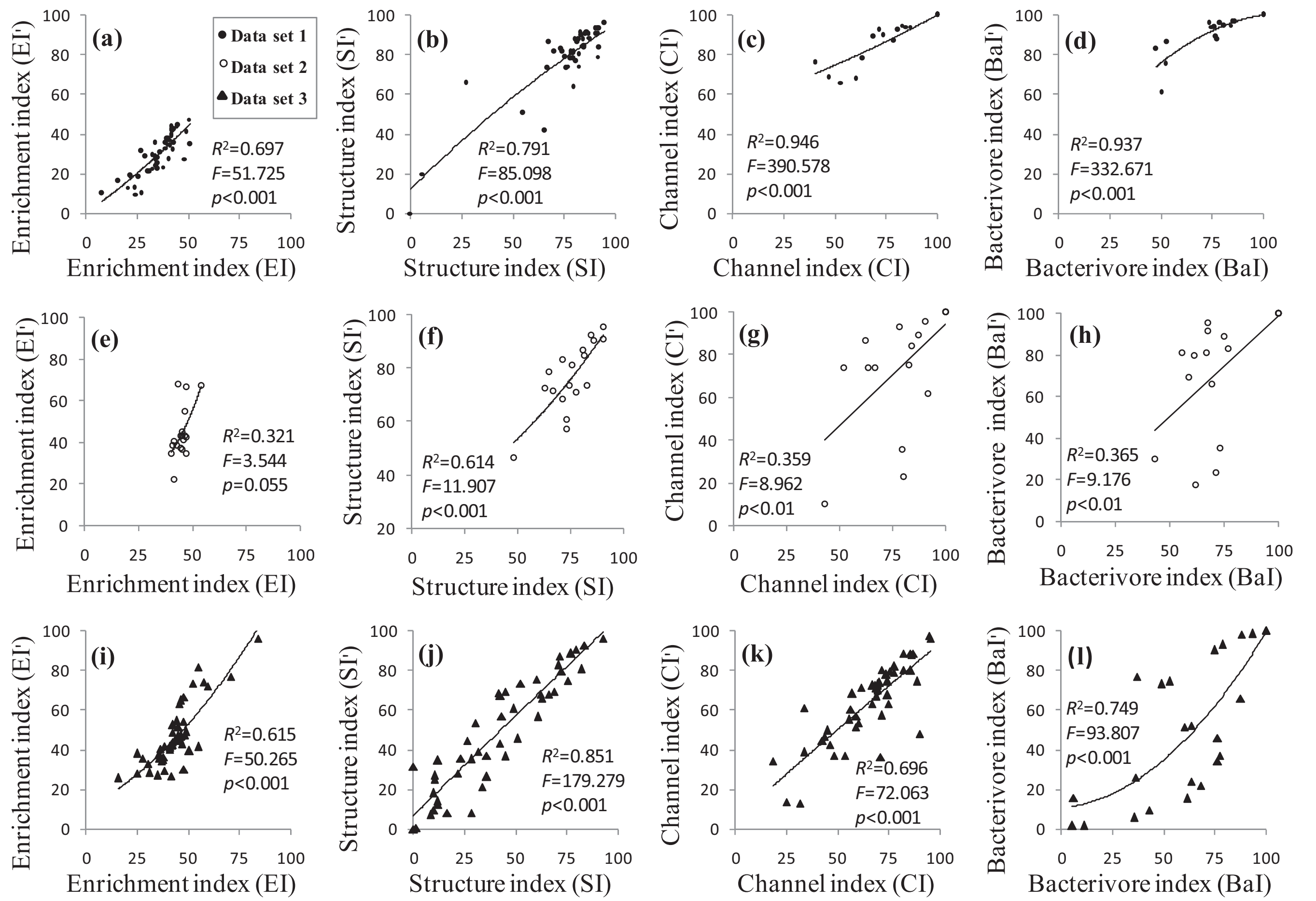

Fig. 2. Quadratic regression of nematode community indices for data set 1 (a–d), data set 2 (e–h), and data set 3 (i–l) that were calculated with a genus-based weighting system (EI′, SI′, CI′, and BaI′) vs. a guild-based weighting system (EI, SI, CI, and BaI). EI′ and EI refer to the enrichment index, SI′ and SI refer to the structure index, CI′ and CI refer to the channel index, and BaI′ and BaI refer to the bacterivore index.

weighting factors; these analyses used the genus-based weighting factor for each genus and also the mean of the genus-based weighting factors within a guild. The quadratic regression analyses were also used to determine how each nematode community index differed depending on which weighting system was used; to do this, we regressed EI′ on EI, SI′ on SI, CI′ on CI, and BaI′ on BaI for the three data sets. ANOVAs were used to analyze the effects of the four levels of each management practice on the nematode community indices derived from data set 1, to analyze the effects of land use types on the nematode community indices derived from data set 2, and to analyze the effect of forest management practices on the nematode community indices derived from data set 3. Differences among the four levels of each management practice of data set 1, among the land use types of data set 2, and among forest management practices of data set 3 were assessed by LSD. SPSS software (SPSS Inc., Chicago, IL) was used for all statistical analyses.

3. Results

The weighting factors obtained with the genus-based system were positively correlated with those obtained with the guild-based system for all the three data sets when the biomasses of individual genera were used (Fig. 1d–f) and also when the mean biomasses of all genera within a guild were used for data set 3 (Fig. 1c). The variances of generic biomasses in each guild were large for all the three data sets (Fig. 1d–f). The average generic biomasses of nematodes within the guilds with guild-based weighting factors of 0.8, 1.8, 3.2, and 5 were 0.32, 1.37, 2.05, and 6.17 μg/ind, respectively, for data set 1 (Fig. 1a), were 0.29, 0.63, 2.35, and 5.16 μg/ind, respectively, for data set 2 (Fig. 1b), were 0.34, 0.42, 2.27, and 7.94 μg/ind, respectively, for data set 3 (Fig. 1c). Quadratic regression revealed significant positive correlations ($p < 0.01$) between both variations of the indices, except EI′ and EI for data set 2 (Fig. 2).

For data set 1, the indices calculated with genus-based vs. guild-based weighting systems showed similar tendencies in response to different levels of management practices (Fig. 3). EI′ and EI were significantly affected by irrigation but not by the other management practices (Fig. 3a). SI′ and SI were significantly affected by fertilization (Fig. 3b); while SI but not SI′ was significantly affected by cutting frequency (Fig. 3b). BaI but not BaI′ was significantly affected by fertilization (Fig. 3d). For data set 2, land use type was found to only significantly affected EI′ (Fig. 4b) and SI (Fig. 4c). Land use type did not significantly affect CI, CI′, BaI, or BaI′ (Fig. 4e–h). For data set 3, vegetation removal significantly affected SI and SI′ (Fig. 5c and d) in both the wet and dry seasons. In addition, the SI′ under control, understory removal, and all plants removal treatments were differed significantly in the dry season (Fig. 5d). However, the SI under control and understory removal treatments were not significantly different in the dry season (Fig. 5c). Moreover, vegetation removal apparently affected the CI′ rather than the CI in the dry season; and vegetation removal apparently affected the CI rather than the CI′ in the wet season (Fig. 5e and f).

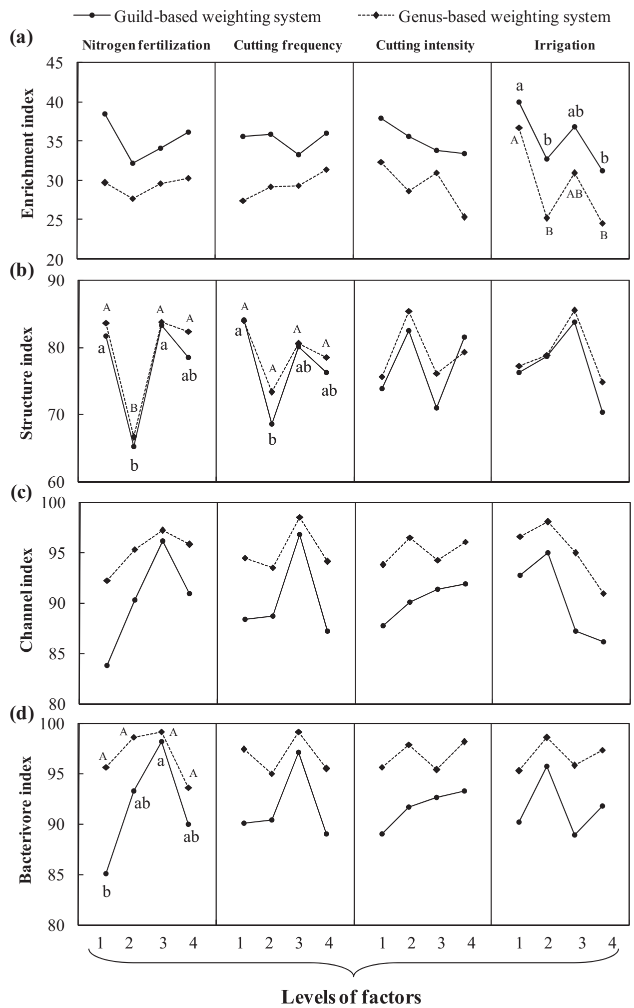

Fig. 3. Nematode enrichment index (EI and EI′) (a), structure index (SI and SI′) (b), channel index (CI and CI′) (c), and bacterivore index (BaI and BaI′) (d) as affected by four levels of nitrogen fertilization, cutting frequency, cutting intensity, and irrigation in a hybrid napiergrass field (data set 1). EI, SI, CI, and BaI were calculated using guild-based weighting factors, and EI′, SI′, CI′, and BaI′ were calculated using genus-based weighting factors. In each panel, indices derived with guild-based weighting factors and having different lowercase letters, and indices derived with genus-based weighting factors and with different uppercase letters, are significantly different at $p < 0.05$.

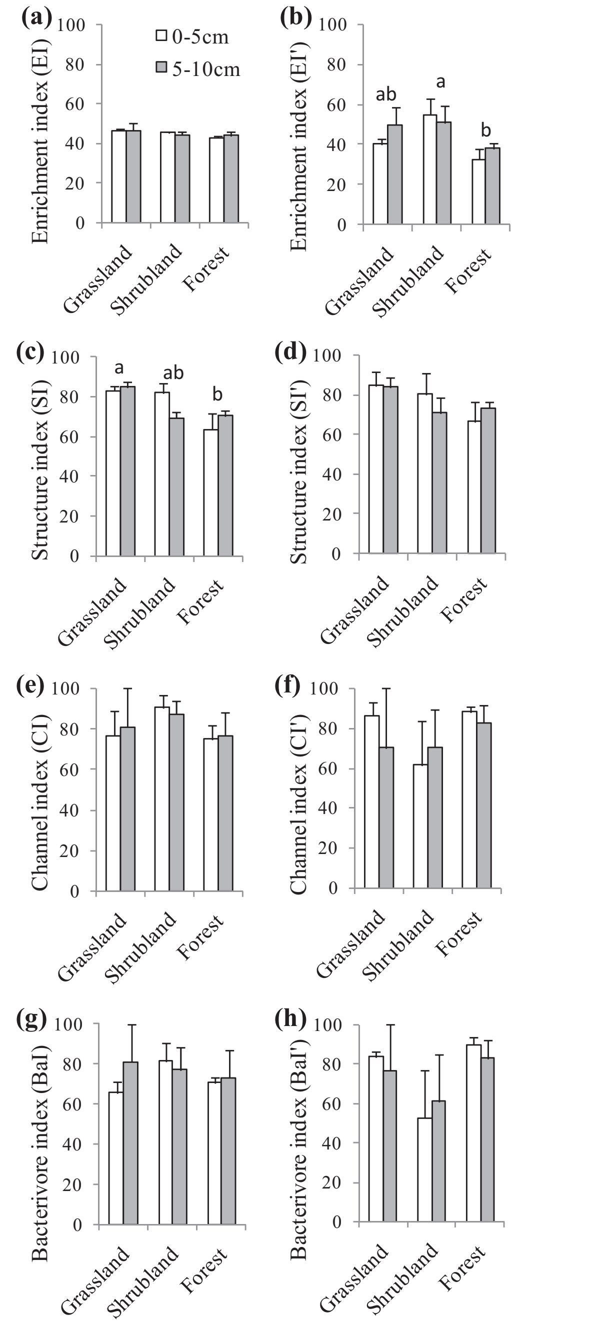

Fig. 4. Nematode enrichment index (EI and EI′) (a and b), structure index (SI and SI′) (c and d), channel index (CI and CI′) (e and f), and bacterivore index (BaI and BaI′) (g and h) at 0–5 and 5–10 cm soil depths of grassland, shrubland, and forest ecosystems of data set 2. EI, SI, CI, and BaI were calculated used guild-based weighting. EI′, SI′, CI′ and BaI′ were calculated using genus-based weighting. Bars indicate standard errors of means. In each panel indices of different ecosystems with different letters are significantly different at $p < 0.05$.

4. Discussion

The regression of guild-based weighting factors on genus-based weighting factors yielded very high R^2 values for all the three data sets, indicating that the genus-based weighting method is a refinement of the guild-based weighting method rather than a radical change from that method. Consistent with our results, Ferris et al. (2001) found a significant correlation between the average guild biomass and guild-based weighting factor of structure component, which was used to support the use of guild-based weighting. However, the genus-based weighting factors varied greatly among the genera within each guild. The information represented by that variability could affect nematode community indices because soil nematode biomass reflects food intake and other important aspects of nematode biology. Therefore the estimates of nematode community indices may be more accurate with genus-based weighting than with guild-based weighting. In support of this, previous studies have often reported that the expected responses of soil nematode genera to a specific disturbance (based on their guilds) differed from their actual responses. For instance, *Aphelenchoides*, *Eucephalobus*, *Heterocephalobus*, and *Wilsonema* were sensitive to tillage but *Anatonchus*, *Clarkus*, *Epidorylaimus*, *Mylonchulus*, and *Tylencholaimellus* were not sensitive to tillage, which contrasted to their inferred responses (Fiscus and Neher, 2002). Additionally, several enrichment opportunistic genera, such as *Mesorhabditis* and *Panagrolaimus*, might not be favored by nitrogen enrichment (Zhao and Neher, 2013). Additionally, the guild-based weighting factor for the Ba1 guild (3.2) is based on the fecundity of Ba1 and is four time greater than the weighting factor for Ba2 nematodes (Ferris et al., 2001, 1996) but is equivalent to the weighting factor of *cp*4

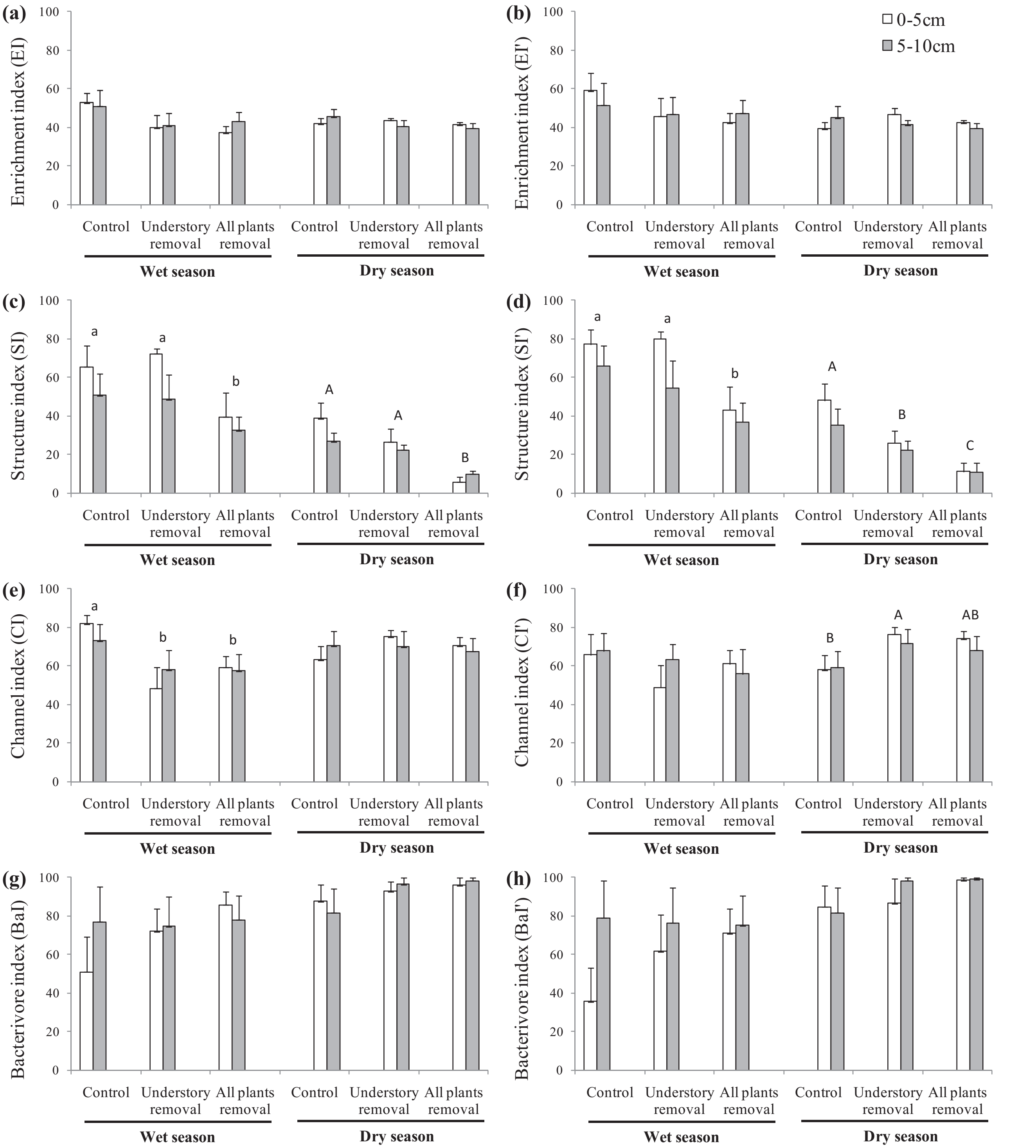

Fig. 5. Nematode enrichment index (EI and EI′) (a and b), structure index (SI and SI′) (c and d), channel index (CI and CI′) (e and f), and bacterivore index (BaI and BaI′) (g and h) under control, understory removal, and all plants removal treatments at 0–5 and 5–10 cm soil depths in the wet season and dry season in plantations of mixed native tree species of data set 3. EI, SI, CI, and BaI were calculated used guild-based weighting. EI′, SI′, CI′ and BaI′ were calculated using genus-based weighting. Bars indicate standard errors of means. Different lowercase and uppercase letters indicate significant ($p < 0.05$) differences among treatments in wet season and dry season, respectively.

nematodes. However, the ratio of the Ba1 fecundity to Ba2 fecundity could differ depending on which genera or species are present in the soil. In this study, the weighting factor would be 0.48 for Ba1 and 2.32 for *cp*4 nematodes in study 1, 2.77 for Ba1 and 2.20 for *cp*4 nematodes in study 2, and 2.55 for Ba1 and 2.16 for *cp4* nematodes in study 3 (data not shown). The contrasting weighting factors for Ba1 were primarily due to the difference in Ba1 nematode genera in these data sets. Although the weighting factors for *cp4* nematodes did not varied as much as those for Ba1 of these data sets, there was still substantial difference among the three data sets, which also were due to the difference in *cp4* nematode genera in these data sets.

When calculated with guild-based and genus-based weighting factors, the patterns obtained for the nematode community indices were usually similar but the index values were different. For instance, the shrubland and forest had contrasting enrichment index with genus-based weighting factors rather than with guild-based weighting factors in the study 2 (Fig. 4a and b). Additionally, understory removal significantly reduced the structure index and channel index with genus-based weighting factors in the dry season (Fig. 5d and f); but the effects of understory removal on the structure index and channel index with guild-based weighting factors in the dry season were not significant in the plantations of mixed native tree species in the study 3 (Fig. 5c and e). Relative to respective indices calculated with guild-based weighting factors, the enrichment index with genus-based weighting factors was more sensitive to land uses; and the structure index and channel index with genus-based weighting factors were more sensitive to vegetation management practices, especially in the dry season. These results were consistent with our hypothesis. Conversely, the genus-based weighting system did not always successfully include useful information. For example, the grassland and forest had contrasting structure indices with guild-based weighting factors rather than with genus-based weighting factors in the study 2 (Fig. 4c and d). In addition, vegetation management significantly affected the channel index with guild-based weighting factors rather than that with genus-based weighting factors in the wet season in the study 3 (Fig. 5e and f). Apparently, the most likely reason for the contrasting results with the two weighting systems was that the weighting factors of the two systems were different.

As noted above, the sensitivity of the indices calculated with one of the weighting systems was not always superior to the sensitivity of the indices calculated with the other weighting system in the current study. One likely reason was that the mean biomass of a nematode genus, which was calculated using documented body size data from literature rather than measured body size data of each specimen, did not represent the real biomass of the nematode genus in a given soil sample. Theoretically, weighting of nematodes on a fine taxonomic level (e.g., genus and species levels) would generate a more accurate evaluation of soil nematode communities than weighting on a coarse taxonomic level (e.g., functional guild level), because the higher the level of taxonomy, the greater the variance of nematodes in the taxon (may vary in biomass, fecundity, and other properties). Additionally, the body sizes of nematodes even within one genus varied greatly (Bongers, 1988; Zhao et al., 2015). Therefore, weighting each specimen may be an unbiased evaluation of nematode community and may be the most accurate approach for a particular study. For the studies that did not measure the body sizes of the each specimen of nematodes (similar to the present study), it would be a more effective way to integrate both weighting systems for the calculation of the nematode community indices to reveal significant treatment effects.

In summary, the proposed method the proposed method or genus-based method which used biomasses of soil nematode taxa as weighting factors is a refinement of the guild-based method of Ferris et al. (2001). The proposed method weights soil nematodes in a fine taxonomic level (genus) rather than in a coarse taxonomic level (functional guild). It was suggested that both weighting systems should be used for the calculation of the nematode community indices in a study in order to better distinguish the treatment effects. In addition, weighting systems based on life history strategies have also been used for other soil organisms, such as mites, springtails and protozoa (Ruf, 1998; Siepel, 1995; Wodarz et al., 1992). Our study could provide insights of methodology for developments and/or refinements of weighting systems of soil organisms.

Acknowledgements

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