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Putting the ‘upstairs–downstairs’ into ecosystem service: What can aboveground–belowground ecology tell us?

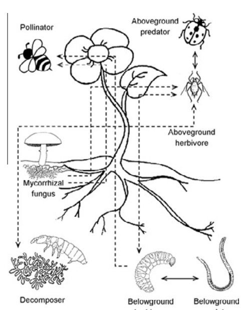
A. Donald A'Bear[a,*], Scott N. Johnson[b], T. Hefin Jones[a]

[a] Cardiff School of Biosciences, Cardiff University, Cardiff, UK
[b] Hawkesbury Institute for the Environment, University of Western Sydney, Sydney, Australia

HIGHLIGHTS

- Aboveground–belowground interactions influence ecosystem function.
- Root and shoot herbivory weaken antagonism of the spatially-separate herbivore.
- Decomposers and mycorrhizae increase shoot herbivore performance or antagonism.
- Shoot herbivory stimulates nutrient cycling by decomposers.
- Root herbivory and mycorrhizae increase floral attractiveness to insect pollinators.

GRAPHICAL ABSTRACT



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ABSTRACT

Interactions between spatially-separated aboveground and belowground biota exert important influences on the functioning of terrestrial ecosystems. Plant root exudates and litter inputs affect root-associated and decomposer sub-communities, which, in turn, regulate nutrient availability and plant growth. Ecosystem services theoretically attributed to specific functional components of aboveground or belowground biota are, therefore, influenced by indirect (plant-mediated) interactions with the wider community. Some recent studies have considered aboveground–belowground interactions in a climate change context, with implications for altered ecosystem service provision. This review is a conceptual discussion of the mechanisms by which aboveground–belowground interactions affect specific ecosystem services: control of herbivores by natural enemies, insect pollination and nutrient mineralization by soil decomposers. While some mechanisms are well-characterized, others are poorly understood. Reducing root and shoot herbivory, in addition to the direct plant benefit, indirectly promotes antagonism of the spatially-separate herbivore by its natural enemies. Soil decomposers and mycorrhizal fungi can increase shoot herbivore performance such that control by natural enemies is weakened, or initiate bottom-up trophic cascades which strengthen antagonism of shoot herbivores. Aboveground herbivory generally stimulates nutrient cycling by decomposers. Root herbivory and mycorrhizal association both appear to increase floral attractiveness to insect pollinators. Mechanisms reflect alterations to plant growth, nutritional quality and chemical defenses. Climate change has considerable potential to alter aboveground–belowground interactions, with largely unexplored implications for biological control, pollination and soil nutrient cycling.

* Corresponding author. Address: Sir Martin Evans Building, Cardiff School of Biosciences, Cardiff University, Museum Avenue, Cardiff CF10 3AX, UK.
E-mail address: ABearAD1@Cardiff.ac.uk (A.D. A'Bear).

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1. Introduction

The functioning of an ecosystem is regulated by the interactions that occur between the organisms within it. Interactions between aboveground and belowground biota, *via* plant-mediated mechanisms, are potentially as important for ecosystem structure and function as those between spatially co-existing species (Bardgett and Wardle, 2010; see Dreyer and Gratton, 2014 for a discussion of linkages between horizontally adjacent habitats). While both aboveground (Bale et al., 2002; Grime et al., 2000) and belowground (A'Bear et al., 2013; Jones et al., 1998) sub-community dynamics and processes are known to be affected by global climate change factors, only recently have studies begun to consider interactions between these spatially-separated biota within a climate change context. Plant inputs to soil (roots, their exudates and litter material) can determine sub-community composition by influencing root-associated and decomposer organisms. These, in turn, regulate plant growth and nutrient availability (Bever et al., 1997; Wardle et al., 2004). Feedbacks of this nature between spatially-separated sub-communities influence plant (Bradford et al., 2002; De Deyn et al., 1993), microbe (De Deyn et al., 2011; de Vries et al., 2012; Kostenko et al., 2012), detritivore (Hedlund et al., 2003; Wardle et al., 1999), herbivore (Bonkowski et al., 2001; Scheu et al., 1999; Wurst et al., 2003) and natural enemy (Bezemer et al., 2005; Gange et al., 2003) activity and population dynamics. As a consequence, ecosystem services (e.g. biological control of herbivore populations by natural enemies, pollination, decomposition and nutrient cycling) theoretically attributed to specific functional units within aboveground or belowground subsystems are, in reality, influenced by indirect interactions with other components of the community (Fig. 1).

Nutrient exchange intimately links aboveground and belowground biota; dead plant material provides the organic carbon required by the soil decomposer subsystem, the activity of which regulates the supply of mineral nutrients to plants, herbivores and natural enemies (van der Heijden et al., 2008). Plant-associated organisms, either aboveground (e.g. leaf herbivores and pollinators) or belowground (e.g. root herbivores and mycorrhizal fungi), influence one another through changes to plant productivity (e.g. due to mycorrhizal association; Gange et al., 2003) or induced defensive chemistry (e.g. terpenoid or glucosinolate production, due to herbivory; reviewed by Bezemer and van Dam, 2005), indirectly influencing higher trophic levels (Gange et al., 2003; Wardle et al., 2004). Belowground inputs, such as root exudates, litter fall and herbivore frass, influence the composition and activity of the decomposer community (Ayres et al., 2007; Jones et al., 1998; Krasnoshchekov and Vishnyakova, 2003). Intense competition also occurs between plants and soil microbes, as they are limited by the same nutrients (Wardle et al., 2004). The wide range of mutualistic, facilitative and antagonistic feedbacks that occur between aboveground and belowground organisms are also influenced when interacting components are affected by changes in the abiotic environment (Stevnbak et al., 2012; Tylianakis et al., 2008). The direct effect of, for example, elevated CO_2, warming or altered precipitation, on one species has the potential to indirectly influence members of the wider community (see also: Schmitz and Barton, 2014; Tylianakis and Binzer, 2013; Welch and Harwood, 2014). Ecosystem structure and function is, therefore, a consequence of this complex network of dynamic interactions.

Previous reviews have considered the ecology of specific aboveground–belowground interactions. These include the interactions between root and foliar herbivores (e.g. Bezemer and van Dam, 2005; Johnson et al., 2012), decomposers and foliar herbivores (e.g. Bardgett et al., 1998; Scheu, 2001), and mycorrhizal fungi

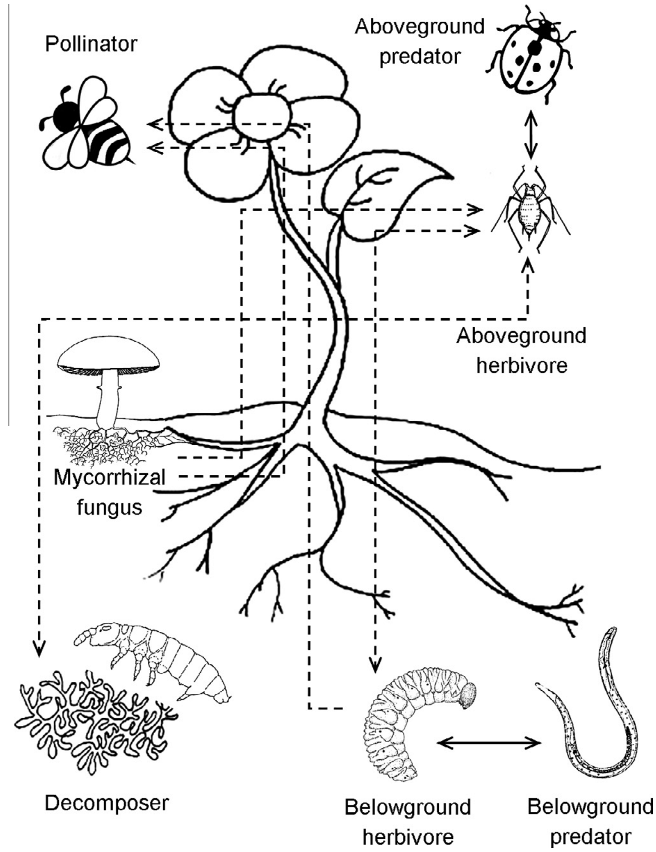

Fig. 1. Plant-mediated (indirect, dashed lines) interactions between aboveground and belowground biota; direct (solid lines) interactions between herbivores and their predators.

and plant community dynamics (e.g. Gange and Brown, 2002; Hart et al., 2003). Several conceptual models have been suggested to describe the mechanisms by which different components of aboveground and belowground communities influence one another (e.g. Bever et al., 1997; Masters et al., 1993; Moore et al., 2003). Mechanistic understanding of these interactions provides the potential to regulate them for biological control and the provision of ecosystem services. The present review is a conceptual discussion of how interactions between aboveground and belowground sub-communities influence ecosystem function and service. We explore the mechanisms by which aboveground–belowground interactions regulate the control of herbivory by natural enemies, pollination and nutrient mineralization by soil biota (Fig. 1). These interactions have implications for biological control, productivity and soil fertility in natural and managed ecosystems. Within the context of each of the aboveground–belowground interactions reviewed, we draw on the limited available evidence to consider the potential for climate change to influence ecosystem service provision mediated by these feedbacks.

2. Effects of belowground biota on aboveground biota and ecosystem services

2.1. Root herbivore effects on natural enemies of aboveground herbivores

Root herbivores have been shown to affect a number of aboveground insect herbivores (reviewed by Johnson et al., 2012). Recent studies have begun to explore the implications of these affects for