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Soil nematode assemblages as bioindicators of primary succession along a 120-year-old chronosequence on the Hailuogou Glacier forefield, SW China

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A B S T R A C T

Successional dynamics in terrestrial ecosystems is important for interactions between aboveground and belowground subsystems. In this study, nematode communities in a *Hailuogou Glacier Chronosequence* from seven stages were investigated to determine whether changes in soil phosphorus (P) and nematode assemblages parallel those observed in aboveground communities, and whether the primary succession in this chronosequence has entered a retrogressive phase after 120 years of succession. The initial 40-year succession, including stages 2, 3 and 4, can be viewed as a build-up phase. Especially at stage 3, vegetation succession from grassland to forest accelerated the accumulation of plant litter and bioavailable P, paralleled with a sharp increase in nematode abundance. The mature phases covering stages 5, 6 and 7 displayed most balanced nematode communities, in which abundance, taxon richness, maturity index and structure index were at highest. However, the last stage 7 appeared to show some retrogressive characteristics, as suggested by the reduced bioavailability of P and a significant decrease in nematode densities, along with the disappearance of some rare genera of nematodes from higher trophic guilds, resulting in decreases in the nematode channel ratio, plant parasite index and enrichment index. Thus, the *Hailuogou Glacier Chronosequence* may enter its retrogressive phase during the next decade or century. A bacterial-based nematode energy channel dominated the chronosequence during the development; by contrast, a fungivore-based channel was activated at the early and late stages, because fungivores are better adapted to nutrient-poor environments. Our results demonstrated that different nematode guilds have contrasting responses to chronosequence stages, possibly due to their different responses to bottom-up and top-down controls. Furthermore, soil nematode communities could be used as sensitive bioindicators of soil health in glacial-retreat areas.

1. Introduction

Elucidating the driving factors of successional dynamics in terrestrial ecosystems is an important issue in ecology, as such knowledge is expected to offer fundamental clues to understanding some basic questions about nutrient limitation that may develop during ecosystem succession: what is the rate of limitation over time and how do species and ecosystems respond to nutrient limitation over successional time (De Deyn et al., 2003)? In some chronosequences, the simultaneous availability of successional stages provides necessary conditions to use a “space-for-time substitution” approach as an alternative for long-term studies on plant and soil biota succession (Pickett, 1989). Despite some methodological shortcomings, this approach is often considered useful for determining long-term successional changes (Walker et al., 2010). The *Hailuogou Glacier Chronosequence*, located on the

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south-eastern fringe of the Tibetan Plateau, provides an excellent place to study the relationship between vegetation succession and soil development (Luo et al., 2012; Zhou et al., 2013; Prietzel et al., 2013a, 2013b). Spatial differences in the lithology of parent rocks, topography, soil-water conditions and climate can be ignored because of small gradients in length (2 km), width (50–200 m) and elevation (127 m from 2855 to 2982 m). Along the approximately 2 km-long belt, a series of sites representing different stages of vegetation succession from pioneer to climax vegetation communities can be readily recognized (Luo et al., 2012). The relatively mild and humid climate on this site allows rapid moraine colonization by plants, causes the accumulation of organic material, and promotes relatively rapid soil development (Alexander and Burt, 1996; Luo et al., 2012). Several studies have investigated how communities develop during primary succession, including pedogenesis (He and Tang, 2008), soil respiration (Luo et al., 2012), plant succession simulation (Yang et al., 2014), soil microbial changes (Zhang et al., 2010), and the availability and transformation of essential nutrients, particularly phosphorus and sulfur speciation (Zhou et al., 2013; Prietzel et al., 2013a, b). However, successional studies have rarely investigated the responses of soil fauna communities to different development stages of ecosystems, and whether these changes parallel those observed in aboveground communities.

Interactions between aboveground and belowground subsystems contribute to ecosystem functioning (De Deyn and van der Putten, 2005). Soil nematode communities are useful biological indicators of soil health, because they form a dominant group of soil organisms and live in various types of soil, including chemically contaminated soil (Yeates, 2003). These communities also represent key links in soil food webs, such as herbivores, bacterivores, fungivores, omnivores and predators, and their trophic structures are closely correlated with soil ecosystem processes (Yeates, 2003). Furthermore, nematodes have short generation times and are sensitive to environmental changes; thus, they can provide adequate resolution required to detect changes in soil communities (Bonger and Ferris, 1999; Williamson et al., 2005). The quality and quantity of organic matter entering soil food webs possibly alter nematode communities (Ugarte et al., 2013; Zhao et al., 2014). Thereby, low ratios of C:N and soluble phenolics:N in soil are often found in forb communities (Eskelinen et al., 2009). By contrast, high ratios are generally observed in shrub land and tree communities. Changes in those ratios may markedly affect soil biota communities, leading to a shift between bacterial and fungal dominated assemblages. There is evidence of more efficient adaptation of fungal-based channels when compared to bacterial-based channels in resource-poor conditions (Sun et al., 2013; Carrascosa et al., 2014). Meanwhile, microbe-feeders are strongly regulated by the top-down control of predators (both top predators and omnivores, or predators that feed on more than one trophic level) (De Mesel et al., 2004). Thus, different trophic groups of nematodes may show contrasting responses to chronosequence stages, as their relative responses to bottom-up and top-down controls differ. Soil organisms are also supposed to play significant roles in nutrient cycling, which may affect the productivity and competition of plant assemblages, with potential effects on vegetation trajectories (Bradford et al., 2002; van der Heijden et al., 2008). However, few studies have considered a single conceptual framework relating both above- and below ground linkages to plant succession.

Furthermore, after a long-term absence of catastrophic disturbances, the maximal plant biomass phase is often followed by a phase of ecosystem decline or a period of 'ecosystem retrogression', during which a long-term reduction in plant biomass and ecosystem process rates occurs (Vitousek et al., 2010). Such decline phases have seldom been compared with build-up phases. For this reason, the former remains poorly understood. It is currently believed that this decline is associated with diminishing plant resources, particularly as for the availability of P, as chronosequences develop (Richardson et al., 2004). However, previous studies on the *Hailuogou Glacier Chronosequence* estimated that biomass accumulation on the oldest sites gradually continues to increase (Luo et al., 2012). Zhou et al. (2013) also found that annual P and nitrogen (N) requirements for plant growth are smaller than the bioavailable stocks of P and N, thus demonstrating that the bioavailable P and N pool of soil presently meets the requirements for plant-growth at the 120-year-old site. However, rapid carbon (C) and N accumulation on the Hailuogou Glacier (He and Tang, 2008), as detected also in many other young chronosequences, and the great increases in soil C:P and N:P ratios in the A horizon at later stages (Zhou et al., 2013) show that future plants might be limited by bioavailable P as C and N deposition. Thus, nematode assemblages, which are vulnerable to environmental changes, together with nutrient dynamics can be used to predict, whether the soil ecosystem in the *Hailuogou Glacier Chronosequence* has entered retrogressive stages.

In the present study, soil properties and nematode communities were examined in the well-characterized *Hailuogou Glacier Chronosequence* after 120 years of succession to test the following hypotheses: (1) based on sensitive nematode assemblages and soil P availability, the *Hailuogou Glacier Chronosequence* has entered a decline phase, and the chronosequence can be divided into distinct build-up and retrogressive stages; (2) soil nematode communities follow the changes in soil fertility and vegetation biomass at different stages of primary succession, thereby highlighting the importance of resource availability; (3) different trophic groups display contrasting responses along the chronosequence, because these groups are affected, to varying degrees, by bottom-up control relative to top-down control and by abiotic factors. Our research has implications for integrated studies on biogeochemical impacts of vegetation changes and belowground communities. Further, our results will contribute to improved predictions of the direction and intensity of primary succession, and also to improved management practices related to nutrient limitation during long-term soil development.

2. Materials and methods

2.1. Study area

The Gongga Mountain (29°30′ to 30°20′ N, 101°30′ to 102°15′ E, 7556 m a.s.l), located on the south-eastern fringe of the Tibetan Plateau, is the highest peak in the eastern part of the Tibetan Plateau and the Hengduan Mountain. The Gongga Mountain lies in the transition zone of the Tibetan Plateau Frigid Zone and the Warm-humid Subtropic Monsoon Zone (Fig. 1). The Hailuogou Glacier, which flows down to the eastern slope of the Gongga Mountain, is the longest monsoonal temperate glacier in the Hengduan Mountain Region (Li et al., 2010). The mean annual air temperature is 3.8 °C, with minimum and maximum means of −4.3 °C in January and 11.9 °C in July, respectively. The total annual precipitation is approximately 2000 mm, rainfall mainly occurring from June to September. The observed recession of the Hailuogou Glacier began in about A.D. 1823, and has accelerated markedly since the early 20th century. This study was conducted on seven sites undergoing long-term primary succession stages from pioneer communities to climax vegetation communities (Fig. 1).

- Stage 1 spans the first 3 years after the glacial retreat. This stage is characterized by coarse gravelly sand and bare soil with some mosses covering 1–5% of surface area.