

# Biodiversity Effects on Soil Processes Explained by Interspecific Functional Dissimilarity

D. A. Heemsbergen,<sup>1,2</sup> M. P. Berg,<sup>1</sup> M. Loreau,<sup>3</sup> J. R. van Hal,<sup>2</sup>  
J. H. Faber,<sup>2</sup> H. A. Verhoef<sup>1\*</sup>

The loss of biodiversity can have significant impacts on ecosystem functioning, but the mechanisms involved lack empirical confirmation. Using soil microcosms, we show experimentally that functional dissimilarity among detritivorous species, not species number, drives community compositional effects on leaf litter mass loss and soil respiration, two key soil ecosystem processes. These experiments confirm theoretical predictions that biodiversity effects on ecosystem functioning can be predicted by the degree of functional differences among species.

Functional redundancy of species is assumed to be a common feature in soils (1–4), and experimental studies that manipulate species number often show an asymptotic response of soil processes, in which the asymptote is reached at low levels of species number (5, 6). Even though species number per se does not appear to be important, the functional diversity of the soil community (that is, the range of species traits that determine their functional role) may affect ecosystem processes (5–7). Functional differences may result in a variety of interactions among species. Because of the diverse and complex nature of these interactions, it may often be difficult to predict changes in ecosystem functioning when species are lost from or introduced into the community. The central question examined in this paper is whether we can predict the effects of changes in species composition on soil ecosystem processes if the functional dissimilarity of species in the community is known.

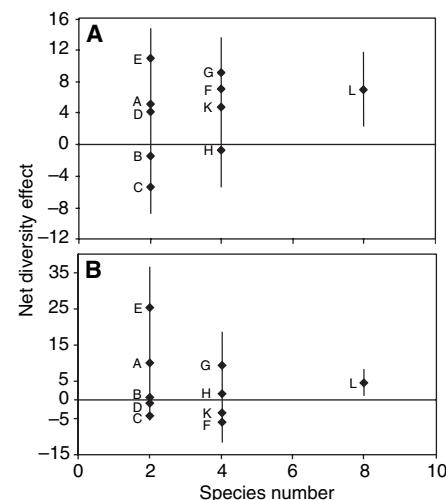
Soil macrofauna plays a critical role in the decomposition of dead organic matter. It is known that species differ in their effects on soil processes (8). For example, each species has a specific mode of affecting litter fragmentation or nitrification, due to contrasting functional attributes. Moreover, the effects of different species on a particular process often differ in strength. These differences may lead to interspecific interactions that result in species mixtures performing better (facilitative interactions) or worse (inhibitory interactions) than would be

expected on the basis of the mere additive effects of single species. The nature (inhibitory, neutral, or facilitative) of these interactions might be related to the degree in which species differ in their impact on soil processes. We hypothesized that species mixtures that contain species with different effects on ecosystem processes (species that are functionally dissimilar as to these processes) show facilitative interactions, irrespective of the number of species or taxonomic groups involved. Functional dissimilarity was assessed in terms of the effects of the various species on four ecosystem process variables: leaf litter mass loss, leaf litter fragmentation, soil respiration, and nitrification, all of which are related to the process of decomposition. Thus, instead of focusing on ecological attributes of species that are associated with their functional impact (9), we directly measured their effect on ecosystem processes.

We manipulated species composition in soil microcosms (10) with an increasing number of macro-detritivores: zero, one, two, four, and eight species per microcosm (table S1). Species were selected from the grassland macrofauna community of a river floodplain (10). Single-species treatments of all eight species were included in the experimental design to quantify their per-capita effects on soil process rates, and these were used to quantify functional dissimilarity among species. To discriminate the effect of species number from other compositional effects on process rates, different two- and four-species combinations were included in the design (table S1). Each species was assigned randomly to multispecies treatments with the following constraints: (i) species were equally represented, and (ii) both two- and four-species combinations contained taxonomic group diversity [one versus two taxonomic groups and two versus three taxonomic groups, respectively (table S1)]. Total earthworm biomass

and total arthropod abundance were kept constant across treatments (10). The microcosms were kept under controlled environmental conditions for 8 weeks (10). The soil processes measured included leaf litter mass loss, leaf litter fragmentation, gross  $\text{NO}_3^-$  productivity, and soil respiration ( $\text{CO}_2$  production) (10).

We observed only a small effect of species number on decomposition processes. Saturation in process rates occurred after more than one species was added (11), and mixtures showed a large variation in the measured soil processes. Net biodiversity effects were calculated (10, 12) to assess whether positive or negative interactions among species could explain the observed variation in soil processes within a diversity treatment. We observed a range of negative, neutral, and positive net diversity effects in two- and four-species treatments (Fig. 1, A and B). For some species combinations [for example, *Lumbricus rubellus* and *Philoscia muscorum* (Fig. 1, combination E)], the net diversity effect on soil respiration and leaf litter mass loss was higher than expected, suggesting facilitation. For other combinations [for example, *Polydesmus denticulatus* and *Oniscus asellus* (Fig. 1, combination C)], a lower effect than expected was observed, suggesting inhibition due to interspecific competition. This shows that communities with the same species number, but different species compositions, had very different effects on soil ecosystem processes.

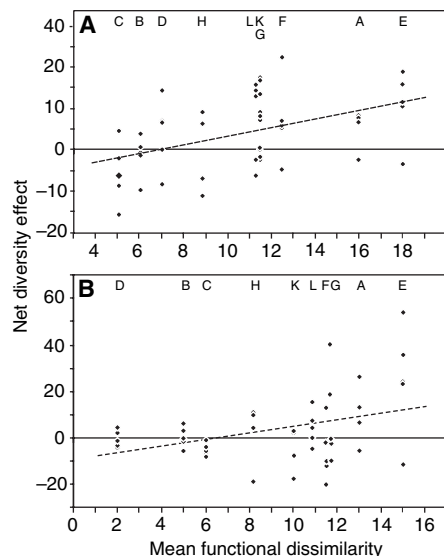


**Fig. 1.** Net diversity effect on soil respiration (A) and leaf litter mass loss (B) in relation to species number. Each dot represents a treatment mean ( $n = 5$  per treatment); error bars represent standard errors. Letters next to the dots refer to the actual species combination given in table S1. A nonsignificant regression between species number and soil respiration (linear regression,  $F_{47, 46} = 1.46$ ,  $P = 0.22$ ) and leaf litter mass loss (linear regression,  $F_{47, 46} = 0.29$ ,  $P = 0.60$ ) indicates that negative or positive net diversity effects were not related to species number.

<sup>1</sup>Vrije Universiteit, Institute of Ecological Science, Department of Animal Ecology, de Boelelaan 1085, 1081 HV Amsterdam, Netherlands. <sup>2</sup>Alterra, Wageningen University and Research Centre, P.O. Box 47, 6700 AA Wageningen, Netherlands. <sup>3</sup>Laboratoire d'Ecologie, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris Cedex 05, France.

\*To whom correspondence should be addressed. E-mail: herman.verhoef@ecology.falw.vu.nl

Overall, net diversity effects showed no conclusive trends with species number (Fig. 1), indicating that species number per se does not explain the observed net effects. Positive net diversity effects occurred in



**Fig. 2.** Net diversity effect on soil respiration (A) and leaf litter mass loss (B) in relation to mean functional dissimilarity ( $\bar{10}$ ) of 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 ( $\bar{10}$ ). 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.

**Table 1.** The effect of single species (mean,  $n = 5$  per treatment) on four soil ecosystem processes related to decomposition. For each species, the total biomass (mean  $\pm$  SE,  $n = 5$  per species) added to the microcosms is given. Significant interspecific differences [one-way analysis of variance over all treatments, with an a posteriori test on interspecific means using least-square differences ( $P \leq 0.05$ ), with an unbalanced structure for all processes] between means within a column are marked with different superscript letters. BC, Bray-Curtis; DW, dry weight.

	Biomass added to microcosm (g)	Litter mass loss (mg day <sup>-1</sup> )	Litter fragmentation (BC similarity in size distribution)	Gross NO <sub>3</sub> productivity (μg g <sup>-1</sup> DW day <sup>-1</sup> )	Soil respiration (μg g <sup>-1</sup> DW day <sup>-1</sup> )
Control	0	25.1 <sup>a</sup>	1	6.72 <sup>a</sup>	81.6 <sup>a</sup>
<i>Aporrectodea caliginosa</i>	0.362 ± 0.013	41.1 <sup>ab</sup>	0.85 <sup>ab</sup>	8.81 <sup>d</sup>	92.9 <sup>b</sup>
<i>Allolobophora chlorotica</i>	0.221 ± 0.014	30.6 <sup>ab</sup>	0.89 <sup>a</sup>	8.29 <sup>c</sup>	89.5 <sup>ab</sup>
<i>Lumbricus rubellus</i>	0.286 ± 0.016	46.6 <sup>b</sup>	0.83 <sup>ab</sup>	9.35 <sup>e</sup>	95.7 <sup>b</sup>
<i>Trachelipus rathkii</i>	0.191 ± 0.010	33.4 <sup>ab</sup>	0.88 <sup>ab</sup>	7.69 <sup>b</sup>	87.0 <sup>ab</sup>
<i>Philoscia muscorum</i>	0.054 ± 0.003	28.1 <sup>a</sup>	0.85 <sup>ab</sup>	7.14 <sup>a</sup>	87.5 <sup>ab</sup>
<i>Oniscus asellus</i>	0.205 ± 0.007	42.1 <sup>ab</sup>	0.78 <sup>b</sup>	7.97 <sup>bc</sup>	87.9 <sup>ab</sup>
<i>Polydesmus denticulatus</i>	0.044 ± 0.004	37.1 <sup>ab</sup>	0.77 <sup>b</sup>	6.99 <sup>a</sup>	83.3 <sup>ab</sup>
<i>Julus scandinavicus</i>	0.289 ± 0.010	30.1 <sup>ab</sup>	0.85 <sup>ab</sup>	9.23 <sup>de</sup>	92.2 <sup>b</sup>
Standardized SE		6.1	0.031	0.18	3.52

species mixtures composed of species with strong differences in single-species effects (Table 1). The epigeic earthworm *L. rubellus* had a large impact on most processes in monoculture. Its strong effect on leaf litter mass loss is a consequence of its ability to transport litter to deeper soil layers. The effect of the endogeic earthworm *Aporrectodea caliginosa* on total soil respiration probably reflected changes in the physical conditions of the soil. Among arthropods, the millipede *P. denticulatus* and the isopod *O. asellus* significantly fragmented leaf litter into smaller particles. These differences in the way different species affect ecosystem processes are critical to understand the effects of species number and composition. Therefore, communities composed of functionally dissimilar species should have stronger effects on process rates than communities consisting of functionally similar species.

We observed a significant positive regression of both soil respiration and leaf litter mass loss against mean functional dissimilarity ( $\bar{10}$ ) (Fig. 2, A and B). Thus, differences in the way in which species influence ecosystem processes tend to generate facilitation. Facilitation was shown in all combinations in which *L. rubellus* was present (Fig. 2, combinations A, E, F, G, and L), probably due to fragmentation and chemical changes in the leaf litter by isopods or millipedes. Inhibition occurred between *O. asellus* and *P. denticulatus* (Fig. 2, combination C). Both species have similar body sizes and showed the strongest comminuting activity (Table 1), suggesting possible competition for leaf litter of a specific fragment size. Neutral net diversity effects were observed for species combinations lacking *L. rubellus* or *O. asellus* and *P. denticulatus* (Fig. 2, combinations B, D, and H).

In this experiment, net biodiversity effects on soil processes were explained by the mean functional dissimilarity of species mixtures. These results suggest that it is not species number but the degree of functional differences between species that is a driver of ecosystem processes, and this effect in turn is due to facilitative interactions among species. 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 enhance ecosystem process rates. If we know how species contribute to multiple species interactions in the community, by an analysis of their functional dissimilarities, we may be able to predict the impact of local species loss or biological invasions on ecosystems. This may also have implications for ecosystem restoration, which may require the introduction of particular functionally dissimilar species or species combinations into impoverished ecosystems.

References and Notes

- O. Andr en, J. Balandreau, *Appl. Soil Ecol.* **13**, 105 (1999).
- M. A. Bradford *et al.*, *Science* **298**, 615 (2002).
- J. Laakso, H. Set al , *Oikos* **87**, 57 (1999).
- J. H. Faber, H. A. Verhoef, *Soil Biol. Biochem.* **23**, 15 (1991).
- J. Mikola, R. D. Bardgett, K. Hedlund, in *Biodiversity and Ecosystem Functioning, Synthesis and Perspectives*, M. Loreau, S. Naeem, P. Inchausti, Eds. (Oxford Univ. Press, Oxford, 2002), pp. 169–180.
- D. A. Wardle, O. Zackrisson, G. H rnberg, C. Gallet, *Science* **277**, 1296 (1997).
- D. Tilman, J. Knops, D. Wedin, P. Reich, in *Biodiversity and Ecosystem Functioning, Synthesis and Perspectives*, M. Loreau, S. Naeem, P. Inchausti, Eds. (Oxford Univ. Press, Oxford, 2002), pp. 21–35.
- D. C. Coleman, D. A. Crossley, *Fundamentals of Soil Ecology* (Academic Press, New York, 1996).
- B. Walker, A. Kinzig, J. Langridge, *Ecosystems* **2**, 95 (1999).
- Materials and methods are available as supporting material on Science Online.
- The relations between species number and soil process rates were best explained by exponential regression (curve fits of linear regression and exponential regression were compared using their residual sum of squares). Leaf mass loss: exponential regression,  $F_{91, 89} = 4.52$ ,  $P = 0.013$ , saturation of process rate after one species; leaf fragmentation:  $F_{91, 89} = 3.81$ ,  $P = 0.026$ , saturation of process rate after one species; gross nitrate productivity:  $F_{91, 89} = 11.21$ ,  $P < 0.001$ , saturation of process rate after one species; soil respiration:  $F_{89, 87} = 10.15$ ,  $P < 0.001$ , saturation after two species.
- M. Loreau, A. Hector, *Nature* **412**, 72 (2001).
- We thank D. Wardle for stimulating discussions. M.P.B. was financially supported by an academy fellowship of the Royal Netherlands Academy of Science. The investigation was supported by the Arts and Sciences Research Council for Earth and Life Sciences (ALW), with financial aid from the Netherlands Organization for Scientific Research (NWO) and from the Dutch Ministry of Agriculture, Nature and Food Quality through DWK program 384.

**Supporting Online Material**  
[www.sciencemag.org/cgi/content/full/306/5698/1019/DC1](http://www.sciencemag.org/cgi/content/full/306/5698/1019/DC1)  
 Materials and Methods  
 Table S1  
 References

23 June 2004; accepted 10 September 2004