



Micro-arthropod community responses to ecosystem retrogression in boreal forest



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ABSTRACT

Explaining the variation in communities of soil organisms across plant communities or ecosystems remains a major challenge for ecologists. Several studies have explored how soil communities are affected along ecosystem successional gradients but most of these are based on relatively short term chronosequences. To address the impact of ecosystem age on micro-arthropod communities, we utilized a 5000 year old post-fire chronosequence, which consists of thirty lake islands differing greatly in time since fire in the boreal forested zone of northern Sweden. The Acari community did not change along this chronosequence, indicating that Acari rapidly (<60 yr) reach equilibrium after forest fire and that they are relatively unresponsive to subsequent long term changes in plant community composition and soil quality. The Collembola community composition, however, showed greater responsiveness to the chronosequence and this was best explained through their functional traits. Notably, the youngest (most recently burned) islands, which had the highest ecosystem productivity and fungal mass turnover, were dominated by soil-dwelling (eu-edaphic) Collembola species that are best positioned to take advantage of resource input to the soil. Although plant community characteristics did not emerge as powerful drivers of the Collembola community, we found that Collembola community composition was related to the quality (N and P) of the soil substrate, which reflects a long term legacy of the plant community. Collembola life history characteristics proved to be important for understanding how abundances of different taxa varied relative to one another across the gradients of plant diversity and substrate quality gradients that occur across long-term chronosequences. The causal connection between vertical stratification of Collembola and substrate quality is at present unclear but is likely to be related to their feeding preferences and microhabitat conditions. Because the soil-dwelling Collembola showed a strong decline in abundance with ecosystem retrogression while surface-dwelling Collembola did not these two life history groups may operate as functionally distinct groups within the soil food web across these long-term chronosequences.

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1. Introduction

Explaining the high diversity and spatial variation of soil organisms within ecosystems and across regional scales is still a major challenge for ecologists. A large part of this challenge arises from the variation in environmental filters behind soil community

assembly that exist across space and time (Ettema and Wardle, 2002; Bardgett *et al.*, 2005). Soil quality and the presence, productivity and diversity of plants are assumed to be the major drivers behind the community composition of soil animals at local scales (Wardle *et al.*, 1999; Nielsen *et al.*, 2010, 2012; Berg, 2012), because in combination they determine habitat and resource availability. However, historical events can determine the strength of these drivers at larger regional scales (Zaitsev *et al.*, 2013). Therefore, to understand the drivers of diversity and community composition of soil animals we need to not only identify the potential environmental filters that exist at present but recognize the

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role of historic events that helped to create these environmental filters and how these may have changed across time.

Studies of ecosystem succession, such as through the use of chronosequences, often enable effective evaluation of the drivers of soil animal communities. There are a variety of reported responses of the soil animal community to successional gradients, which emerge because different successional gradients differ in various factors such as the type of vegetation present, abiotic properties and the time span of the succession (Hågvar, 1982; Hågvar and Abrahamsen, 1984; Zaitsev et al., 2002; Hågvar et al., 2009; Schrama et al., 2012; Zaitsev et al., 2013) as well as the nature of the disturbance that initiated the succession (Chauvat et al., 2011; Perez et al., 2013). Further, most studies on how soil animal communities respond to succession have focussed on their composition, species richness and diversity, while few have focused on the functional trait spectra of soil organisms, despite the insights that can be gained about community responses through the use of trait-based approaches (McGill et al., 2006; Ackerly and Cornwell, 2007; Suding et al., 2008; Messier et al., 2010). For instance, grouping micro-arthropod species according to their vertical distribution across the soil-litter profile (e.g., into epi-edaphic, hemi-edaphic and eu-edaphic life history categories) incorporates various traits related to physiological acclimation and dispersal ability (Gisin, 1943; van Dooremalen et al., 2013) and has been very successful in explaining community responses to changes in plant diversity, soil quality, moisture availability, habitat fragmentation and disturbances (Berg and Bengtsson, 2007; Krab et al., 2010; Makkonen et al., 2011; Bokhorst et al., 2012, 2013). Eu-edaphic or soil-dwelling species which feed on fungi and plant roots should be most responsive to soil quality and root exudates (Milcu et al., 2010) while hemi- and epi-edaphic species that live in the litter layer and associated plants may benefit from a greater diversity in habitat structure provided by aboveground plant parts (Sabais et al., 2011).

Our efforts to explore soil community responses along gradients of vegetation succession would benefit from utilizing long-term chronosequences that incorporate a wide range of plant diversity and soil fertility and that also include large potential shifts in functional traits of the soil community. In very long term chronosequences (i.e., where ecosystems have remained undisturbed for millennia or beyond) ecosystem succession proceeds to a state of 'ecosystem retrogression' that is characterized by increasing limitation of nutrients (notably nitrogen (N) and phosphorus (P)), impairment of decomposition processes, and reduced plant standing biomass and productivity (Walker et al., 1987; Wardle et al., 2004; Peltzer et al., 2010). Several long term chronosequences that have undergone retrogression have been identified in a range of ecosystems around the world (Walker and Syers, 1976; Vitousek et al., 1995; Parfitt et al., 2005; Selmanns and Hart, 2010; Laliberté et al., 2012) and these sequences show at least partly similar responses for a range of aboveground and belowground properties. Retrogressive chronosequences allow for powerful tests of how belowground communities respond to long term changes in the plant community and soil environment, without the strong legacies of human activity often present in shorter term chronosequences. A handful of studies have explored the responses of nematode communities and soil macrofauna to ecosystem retrogression (Williamson et al., 2005; Doblas-Miranda et al., 2008; Jonsson et al., 2009) but to our knowledge the response of micro-arthropod (mite and springtail) communities remains largely unexplored. This is despite their high diversity and crucial role in driving belowground ecosystem processes in many ecosystems worldwide (Filser, 2002; Wall et al., 2008).

For the present study we used a well-studied chronosequence consisting of thirty islands lacking a history of major anthropogenic disturbance in northern Sweden and spans ca. 5000 years. This

chronosequence results from the variation in fire frequency across islands with larger islands burning more frequently due to lightning strikes relative to smaller islands (Wardle and Zackrisson, 2005). This generates a chronosequence of islands differing in time since the most recent fire. As time since fire increases (and island size decreases), quality of litter inputs and litter decomposition rates diminish, leading to significant humus accumulation on the smaller islands, causing available nutrients in the soil to be locked up (Wardle et al., 2012a). In addition, there is a shift in the fungal community, with fungi that produce better protected hyphae reaching a greater abundance on the smaller islands (Clemmensen et al., 2013). Furthermore, the poorer resource quality on the smaller islands leads to reduced intensity of plant competition and greater coexistence of plant species (Wardle and Zackrisson, 2005; Wardle et al., 2008) and thus greater plant species diversity (Wardle et al., 2012a). Therefore, this island chronosequence provides a natural gradient in plant species richness, diversity and soil quality, which allows testing of the impact of these factors on the soil micro-arthropod community. We hypothesize that 1) abundances of micro-arthropods will decline with decreasing island size and as time since fire and retrogression proceeds, because of poorer quality of resources; diversity and richness of taxa will meanwhile be greater on small islands despite predictions to the contrary from island biogeography theory (MacArthur and Wilson, 1963), because of greater plant diversity and therefore habitat heterogeneity (Wardle, 2006). However, the response to island size will vary for different micro-arthropod groups and we therefore also hypothesize that 2) the community composition on the larger islands will be dominated by soil-dwelling (eu-edaphic) species due to the higher soil fertility on those islands (Hågvar, 1982) while surface-dwelling (hemi- and epi-edaphic) species will dominate the plant species-rich but less fertile smaller islands. By addressing these hypotheses we aim to provide a better insight in the driving roles of vegetation succession and ecosystem change, and concomitant shifts in plant diversity and soil quality on the community structure of soil micro-arthropods.

2. Materials and methods

The study area consisted of 30 forested islands of contrasting sizes in two neighbouring lakes in northern Sweden: Lakes Uddjaure and Hornavan (65° 55' N to 66° 09' N and 17° 43' E to 17° 55' E). All islands were formed following the retreat of land ice about 9000 years ago. The mean annual precipitation is 750 mm, and the mean temperature is 13 °C in July and –14 °C in January. The only major abiotic extrinsic factor that varies among islands is the history of lightning ignited wildfire, with larger islands having burned more frequently than smaller islands because of their larger area to intercept lightning; time since the most recent fire varies among islands from 60 to over 5000 years (Wardle et al., 1997, 2003a). Consistent with previous studies on this system (Wardle et al., 2003a; Wardle and Zackrisson, 2005; Clemmensen et al., 2013), we divided the islands into three size classes with 10 islands per class: large (>1.0 ha), medium (0.1–1.0 ha) and small (<0.1 ha), with a mean time since last major fire of 585, 2180 and 3250 years, respectively (Wardle et al., 2003a). As such, the three island size classes represent stages of early, mid and late succession respectively. On larger islands the vegetation is dominated by early successional species such as *Pinus sylvestris* and *Vaccinium myrtillus*, while late successional species such as *Picea abies* and *Empetrum hermaphroditum* dominate on small islands (Wardle et al., 1997). Previous studies on these islands have shown that as islands become smaller and time since fire increases, they enter a state of 'ecosystem retrogression' (Peltzer et al., 2010) in which there is a

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