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Linkages between below and aboveground communities: Decomposer responses to simulated tree species loss are largely additive

Becky A. Ball^{a,*}, Mark A. Bradford^{a,b}, Dave C. Coleman^a, Mark D. Hunter^{c,d}

^a Odum School of Ecology, University of Georgia, Athens, GA 30602, USA

^b School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA

^c School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109, USA

^d Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA

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ABSTRACT

Inputs of aboveground plant litter influence the abundance and activities of belowground decomposer biota. Litter-mixing studies have examined whether the diversity and heterogeneity of litter inputs affect decomposer communities in ways that can be predicted from monocultures. They have mainly attempted to detect non-additive effects of litter mixing, although individual species effects (additivity) as well as species interactions (non-additivity) may alter decomposition rates. To determine potential impacts of plant species loss on aboveground-decomposer linkages, we assessed both additive and non-additive effects of litter mixing on decomposer communities. A full-factorial litterbag experiment with leaves from four deciduous tree species was conducted, to assess responses of bacteria, fungi, nematodes, and microarthropods. Data were analyzed using a statistical method that first looked for additive effects based on the presence or absence of species and then any significant species interactions. We observed almost exclusively additive effects of all four litter species on decomposer biota, with each species exerting effects on different aspects of the community. These results imply that the consequences of species loss for the decomposer community will be largely predictable from knowledge of single species litter dynamics. The two species at opposite ends of the quality spectrum exerted the most effects. Highquality Liriodendron tulipifera supported a more diverse arthropod community and drove bottom-up effects on the decomposer food web. Low-quality Rhododendron maximum had negative effects on most groups of biota. Litter of mid-quality species exerted fewer effects. The influence of litter species richness on the Tylenchidae (nematodes) was the only non-additive effect of litter mixing. Together, these data demonstrate an effect of plant community composition on decomposer biomass, abundance, and diversity, confirming a link between above and belowground communities. We were able to identify the species to which the decomposer community is most sensitive, aiding predictions of the consequences of the loss of these dominant species on the decomposer community, with potential feedbacks for organic matter and nutrient turnover.

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1. Introduction

Decomposer biota, including microbes and invertebrate fauna, play a pivotal role in litter decomposition and through their feeding activity drive the amount and timing of organic matter turnover and mineral nutrient availability (Seastedt, 1984; Beare et al., 1992; Hunter et al., 2003). Control over the availability of resources for plant productivity forms a feedback from belowground systems to aboveground processes and communities (De Ruiter et al., 2005). Recently, there has been increasing interest in effects that operate in the opposite direction. That is, how aboveground systems affect belowground communities and processes (Scheu et al., 2003; Wardle et al., 2004; Bardgett et al., 2005; De Deyn and Van der Putten, 2005; Wardle, 2006; Nilsson et al., 2008). With this focus in mind, much research has been conducted to determine how plant communities might affect soil processes and decomposer communities. Since a major influence of plants on the soil system is through litter (e.g. Negrete-Yankelevich et al., 2008), there has been a large focus specifically on the effects of altered plant litter characteristics on decomposer communities, through litter quality

^{*} Corresponding author. 6182 Steele Hall, Environmental Studies Program, Dartmouth College, Hanover, NH 03755, USA. Tel.: +1 603 646 1689; fax: +1 603 646 1682.

E-mail address: rebecca.a.ball@dartmouth.edu (B.A. Ball).

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(Saetre and Bååth, 2000; Gonzalez and Seastedt, 2001), species and functional diversity (Bardgett and Shine, 1999; Wardle et al., 2003; Milcu et al., 2006; Wardle et al., 2006), and resource heterogeneity (Blair et al., 1990; Hansen, 1999; St John et al., 2006).

From this interest, many litter-mixing studies have been conducted to determine whether decomposer communities and their impacts on decay dynamics differ under multi-species mixtures when compared to monocultures (reviewed by Gartner and Cardon, 2004). Additive effects on biota result from the independent influence of individual litter species, where diverse litter mixes may support abundant and diverse decomposer communities that are simply combinations of those that occur in litter monocultures (Johnson et al., 2006). Specifically, if decay dynamics in mixtures are the sum of their parts, biota of single litters can be used to predict biota colonizing multi-species litter layers. Alternatively, non-additive effects emerge if decomposer communities in mixture are not simple averages of those in monoculture. That is, they are unpredictable based solely on studying litter monocultures. A number of studies have attempted to identify non-additive effects of litter mixing on a variety of decomposition parameters, both in terrestrial (reviewed by Gartner and Cardon, 2004; Hättenschwiler et al., 2005) and aquatic (Lecerf et al., 2005; LeRoy and Marks, 2006; Swan and Palmer, 2006) systems. Results vary among studies (see Gartner and Cardon, 2004), perhaps in part because of differences in the parameters measured. Biotic assessments vary from measurements of abundance, density, biomass, or activity and describe various different groups of decomposers. Additionally, studies have also been conducted under a variety of plant richness levels and covering different time spans (e.g. those reviewed by Gartner and Cardon, 2004).

Under scenarios of global environmental change, many systems are at risk of losing dominant plant species (Grime, 1997; Vitousek et al., 1997; Loreau et al., 2001; Ellison et al., 2005). While previous litter-mixing studies have explored consequences of species loss, they generally tested for non-additivity, where interactions among species are the focus. However, individual (additive) effects based on the identity of species may also have a major impact on ecosystem processes (Gross and Cardinale, 2005; Schläpfer et al., 2005). That is, the loss of a particular species from a system may have a large impact on the decomposer community, even if its role in mixture dynamics is additive. Statistical methods used in littermixing studies to test for non-additive effects commonly are not designed to also test whether individual species have significant additive effects in mixture (see Ball et al., 2008); that is, whether species are functionally redundant or not. To predict accurately the consequences of species loss for ecosystem functioning, it is necessary to consider both additive and non-additive effects of species loss, reflecting either an independent influence of species on ecosystem functioning (additivity) or emergent dynamics that arise due to species interactions (non-additivity).

To determine the potential consequences of species loss on decomposer communities, we conducted a three-year, full-factorial litter-mix study in a southeastern US temperate forest. We used leaf litter from four co-dominant tree species, which differed markedly in initial chemical quality and so might each be expected to have pronounced effects on decomposer communities (Wardle and Lavelle, 1997). To obtain a comprehensive understanding of the decomposer community responses to litter mixing, we measured many commonly studied groups of decomposers over the course of two years: microbes, nematodes, microarthropods, and small macroarthropods. To analyze these data, we used a statistical model that sequentially tests first for additive effects of the loss of each component litter species, then whether any of the remaining variance is explained by interactions among the litter species. Significant interactions are indicative of non-additivity and were explored using post hoc analyses to determine whether non-additive effects were explained by richness and/or composition (Mikola et al., 2002; Drake, 2003). The strength of the approach is that we can first ask whether loss of a particular species is likely to affect community structure (Ball et al., 2008). If it does, we can then ask whether its loss is likely to be additive or whether the consequence of its loss will be dependent (i.e. non-additive) on the presence of some or all of the other species in the community. We hypothesized that, given the gradient in initial litter quality, structure, and decomposition rate, there would be compositional effects of litter mixing on the decomposer community, suggesting a feedback between aboveground plant communities and belowground communities. Specifically, we hypothesized that (1) both high- and low-quality litters will influence decomposer communities, due to the fact that high-quality litter (with high nutrient content and low secondary metabolites) should provide a better resource to support a larger decomposer community (Wardle et al., 2006) and lowquality litter with lower nutrient content and more structural compounds (e.g. lignin) should provide a poor resource but more habitat complexity (Hansen and Coleman, 1998) for the decomposer community. We also hypothesized that (2) individual species effects will be non-significant (i.e. neither significantly additive or non-additive and hence functionally redundant) when in mixture with species of similar quality, but will support a significantly larger and more diverse decomposer community when in mixture with litter species of markedly different quality (sensu Wardle, 2002). Given the high degree of variation in observations of additive or non-additive effects of litter mixing on decomposer biota (Gartner and Cardon, 2004), we felt that we could not reliably hypothesize whether significant species effects in mixture will likely be due to species identity or interactions.

2. Materials and methods

2.1. Study site

The experiment was conducted at Coweeta Hydrologic Lab (US Forest Service) in the southern Appalachians near Otto, North Carolina, USA (35°00'N, 83°30'W; elevation 1300 m). The area is a deciduous hardwood forest, comprised largely of oaks (Quercus spp.), tulip poplar (Liriodendron tulipifera), maples (Acer spp.), birches (Betula spp.), and riparian stands of eastern hemlock (Tsuga canadensis), with an abundant evergreen understory comprised mainly of Rhododendron maximum (rhododendron) and Kalmia latifolia (mountain laurel). The mean annual temperature over the duration of the experiment was 14 °C. Mean monthly temperature varied with season, and followed the same annual pattern of peak temperatures in July-August and minimum temperatures in December-February (National Climatic Data Center, Appendix 1 (supplementary material - online)). The mean annual rainfall was approximately 1700 mm, generally with moderate levels of precipitation (approx. 12 cm month⁻¹) except during late summer peaks and autumnal minimums. The study was conducted in Watershed 20 on Ball Creek, which drains into Coweeta Creek, a tributary of the Little Tennessee River. A tropical storm in September 2004 temporarily flooded the low areas of the riparian zone.

2.2. Experimental design

Litters from four co-dominant tree species were used: *L. tulipifera* L. (tulip poplar, L), *Acer rubrum* L. (red maple, A), *Quercus prinus* L. (chestnut oak, Q), and *R. maximum* L. (rhododendron, R). The litters from these species cover a range of chemical compositions and decay rates in monoculture (Table 1; Ball et al., 2008). Senesced leaves of each species were collected in October 2003 and air-dried Download English Version:

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