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Positive plant microbial interactions in relation to plant performance and ecosystem function

Tree invasion of heather moorland: impacts of birch and pine on microbes, microfauna and decomposition

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Summary

Understanding links between above and belowground communities is important to be able to predict how land management may influence the diversity and activity of belowground food webs, and consequently, how associated ecosystem processes like decomposition may be affected. Changes in land management will often result in altered aboveground species richness and can transform the composition of plant communities. These changes aboveground can have both positive and negative impacts on the belowground system, and furthermore, may feedback to the plant community (Bezemer *et al.*, 2006). In turn, a large body of work has developed from experimental plant communities focusing on the relative importance of plant species richness per se and the traits of dominant plants in driving soil patterns and processes. Fewer studies have examined these relationships in relatively undisturbed semi-natural habitats and it is often questioned as to what extent findings from experimental systems can successfully explain patterns in their semi-natural counterparts.

Secondary succession from heather moorland to native woodland is an increasingly common phenomenon following changes in land management; this regeneration in upland systems is encouraged by conservation policy in the UK. The cessation of regular burning or reductions in grazing pressure in moorland habitats allows tree seedlings to invade and establish. Subsequently, plant community composition, detrital inputs and soil properties are altered as regenerating native woodland ages (Miles, 1981). The consequences of these direct and indirect effects of tree regeneration for belowground communities are poorly understood. Here, we explore the relationship between above and belowground communities in this successional system using data from: i) a correlative study on two natural chronosequences from heather moorland to birch woodland, ii) a manipulative litterbag experiment in the field examining detrital richness and composition, and iii) an outdoor mesocosm experiment comparing the effects of birch and pine saplings. The broad findings of these different approaches are discussed with the aim of disentangling the potential mechanisms by which trees may impact microbes, nematodes and decomposition.

In the chronosequence study, the development of birch stands on moorland induced a complete transformation in the composition of ground vegetation with greater species richness and a switch from *Calluna* to grass dominated cover. In addition, soil pH increased and the depth of soil organic matter was reduced. These changes in the plant community and soil properties were

associated with differences in the size and composition of the microbial community, as measured using Phospholipid Fatty Acid (PLFA) markers, and differences in nematode abundance, trophic structure and diversity (Keith *et al.*, 2009). The quantity of both total and fungal PLFAs declined from moorland to birch woodland stands. In contrast, there was an increase in total nematode abundance and the prevalence of higher trophic levels (i.e. predatory nematodes). This resulted in an apparent inverse relationship between microbial PLFAs and nematode abundance across all samples. However, despite these distinct responses to birch invasion of moorland there were increases in both the relative contribution of bacterial PLFAs and bacterial feeding nematodes to their respective groups. These findings highlight the change in the relative importance of fungal-based and bacterial-based energy channels between moorland and birch woodland. This is supported by the increase in decomposition rates and decrease in the depth of organic matter from moorland to birch woodland.

Since changes in PLFA and nematode composition were associated with the change to more productive ground vegetation and its higher litter quality under birch, and because nematode diversity was also positively related to plant diversity (Keith *et al.*, 2006), a manipulative litterbag experiment was carried out at one of the chronosequence sites to examine the role of detrital richness and composition in shaping the decomposer system. The leaf litter of five species from secondary succession on moorland was used (*Calluna vulgaris, Vaccinium myrtilus, Deschampsia flexuosa, Betula pendula, Pinus sylvestris*) with replication of the 31 possible litter combinations. Increasing plant litter richness generally had little effect on the quantity of PLFAs, nematode abundance and decomposition rates in litterbags. However, while there were limited effects on the *mean* there were consistent decreases in the *variability* of nematode abundance and decomposition rates with increasing litter richness (Keith *et al.*, 2008). This suggests that variability in the decomposer system may be buffered, and hence stability increased, with greater litter richness (McCann, 2000; Keith *et al.*, 2008).

Litter composition had a far stronger influence on PLFAs (both fungal and bacterial) and decomposition in litterbags. The presence of *Deschampsia* had the greatest impact with positive effects on bacterial and fungal PLFAs, and decomposition; *Betula* had similar effects but these were less pronounced. Conversely, the presence of *Calluna* and *Vaccinium* had a negative effect on decomposition, while *Calluna* and *Pinus* had a negative effect on bacterial PLFAs. In turn, *Calluna* and *Pinus* litter were found to promote a greater importance of the fungal-based energy channel compared with the other litter species. A trend of increased fungivorous nematode abundance in *Calluna* and *Pinus* also suggests that litter effects on nematode community structure may be mediated via the microbial community. These findings are in agreement with the increased importance of the bacterial-based energy channel from *Calluna*-dominated moorland to birch woodland. The differences demonstrate that functional composition or identity of the dominant litter species is likely to be more important than litter richness in determining both the structure of the decomposer community and decomposition rates.

We conducted a mesocosm experiment to examine the potential direct impacts of trees on the decomposer system in isolation from confounding differences met in the correlative study. The addition of birch and pine leaf litter had limited effects on soil nematodes, only reducing predatory nematode abundance, but in comparison, the presence of tree roots markedly altered nematode abundance and trophic structure with both birch and pine roots sustaining greater total, fungal feeding and predatory nematode abundance (Keith *et al.*, 2009). There were also strong positive relationships between root biomass and total nematode abundance, and between fungal PLFAs and fungal feeding nematode abundance, thereby demonstrating the positive impact of belowground tree inputs.

Birch and pine also had specific impacts on nematode groups with pine roots promoting bacterial feeders and birch roots promoting root-hair feeders. Furthermore, while there was no difference in the quantity of total, bacterial and fungal PLFAs between birch and pine root treatments, the multivariate composition of the microbial PLFAs was significantly distinct between these

contrasting tree species. The increases in the abundance of different nematode trophic groups, and distinct microbial PLFA composition, in the presence of birch and pine roots indicate that the positive impact of trees on decomposers is species-specific, and that the outcome of interactions may depend upon the focal component of the soil food web.

Together, these findings show that native tree invasion of moorland can have a tremendous impact on the decomposer community and decomposition by controlling detrital inputs, both directly, and indirectly via changes in the composition of ground vegetation. Differences in the quality and quantity of detrital inputs can influence belowground biodiversity and trophic structure by modifying soil physico-chemical properties and controlling resource availability. Thus, changes in land management in these systems can have important implications for the interactions between plants, decomposers and decomposition.

Key words: Soil biodiversity, native woodland, secondary succession, nematodes, PLFA, litterbag

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