

# **Convergent patterns in multitrophic biodiversity effects on yield across ecosystems**

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In ecosystems managed for food or fiber production, there is often no space for biodiversity – for example, intensive cereal monocultures are usually managed towards optimized yields using herbicides, fungicides and insecticides. In such systems, biodiversity is essentially unwanted - except, maybe, when it improves soil health or Carbon fixation. Consequently, it has been difficult to convincingly show if and where biodiversity is economically important in intensive production systems.

Biodiversity experiments have tried to provide theoretical evidence and justification for positive biodiversity effects on ecosystem properties, including productivity (Spehn et al. 2005). They originated in the 1990s in grassland and savannah ecosystems, with recent extensions to tree biodiversity experiments (Bruehlheide et al. 2014). Throughout these experiments, productivity has often been shown to increase with plant diversity (i.e. the diversity of primary producers). However, most plant-based production systems consist of only one or a few plant species. Are there any generalizable mechanisms by which increased plant biodiversity would lead to higher productivity (and, hence, increased yields)?

In recent years, the focus has moved away from looking only at the plants (as primary producers) to also considering various other trophic levels of organisms and their responses to changes in plant diversity. Wouldn't it be great to be able to show that these groups of organisms also play a role in production systems? Up until a few years ago, studies provided lots of evidence for enhanced overall biodiversity across trophic levels in systems with higher numbers of plant species. However, these studies lacked a proof that multitrophic communities were also linked to ecosystem services and, ultimately, yield (Scherber 2015). Luckily, all of this has changed now, due to an exciting new study published in Nature Ecology and Evolution by Li et al. 2023.

The study was conducted within the framework of the BEF-China experiment (Bruehlheide et al. 2014), a subtropical tree diversity experiment ([www.bef-china.com](http://www.bef-china.com)) at Xingangshan, Dexing, Jiangxi, China (Site A: 29.1123N 117.9197E; Site B: 29.0837N 117.9255E). There were 566 experimental plots, each measuring 25.8 x 25.8 m that had been planted in 2009 and 2010. Initial tree planting density was 400 tree individuals per plot. Tree species richness ranged from monocultures to mixed stands with 2, 4, 8, 16 or 24 species. The authors estimated primary productivity (based on basal diameter and height measurements), measured plant functional traits related to plant growth and arthropod herbivory, and collected arthropods on a subset of 47 plots using beating samples and trap nests. Additionally, predation rates by birds and arthropods were measured using a dummy caterpillar approach.

The authors turned to a particular statistical toolbox for data analysis, structural equation models. Such models allow complex causal hypotheses to be tested against data. Recent developments even allow to account for non-normality, non-linearity and random effects (Douma and Shipley 2022).

One of the great things about Li et al.'s paper is that it directly extends previous attempts to understand plant diversity effects on multitrophic systems. A previous study published in Nature about a decade ago (Scherber et al. 2010) had looked at grassland plant diversity effects on multitrophic interactions, indicating bottom-up effects of plant diversity on higher trophic levels both aboveground and in the soil (**Figure 1a**). In that study, aboveground plant biomass had been seen rather as a proxy for food provisioning and vegetation structure, rather than as a final outcome variable. Concentrating only on the aboveground part of the dataset, and turning plant productivity into an outcome variable (i.e. a variable only receiving arrows) shows that bottom-up effects remain a dominant mechanism in grassland ecosystems (**Figure 1b**), and the strongest (yet non-significant) path goes from plant diversity to productivity (path coefficient=0.62, dashed arrow).

In Li et al.'s study (**Figure 1c**), this direct path from tree diversity to productivity (timber volume) is basically absent, and there is a strong and significant positive effect of natural enemies on timber volume. Additionally, higher herbivore diversity is apparently reducing timber volume (red dashed arrow).

Li et al. are of course not the first to look into multitrophic biodiversity effects. For example, already back in the 1990s, Mulder et al. 1999 used soil and foliar insecticides to remove whole insect communities from experimental grassland plots and found strong increases in aboveground plant biomass under arthropod removal. However, the authors used a blanket exclusion of all arthropods (both herbivores and their natural enemies), not allowing for more fine-grained mechanistic insights. Recently, within the framework of two large grassland biodiversity experiments (Jena/Germany and Cedar Creek/ Minnesota, USA), Barnes et al. 2020 reported that plant diversity reduces loss of primary production to herbivores, indirectly benefiting predators in species-rich ecosystems. Studies directly manipulating diversity of higher trophic levels (and then investigating effects on primary productivity) are much rarer and much more difficult to set up. One example is a study by Deraison et al. who manipulated herbivore species richness and functional group identity, experimentally showing that impacts on aboveground plant biomass are indeed stronger if more herbivore species are present.

The analyses of Li et al now open up an exciting avenue – their study is among the first to show that multitrophic interactions modify the relationship between plant diversity and productivity. Could such a finding be translated into various different ecosystem types, including arable farming? There are some first studies looking into cropping system diversification that also indicate beneficial effects of crop diversity for different groups of arthropods (Brandmeier et al. 2021). Such findings are also backed up by recent meta-analyses pointing into a similar direction.

Li et al.'s paper just has come at the right time – providing a generalizable framework to test multitrophic biodiversity effects on productivity. It is now time to employ there hypothesis framework across different ecosystem contexts – extending the viewpoint from forests to grasslands, arable land, and potentially also aquatic ecosystems such as aquaculture. If higher trophic levels consistently keep pests under control, then this should lead to a mind shift in our overall approaches to managing production ecosystems. Managing multitrophic networks without losing yield is certainly a challenge for agriculture, forestry and fisheries alike.

## **Compliance and ethics**

82 The author(s) declare that they have no conflict of interest.

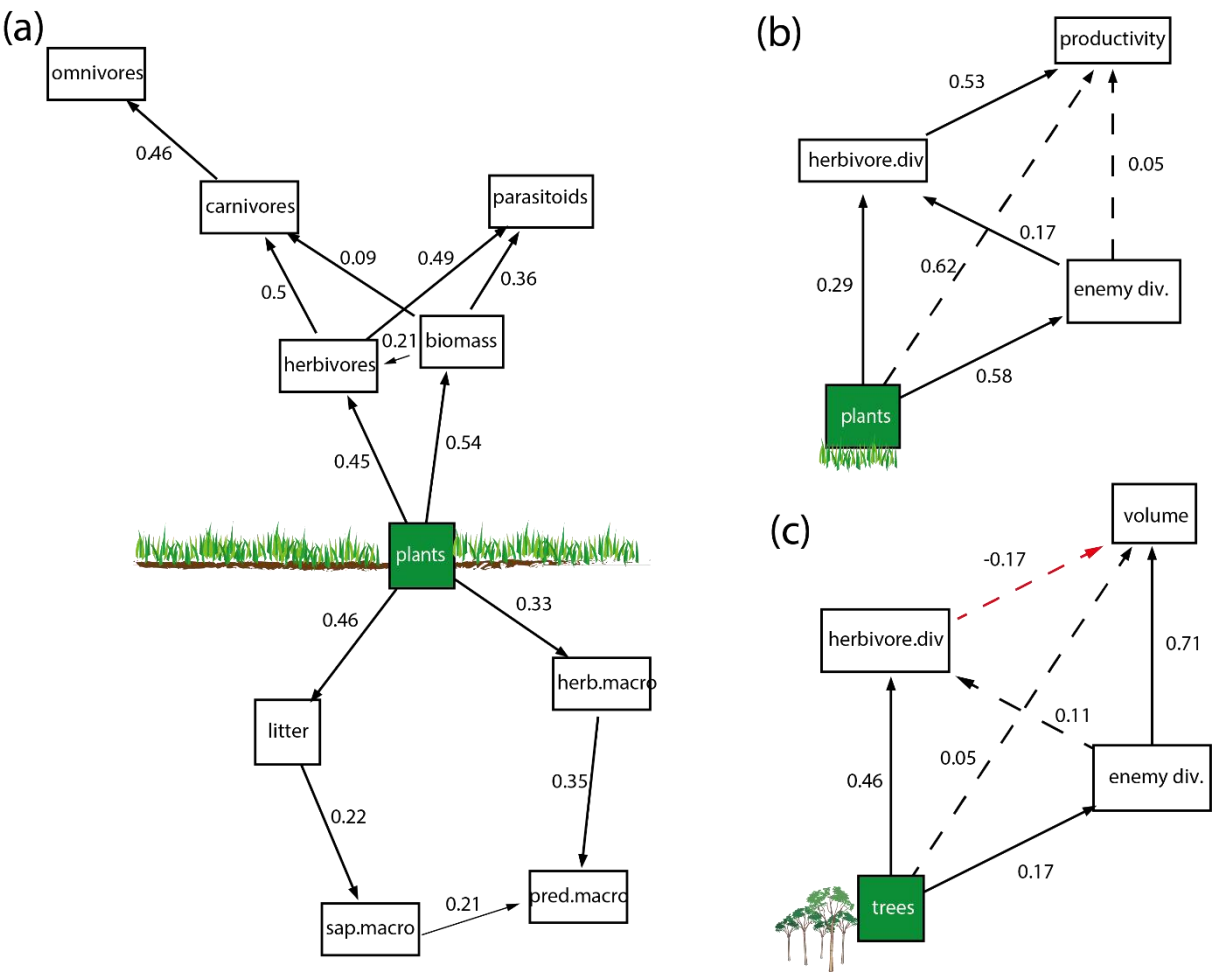
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120 **Figure 1** Convergent structural equation models (SEM) on multitrophic biodiversity effects on yield  
121 across ecosystems.

122 (a) a reanalysis of the data presented in Figure 3 of Scherber et al. (2010). The path diagram shows  
123 abundance data and standardized path coefficients calculated from individual generalized linear  
124 models. (b) SEM on the aboveground part of the data, using species richness (not abundance) of  
125 herbivores and enemies; parasitoids and carnivores are combined into "natural enemies" for  
126 comparison with Li et al.'s paper. (c) SEM for Li et al.'s data, based on aggregate values and also  
127 using species richness of herbivores and enemies. SEMs in (b) and (c) are saturated to allow for  
128 estimates of all paths. All analyses were done using piecewise SEMs based on generalized linear  
129 models with negative binomial errors for count data and Gaussian or Gamma errors for continuous  
130 data. Plant species richness was log-transformed in both analyses. N=50 for Fig. 1a,b; N=47 for Fig.  
131 1c.

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