The Selective Effects of Environmental Change on the Functional Diversity of Soil Decomposers

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Abstract: Whether decomposition can be affected by the biodiversity of soil organisms is an important question. Biodiversity is commonly expressed through indices that are based on species richness and abundances. Soil processes tend to saturate at low levels of species richness. A component of biodiversity is functional diversity, and we have shown that the absence of the influence of species richness on decomposition switched into a positive relationship between fauna diversity and decomposition when we expressed biodiversity in terms of interspecific functional dissimilarity. Communities with functionally dissimilar species are characterized by complementary resource use and facilitative interactions among species. It is suggested that the effects of environmental changes on ecosystem functions such as decomposition can be better understood if we have more knowledge about the selective effect of these changes on specific facets of soil biodiversity, such as functional diversity.

Keywords: functional dissimilarity; soil organisms; decomposition; environmental changes

1. Background and History of the Topic

One of the early attempts to synthesize the knowledge that was obtained from studies determining the interrelationships between specific groups of organisms on plant litter decomposition was the publication of *Biology of Plant Litter Decomposition*. The editors [1] stressed that these two volumes are unique in that they treat ecological problems in a truly biological manner. Two years later, the 17th Symposium of the British Ecological Society was devoted to *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*. The editors [2] stipulated the general emphasis should be placed on the functional roles of organisms in nutrient cycling processes rather than on detailed aspects of their biology. In the Special Publication Series of the British Ecological Society (number 4): *Ecological Interactions in Soil; Plants, Microbes and Animals*, the editors [3] shift the focus to more complex (higher order) interactions. In 1989–1992, my group at the VU University Amsterdam was linked to two big European projects on forest litter decomposition, DECO and CORE, in which the effects of climate change on decomposition were studied, a study that was financed by the Commission of the European Communities and the European Science Foundation. In the DECO project, litterbags with constant litter quality were incubated in 13 European countries in order to unravel the influence of the physical and chemical climate.

In the CORE project, the forest soil columns in lysimeters were transplanted between different pine forests in a reciprocal way. The results were published in the proceedings of the first European Symposium on Terrestrial Ecosystems: Responses of Forest Ecosystems to Environmental Changes, edited by [4]. In addition to the CORE project, food web dynamics in relation to decomposition and nutrient flow were studied [5]. Using a community food web model [6,7], the contribution of functionally defined groups of organisms to decomposition was determined [8]. It became clear that the decomposition of litter across a climate gradient with different nutrient deposition levels (Nitrogen) could...
only be understood with more knowledge of the position, composition, and functional diversity of the soil decomposer community [9].

2. Recent Developments

2.1. Diversity and Decomposition

In their recent article “Diversity meets decomposition”, Gessner et al. [10] mention that the detritus-based food web is supported by 90% of the 100 gigatons of terrestrial plant biomass that is produced every year and that enters the dead organic matter pool. They raise the question of how changes in the biodiversity of this soil food web will affect this vital component of soil functioning. Based on their analysis of their experiments determining leaf decomposition in forest floors and streams, they suggest that changes in species diversity within and across trophic levels can significantly alter decomposition.

Biodiversity is commonly expressed through indices based on species richness and species abundances [11]. Soil process rates tend to saturate at low levels of species richness [12], showing an important degree of redundancy and a weak impact of taxonomic richness on soil process rates.

2.2. Functional Diversity

An important component of biodiversity is functional diversity, which concerns the impact that organisms have on ecosystems. Petchey and Gaston [13] showed good experimental and analytical evidence that functional diversity can provide a link between organisms and ecosystems. In our study, which used eight detritivore species from different taxonomic groups, we did not find any influence of species richness on litter decomposition [14]. However, when we expressed fauna diversity in terms of interspecific functional dissimilarity rather than taxonomic richness, a clear positive relationship was found between fauna diversity and two key soil ecosystem processes: leaf litter mass loss and soil respiration (Figure 1).

Functional dissimilarity is independent of the number of species and describes the unshared functional space among the species in their community [15]. Communities with functionally dissimilar species are likely to show less competitive interactions than communities consisting of species with similar functional attributes. In communities with functionally dissimilar species, complementary resource use and/or facilitative interactions among species are more likely to occur.

These results are in line with those of Coulis et al. [16]. They created trait-based functional dissimilarity gradients using five assemblages of two detritivore species and five mixtures of two plant litter species. Functionally dissimilarity explained up to 20% of the variation in the response variables. Detritivore functional dissimilarity had stronger effects when combined with increasingly dissimilar litter mixtures. This suggests that trait dissimilarity interacts across trophic levels (see also [10]).

Referring to our novel experimental design [14] which has been proven to be powerful for the detection of diversity effects of litter-consuming soil fauna on decomposition, Frainer et al. [17] created a continuous gradient of litter chemistry trait variability within species mixtures to assess the effects of litter dissimilarity on three related processes in a natural stream: litter decomposition and the dynamics of fungal decomposers and nutrients. They did not find any relationship between the decomposition rates and litter trait dissimilarity, nor did they find any effects of trait dissimilarity on fungal biomass accrual or changes during the decomposition of nitrogen nor in the phosphorus concentrations in individual leaf species. According to the authors, the effects of litter diversity on decomposition are less pronounced than effects on terrestrial primary productivity, at least in streams.
Figure 1. Net diversity effect on soil respiration (A) and leaf litter mass loss (B) in relation to mean functional dissimilarity of the species in the community. Each series of dots represents a treatment (n = 5 replicates per treatment; some dots overlap). Letters at the top of the figure refer to the species combination given in Table S1 (See [14]); Supporting Online Material). A significant positive regression between the mean functional dissimilarity of the communities and the net diversity effect for soil respiration (linear regression, F 47,46 = 11.97, p = 0.001) and leaf litter mass loss (linear regression, F 47,46 = 7.48, p = 0.009) indicates that positive net diversity effects are more pronounced in communities consisting of functionally dissimilar species. Functional dissimilarity was related to neither species number nor taxonomic group number. From [14]. Reprinted with permission from AAAS.

In a recent FAO report on soil biodiversity [18] it is stated that one of the most important facets of soil biodiversity has been shown to be the functional dissimilarity among soil organisms, spanning large gradients from microorganisms to macrofauna [14,19,20].

As stated in our study [14], the species-specific contribution to the range of functional dissimilarities in a community might be an important mechanism by which biodiversity generates positive interactions that influence ecosystem process rates. If, by an analysis of their functional dissimilarities, we know how species contribute to multiple species interactions in the community, we may be able to predict the impact of environmental changes on ecosystems.
Controlling environmental gradients and species richness as the sole biodiversity index, both directly and randomly manipulated, were the characteristics of the early Biodiversity–Ecosystem Function (BEF) experiments [21].

In a recent meta-analysis of 69 independent studies reporting 660 observations of the impacts of two important drivers of global change: (chemical stressors and nutrient enrichment) on animal and microbial decomposer diversity and litter decomposition, Beaumelle et al. [22] show that declines in the diversity and abundance explain reduced litter decomposition. The authors mention that the effect of these changes in decomposer diversity and abundance might have also caused changes in the community and food web structure. Underlying changes in keystone species, functional and vertical diversity as well as dominance patterns may have caused these changes in decomposition [22]. They stress the importance of future synthesis work addressing the effect of shifts in functional diversity on decomposition. This implies that the effects of environmental change on ecosystem functions can only be understood if we know the selective effect of environmental change on facets of biodiversity, such as functional diversity.

2.3. Environmental Change and Diversity

If we want to understand the effects of environmental change on decomposition, we should have a clear idea of the dominant controls on litter decomposition. In their recent article on this subject, Bradford et al. [23] re-analyzed the data of a classical regional-scale decomposition experiment [24], which was previously used to demonstrate the predominance of climate as a regulator of litter decomposition rates. In Figure 2, the decomposition triangle shows the classical conceptualization of the dominant factors regulating litter decomposition rates (see [25]) The fundamental controls on decomposition rates were indicated to be physico-chemical environment, litter traits, and decomposer organisms. The authors separated the first control factor into climatic and edaphic factors, emphasizing the primacy of climate. Regional-scale decomposition studies emphasized the importance of climate, whereas studies at broad spatial scales mention litter quality as the dominant control factor. As mentioned by Bradford et al. [23], these paradigms assume that the activities of decomposer organisms are regulated by climate and litter quality and that they do not exert independent control on decomposition rates. However, using a soil community food web model, Berg et al. [8] show signs of the independent effects of soil fauna on the decomposition of coniferous litter in a 2.5 year litterbag study. The small to insignificant role of soil fauna as found in broad-scale litterbag studies (e.g., [26,27]) might be the result of the use of low replication litterbags, reducing the precision in the resulting parameter estimates.

In a recent meta-analysis on litterbag studies, the effect sizes of soil fauna on litter decomposition rates at global and biome scales were quantified, and the interactions between climate, litter quality, and soil fauna were assessed [28]. The effects of soil fauna on litter decomposition across biomes appeared to be differently modulated by climate and litter quality. Based on these data, the authors advocate for the inclusion of biome-specific soil fauna effects on litter decomposition to reduce the unexplained variation in large-scale decomposition models (Figure 3).
Beaumelle et al. [22] show that declines in the diversity and abundance explain reduced impacts of two important drivers of global change: chemical stressors and nutrient en-litter decomposition. The authors mention that the effect of these changes in decomposer decomposition experiment [24], which was previously used to demonstrate the predominance of climate as a regulator of litter decomposition rates. In Figure 2, the decomposition triangle shows the classical conceptualization of the dominant factors regulating litter decomposition rates, which is modified here to represent the contemporary paradigms. The decomposer organisms are shown in small font to emphasize that under contemporary paradigms, climate and litter quality are considered to be the dominant factors regulating the rate at which organic matter decomposes. Modified from Bradford et al. [23].

As stated by Bradford et al. [23], “there is growing evidence that for soil processes the majority of process-level variation occurs at finer and not broader spatial scales” (see, e.g., [8,29–31]). Furthermore, in their meta-analysis of responses of soil biota to global change, Blankinship et al. [32] stress that their analysis was focused on abundance measurements and not the community composition of individual taxa and trophic groups. They underline that functional differences within a trophic group can be just as important as species richness and population size for ecosystem functioning [14,33]. It was suggested by Wardle, Verhoef, and Clarholm [34], that anthropogenic global change phenomena have

![Diagram](https://example.com/diagram.png)

**Figure 2.** The decomposition triangle is the classical conceptualization of the dominant factors regulating litter decomposition rates, which is modified here to represent the contemporary paradigms. The decomposer organisms are shown in small font to emphasize that under contemporary paradigms, climate and litter quality are considered to be the dominant factors regulating the rate at which organic matter decomposes. Modified from Bradford et al. [23].

![Diagram](https://example.com/diagram.png)

**Figure 3.** Mean effect size of soil fauna exclusion on litter decomposition rates (lnRR(k)) at the global scale, agro-ecosystems, cold or dry, humid grasslands, coniferous forests, deciduous forests, tropical dry forests, tropical wet forests. The bars around the means are bias-corrected with 95% bootstrap confidence intervals. Negative mean effect sizes indicate slower litter decomposition in the litterbags without soil fauna. Modified from Garcia-Palacios et al. [28].
a range of direct and indirect effects on soil food web composition and activity, manifesting themselves at the ecosystem level (Figure 4).

This was also suggested for soil communities that are influenced by repeated disturbances, e.g., land use change coupled with exceptional climatic conditions, where interactions between competing species or trophic levels are seriously disrupted [35].

Similarly, it was suggested that temperature changes should be studied in relation to the interactions between key species or functional species groups rather than thermal tolerance or the dispersal ability of individual species [36].

The strength of soil biodiversity effects may depend on specific traits that are lost from the system through environmental change. Functional dissimilarity among soil organisms spanning large gradients from microorganisms to macrofauna ([14,19,20] is one of the most important facets of soil biodiversity. Thus, environmental changes that reduce this functional dissimilarity are likely to negatively influence a multitude of different soil-mediated ecosystem functions.

2.4. Conclusions

This suggests that future studies determining the effect of environmental changes on decomposition should be characterized by an approach in which climate and litter quality changes are studied in the context of their selective effects on the functional diversity of soil decomposers.

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