



Phylogenetic structures of soil nematode communities along a successional gradient in an unreclaimed copper mine tailings site



Jin-tian Li, Shao-peng Li, Yong-jian Chen, Pu Jia, Zheng-shuang Hua, Sheng-long Wang, Yong-sheng Song, Bin Liao, Wen-sheng Shu*

State Key Laboratory of Biocontrol and Guangdong Key Laboratory of Plant Resources, School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, PR China

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ABSTRACT

Analysis of the phylogenetic structure of biological communities by examining the extent to which community members are more closely related (phylogenetically clustered) or less closely related (phylogenetically overdispersed) than expected by chance has recently been proven to be a promising approach to gain insight into the factors governing the community assembly. However, to date there aren't any studies that have quantitatively examined the community structure of soil nematodes in a phylogenetic framework, despite their crucial roles in soil food webs and nutrient cycling processes. Here, we explored the phylogenetic structures of soil nematode communities along a successional gradient in an unreclaimed copper (Cu) mine tailings site to reveal the potential determinants of the soil nematode community assembly. Unexpectedly, we found little evidence that the phylogenetic distance of the co-occurring soil nematodes increased along this gradient. In contrast, phylogenetic structures of the soil nematode communities along the gradient appeared to show a weak tendency toward clustering (i.e. nematodes tend to co-occur with other closely related nematodes more often than expected by chance). On the other hand, when different soil nematode groups characterized by feeding habits were taken into account separately, we unveiled contrasting phylogenetic community structures: bacterial-feeding (BF), plant-feeding (PF), and omnivore-predator (OP) nematode communities tended to be phylogenetically clustered; whereas, fungal-feeding (FF) nematode communities exhibited a tendency toward phylogenetic overdispersion. Moreover, the net relatedness indices of nematode communities characterized by different feeding habits were shown to be correlated with distinct soil chemical properties (such as diethylene triamine pentaacetic acid extractable Cu for BF and cation exchange capacity for FF), indicating that the assembly processes of these communities were not neutral and might have been largely driven by the respective soil chemical properties. Collectively, our results provided novel insight into the factors driving the assembly of soil nematode communities, highlighting the potential for future studies on nematodes to benefit from a community phylogenetics approach.

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1. Introduction

Understanding the factors that determine soil biological community composition and structure is a central theme in soil biology. Although both deterministic and stochastic factors are thought to play important roles in shaping biological community composition and structure, there is still extensive debate about the relative importance of these various factors (Hille Ris Lambers et al., 2012).

Traditional niche-based theories propose that deterministic factors, such as interspecific competitions and environmental filters, drive the assembly of communities, and thus govern community composition and structure (Chesson, 2000). In contrast, contemporary neutral theories emphasize the importance of stochastic factors, such as chance colonization, random extinction, and ecological drift (Hubbell, 2001; Zhou and Zhang, 2008).

It is not until recently that ecologists began to infer the relative importance of deterministic and stochastic factors in shaping community composition and structure from the patterns of phylogenetic community structure, by integrating the newly available phylogenetic information with community data (Webb, 2000; Webb et al., 2002). In the 'ecophylogenetic' framework

* Corresponding author.

E-mail addresses: shuws@mail.sysu.edu.cn, zsushuwensheng@163.com (W.-s. Shu).

developed by Webb and his coworkers (Webb et al., 2002), if traits related to community assembly are phylogenetically conserved, then: (i) a community consisting of species that are more closely related than expected at random (i.e. phylogenetic clustering) is presumed to be largely structured by environmental filtering; (ii) a community comprising species that are less closely related than expected by chance (i.e. phylogenetic overdispersion) is assumed to be largely shaped by competitive exclusion; and (iii) a community consisting of species that are randomly distributed on the phylogeny (i.e. random phylogenetic dispersion) is expected to be largely generated by neutral assembly, where stochastic factors dominate. This heuristic framework for phylogenetic community ecology can serve as a simple and efficacious means to: (i) assess whether communities are largely shaped by niche-based assembly rules or by neutral processes; (ii) reveal the importance of evolutionary history of species in the assembly process of communities; and (iii) infer regional, continental and global processes occurring over deep evolutionary time scales from short-term local processes (Cavender-Bares et al., 2009). It has been widely employed to document patterns of phylogenetic structures of communities of different major taxa and trophic levels in a broad range of contexts (see Vamوسي et al., 2009 for a recent review), providing a more nuanced view of the mechanisms dominating the assembly of communities.

The phylum Nematoda is the second largest one in the animal kingdom beneath the Arthropoda (Hugot et al., 2001) and nematodes are most ubiquitous invertebrates in various habitats (Lee, 2002). Although most nematodes living in soils are very small (typically 50 μm in diameter and 1 mm in length; Ingham, 2000), they play a core role within the soil food webs by linking primary consumers (bacteria and fungi) to higher trophic levels and perform crucial functions in nutrient cycling in soils through mineralizing elements locked in microbial biomass (Yeates, 2010). Indeed, nematodes are well represented in all feeding levels of the soil food webs. Based on their feeding habits, nematodes can be roughly divided into four trophic groups: bacterial-feeding (BF), fungal-feeding (FF), plant-feeding (PF), and omnivore-predator (OP), with members of each group having highly similar feeding traits (largely buccal size and buccal armature; Yeates et al., 1993; Bongers and Bongers, 1998; Lee, 2002).

There is considerable evidence that the composition and structure of soil nematode communities can be used to develop indices that are indicative of status and function of the soil food web (Ferris et al., 2001). For this reason, soil nematode community structure has been proposed as a bioindicator of soil disturbance, nutrient pulse and pollution (Bongers and Ferris, 1999; Ekschmitt et al., 2001). Despite these, we still have a relatively limited understanding of the factors that govern the community assembly of nematodes in the environment. Continuous efforts had been made to improve our knowledge about the effects of biotic and abiotic factors on soil nematode community composition. For example, Viketoft et al. (2009) found that aboveground plant identity had stronger impacts than plant diversity on soil nematode community composition, while Veen et al. (2010) revealed that vertebrate herbivores (cattle and rabbits) could alter soil nematode community composition through modifying associated plant community composition. On the other hand, it has been frequently demonstrated that abiotic factors (such as soil moisture, nitrogen and carbon) also may have a substantial influence on soil nematode community composition (Landesman et al., 2011; Wei et al., 2012; Viketoft, 2013). To date, however, little is known about the major factors driving the assembly of nematode communities, and no studies have quantitatively examined the structure of soil nematode communities in a phylogenetic framework. This represents a critical gap in our knowledge on soil biology.

To help fill this gap, we characterized the potential patterns of phylogenetic structure of soil nematode communities along a successional gradient in an unreclaimed copper (Cu) mine tailings site. The mine tailings site was chosen since it has similar characteristics to primary soils (e.g. macronutrients deficiency, low soil organic matter and a lack of seed bank) and is undergoing a natural succession that is comparable to primary succession (Huang et al., 2011), providing an excellent opportunity to study the shifts of phylogenetic structure of soil nematode communities undergoing primary succession. In addition, mine tailings sites often have a reduced complex soil nematode community (Hohberg, 2003; Shao et al., 2008), where more complete sampling might be feasible (Vamوسي et al., 2009). We expect that the major driver of the assembly of nematode communities will shift from environmental filtering to competitive exclusion along the successional gradient (Letcher, 2010; Norden et al., 2012), since the overall environmental conditions of the mine tailings site would have become less hostile as the primary succession proceeded (Huang et al., 2011). If so, the phylogenetic structure of soil nematode communities is likely to exhibit a tendency toward overdispersion along the successional gradient, considering that less hostile environment tends to favor phylogenetic overdispersion (Webb et al., 2002; Cavender-Bares et al., 2009; Letcher, 2010; Norden et al., 2012).

2. Materials and methods

2.1. Study site

Our study was conducted in an unreclaimed Cu mine tailings site, located in Anhui Province, China (30°54' N, 117°53' E). The site covers an area of 36.4 ha, was used to deposit mine tailings from the Shi-zi-shan Cu Mine near Tong-ling City and has been abandoned to revegetate naturally since November 1991. This region is characterized by a humid subtropical climate, with a mean annual temperature of 16.2 °C and a mean annual precipitation of 1340 mm.

2.2. Sampling

In a field survey conducted in 2007, we found that the unreclaimed mine tailings site consisted of bare Cu mine tailings and various patches colonized by algae, algae-mosses, mosses and vascular plants, which can be considered to represent sequential stages of primary succession on highly degraded lands (Zaady et al., 2010; Huang et al., 2011; Kuske et al., 2012). To investigate the potential patterns of phylogenetic structure of soil nematode communities undergoing primary succession by a space-for-time substitution approach, we collected soil samples along this successional gradient in the unreclaimed Cu mine tailings site (refer to Huang et al., 2011 for some more details): bare mine tailings (BMT), patch with colonization of algae (PCA), patch with colonization of algae-mosses (PAM), patch with colonization of mosses (PCM), and patch with colonization of vascular plants (PCV; dominant species: *Imperata cylindracavar* var. *major*, *Zoysia japonica*, *Hippochaete ramosissimwn*, and *Cynodon dactylon*). For each seral stage along the successional gradient, five 2 m \times 2 m sampling plots were randomly selected. Within each sampling plot, 5 soil samples were collected from the top 20-cm layer by scraping off surface material with a sterile spatula, and mixed thoroughly in the field to make a composite soil sample, which was divided into two subsamples and used for nematode and chemical analyses respectively.

2.3. Nematode identification

Nematodes were extracted from 100 g soil of each subsample for nematode analysis using the Baermann funnel method

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