

Investigating plant-soil feedbacks in tropical montane forest trees

Iveren Abiem^{1,2,3}  and Hazel M. Chapman^{1,3}

Short Communication

Cite this article: Abiem I and Chapman HM (2025). Investigating plant-soil feedbacks in tropical montane forest trees. *Journal of Tropical Ecology*. **41**(e18), 1–5. doi: <https://doi.org/10.1017/S0266467425100060>

Received: 17 June 2024

Revised: 3 March 2025

Accepted: 29 April 2025

Keywords:

Afromontane forest; Ngel Nyaki Forest Reserve; Nigeria; plant-microbe interactions; seedlings; shade-house experiment; species coexistence

Corresponding author:

Iveren Abiem; Email: abiemiveren@gmail.com

¹Department of Plant Science and Biotechnology, University of Jos, Jos, Nigeria; ²School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand and ³Nigerian Montane Forest Project, Yelwa Village, Taraba State, Nigeria

Abstract

Plant-soil microbial interactions play a central role in maintaining biodiversity and coexistence in terrestrial ecosystems. However, to what extent plant-soil feedbacks (PSFs) operate in tropical Afromontane forests remains unclear. In this study, we conducted a PSF shade house experiment using six tree species exhibiting diverse life-history strategies and abundances in a sub-tropical montane forest in Nigeria. Seedlings were grown under controlled conditions in sterilised soil with or without soil inoculum collected under mature trees of each of the six species. We assessed whether conspecific tree seedlings' performance was altered in comparison to heterospecific seedlings when grown in the soil of their adult trees. Seedling growth did not significantly differ between inocula from conspecific and heterospecific adults in five of the six species tested, indicating no evidence of PSFs. In *Garcinia smeathmannii*, we found a significant increase in seedling growth when grown in conspecific soil inocula. Given that no PSFs were observed in five out of six species, our study suggests that PSFs may play a limited role in the performance of some species in this Afromontane ecosystem. Nonetheless, the facilitative interaction noted in *Garcinia smeathmannii* indicates a nuanced ecological dynamic worth further exploration.

Introduction

Increasing evidence suggests that interactions between plants and their soil are important determinants of the structure of plant communities through plant-soil feedbacks (PSFs). PSFs arise through plants changing the biotic and abiotic properties of the soils they inhabit, which may then influence plant growth (Bever 2003, Van Der Putten *et al.* 2013). A plant species may influence soil conditions in a way that supports its growth (positive feedback) or hinders its development (negative feedback). Positive PSFs arise through the accumulation of soil nutrients (Berendse 1990, Chapman *et al.* 2006, Wardle 1999) or symbiotic mutualists (Klironomos 2002, Van Der Putten *et al.* 2016) and may eventually lead to clumped distribution patterns or monodominance (Crawford & Knight 2017, Dickie *et al.* 2014, Teste *et al.* 2017). Positive PSFs could be used to explain conspecific facilitation when a plant modifies its soil environment in a way that has positive effects on its conspecifics (Reinhart *et al.* 2021). Negative feedbacks are generated through nutrient depletion (Berendse, 1994) or changes in litter quality and nutrient cycling (Bennett & Klironomos 2018), or the accumulation of soil pathogens (Bever *et al.* 2015, Chung & Rudgers 2016, Smith-Ramesh & Reynolds 2017, Van Der Putten *et al.* 2016.). Soil microbial effects tend to be much stronger than nutrient effects (Ke *et al.* 2015) and are most pronounced at the seedling stage. Negative soil feedbacks occur when a plant modifies its soil biota in a way that inhibits conspecific more than heterospecific neighbours (Bever *et al.* 2015, Mangan *et al.* 2010).

Evidence suggests that rare species are more prone to negative PSFs than abundant species (Klironomos 2002, Maron *et al.* 2016, Thakur *et al.* 2021). Plants' traits may also help predict the direction of PSFs; fast growth rates and larger specific leaf areas are associated with more negative values (Maron *et al.* 2016, Xi *et al.* 2021, Xi *et al.* 2023) while larger seed size is associated with more positive (or less negative) values (Xi *et al.* 2021). Thus, fast-growing, small-seeded plants investing less in traits associated with natural enemy defence are predicted to have more negative PSFs than slower-growing, large-seeded species (Xi *et al.* 2021). Shade tolerance can also influence the direction of PSFs; shade-tolerant species tend to be slower growing and allocate more resources towards enemy defence, thus having a less negative PSF (Xi *et al.* 2021).

In this study, we explored the relative contribution of soil biota in generating negative feedback across six plant species with different abundances, seed traits and shade tolerance in a West African montane forest. A shade-house experiment was used to assess PSFs on plant performance. Our specific question was: Does the performance of conspecific seedlings differ when grown in the presence of soil biota associated with their adult trees compared to the soil biota of heterospecific adults? Earlier studies in this forest demonstrated weak or non-existent

© The Author(s), 2025. Published by Cambridge University Press. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

Table 1. Plant species used in the experiments and their families, growth form, shade tolerance and the density of adult trees/hectare in the 20.28 ha ForestGEO Plot. Details of species shade tolerance extracted from Abiem *et al.* 2021

Species name	Family	Growth form	Density (trees/ha)	Shade tolerance
<i>Anthonotha noldeae</i>	Fabaceae	Canopy	42	Pioneer
<i>Chrysophyllum albidum</i>	Sapotaceae	Canopy	57	Shade tolerant
<i>Deinbollia pinnata</i>	Sapindaceae	Understory	159	Shade tolerant
<i>Entandrophragma angolense</i>	Meliaceae	Emergent	5	Non-pioneer light demanding
<i>Garcinia smeathamannii</i>	Clusiaceae	Understory	608	Shade tolerant
<i>Ekebergia capensis</i>	Simaroubaceae	Canopy	<0.1	Pioneer

Table 2. Statistical results from the shade house experiment evaluating the biomass in seedlings of *Anthonotha noldeae*, *Chrysophyllum albidum*, *Deinbollia pinnata*, *Entandrophragma angolense*, *Garcinia smeathamannii* and *Ekebergia* sp. in potted soils containing live inoculum from conspecific or heterospecific adult trees

Species	F-value	P-value
<i>Anthonotha noldeae</i>	0.539	0.743
<i>Chrysophyllum albidum</i>	1.803	0.233
<i>Deinbollia pinnata</i>	0.264	0.925
<i>Entandrophragma angolense</i>	1.780	0.198
<i>Garcinia smeathamannii</i>	4.387	0.013
<i>Ekebergia</i> sp.	2.391	0.100

negative density/distance effects associated with Janzen-Connell effects (Abiem *et al.* 2021, Matthesius *et al.* 2011), which were outweighed by facilitation (Abiem *et al.* 2021). This study is the first, to our knowledge, to investigate PSFs in an Afrotropical forest.

Methods

Study site

Our study was based in the Ngel Nyaki Forest Reserve on the Mambilla Plateau in southeast Nigeria (7.0876°N, 11.0534°E, ~1650 m a.s.l.). The 46 km² reserve comprises mainly degraded, grazed savannah but includes two forest fragments, the Ngel Nyaki fragment being approximately 5.2 km² in area (Yadok *et al.* 2019). The forest is a sub montane to mid altitude forest (Chapman *et al.* 2004). The climate is characterised by an average annual precipitation of ~2300 mm, which falls between the months of April and October and a mean monthly maximum and minimum temperatures for the wet and dry seasons as 25.6 and 15.4°C, and 28.1 and 15.5°C respectively (Unpublished data from Nigerian Montane Forest Project). The soil is volcanic and has a high clay content with a pH ranging between 6 and 6.5 (Chapman & Chapman 2001).

Seedling species

We conducted a multispecies shade house experiment using six target species which vary in density and represent a range of ecological characteristics (Table 1). We included the most common species in the 20.28 ha ForestGeo plot *Garcinia smeathamannii* (608 individuals/ha) and *Deinbollia pinnata* (159 individuals/ha); not so

common species, *Entandrophragma angolense* (5 individuals/ha); and a rare species, *Ekebergia capensis* (<0.1 individuals/ha). *G. smeathamannii* is a small understory tree forming monospecific stands with evidence of clonal reproduction through root suckers (Tembe & Deodhar 2011).

Experimental setup, data collection and analysis

We collected fruits from at least three individual trees each of *Entandrophragma angolense* (Meliaceae), *Chrysophyllum albidum* (Sapotaceae), *Deinbollia pinnata* (Sapindaceae), *Anthonotha noldeae* (Fabaceae), *Ekebergia* sp (Meliaceae) and *Garcinia smeathamannii* (Clusiaceae). Seeds were removed from the fruits of plants and surface sterilised for 1 minute in 50% commercial bleach solution (sodium hypochlorite) and then washed thoroughly with distilled water. These seeds were planted in seed trays filled with steam-sterilised sand and raised for two months before they were transplanted.

Our inoculum for each species was soil collected from 2 m away from the base of three adult trees per species and homogenised (Adopted from Mangan *et al.* 2010). All the soil (a combination of 1 part forest soil and 3 parts sand) for the experiment was steam sterilised to remove biotic differences among the treatments. We filled 192 polypots (10 cm diameter × 20 cm depth) with this sterilised soil mixture and then added to each pot about 50 ml (5% of the total soil volume) of inoculum, each polypot being inoculated with the inoculum of one tree species. One seedling of each of the six tree species in the experiment was planted in each pot. Our experiment included conspecific combinations where we planted the seedling of each species in inoculum from conspecific adults, and heterospecific combinations where seedlings of each species were planted with inoculum of each of the five other species individually. The conspecific combination was replicated five times for each species and the heterospecific combination was replicated three times for each species. As a control, two replications of the plant-inoculum combinations were set up using sterilised inoculum, to account for differences from abiotic factors. The pots were placed randomly on two benches in the middle of the shade house and watered every other day for six months. The shade house comprised a wooden frame lined with mosquito netting and covered with a grass-thatched roof. Seedling growth and survival were recorded every two weeks for six months, after which all the plants were harvested, and their total biomass was estimated. We calculated the relative growth rate (RGR) for each individual for the six-month period as $\log(\text{size}_{t+1}) - \log(\text{size}_t) / \text{time}$, where size_{t+1} and size_t corresponds to the height of seedlings at the end of the six-month period of experiment and the start of the experiment respectively.

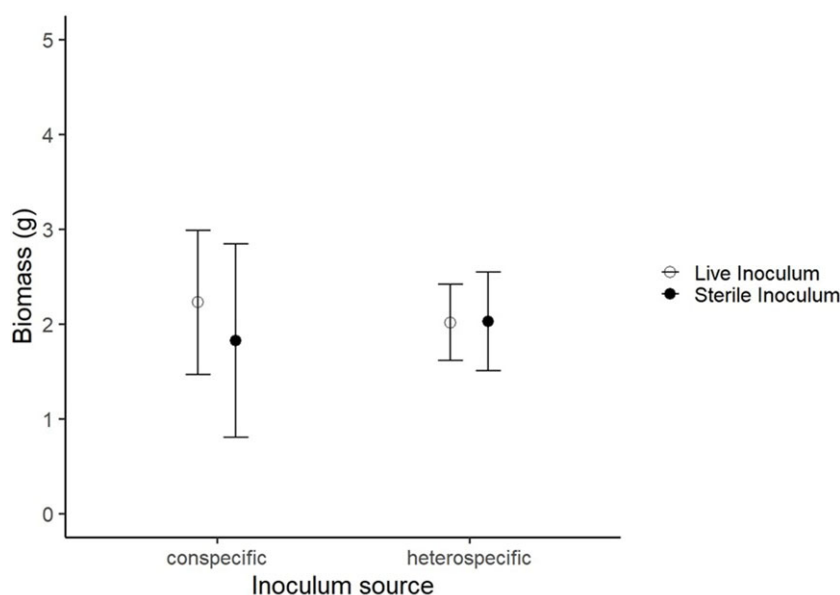


Figure 1. Mean ($\pm$ SE) seedling biomass across live and sterile inocula from conspecific and heterospecific adults.

We analysed the data using the Two-way Analysis of Variance (ANOVA) test to examine if seedling biomass differed between sterile and live soil inoculum sources (conspecific and heterospecific). We also carried out ANOVA test at the species level to test if biomass differed across inoculum sources (conspecific and heterospecific species).

Results

Effects of plant-soil feedback on plant biomass and growth rate

A total of 165 seedlings survived the experiment and for these, we measured biomass and relative growth rates. We found little evidence for plant-soil feedback; across five of the six species used in the experiment (Figure 2). Seedling biomass did not differ among those grown in inocula from conspecific adults versus heterospecific adults, or between the live biota and sterile inocula (Figure 1).

The biomass of *G. smeathmannii* seedlings did show significant variation across live inocula ($F_{5,19} = 4.387$, $P = 0.013$, Table 2; Figure 2).

Discussion

Despite the variation among species in abundance, shade tolerance and seed sizes, we found no evidence of PSFs in five of the six species used in our experiment. This is contrary to the findings from many other studies across a range of locales and vegetation types which report negative (Bezemer *et al.* 2018, Klironomos 2002, Kulmatiski *et al.* 2008, Mangan *et al.* 2010) and sometimes positive (Bauer *et al.* 2015, Smith & Reynolds 2015) conspecific PSFs. The only significant PSF we observed was in *Garcinia smeathmannii*. *G. smeathmannii* is the most abundant species in the Ngel Nyaki ForestGEO plot, so theoretically, if any species did show a positive PSF it should be *G. smeathmannii*; because being an abundant tree species could mean that it is less susceptible to the harmful effects of its associated soil community than a rare tree species (Mangan *et al.* 2010). In a study in Barro Colorado Island

(BCI), Mangan *et al.* (2010) reported that less common species showed stronger negative feedbacks than common species. Again, in a meta-analysis of results from 22 experiments, Reinhart *et al.* (2021) showed that harmful soil biota impacted rare species more. However, the strength and direction of PSFs are often context-dependent (Bennett and Klironomos 2019, De Long *et al.* 2019, Xi *et al.* 2023) and the results of experiments in glasshouses and shade houses may not be applicable to field conditions. Schittko *et al.* (2016) argue that negative PSFs are more likely to be found under glasshouse conditions than in nature. Also, *G. smeathmannii* is an understory species in Ngel Nyaki Forest and studies have shown that light levels can influence the strength of PSFs in understory species (Smith & Reynolds 2015, Xi *et al.* 2020, Xi *et al.* 2023). Plus, positive PSFs in these shaded plants may be facilitated by ectomycorrhizal fungal communities, which improve their nutrient acquisition. There is however very little that is known about the link between ectomycorrhizal fungi and seedlings of monodominant trees in the tropics (Delevich *et al.* 2021).

Given the context and the small sample size of our experiment, we cannot adequately conclude that there are positive effects; however, results from a community-wide study on density dependence (Abiem *et al.* 2021) suggested the possibility of facilitation (Goldenheim *et al.* 2008), or pathogen suppression by mycorrhizal fungi (Liang *et al.* 2015). An alternative explanation may be that the relatively drier and colder environment of Ngel Nyaki Forest does not support as many species-specific pathogens that generate strong negative feedback as in more tropical climates. Pathogens are especially abundant in warmer and wetter environments (Comita & Engelbrecht 2014, Inman-Narahari *et al.* 2016) such as lowland tropical forests which have reported strong negative conspecific density dependence (Lamanna *et al.* 2017). Alternatively, there is the possibility that factors other than soil biota may be causing the conspecific negative effects that are observed in Ngel Nyaki Forest; for instance, distance-dependent herbivory was reported on some plant species by Matthesius *et al.* (2011).

Plant-soil feedbacks (PSFs) are a mechanism through which soil microbes influence species diversity in plant communities. However, the consistency of PSFs among plant species remains unclear.

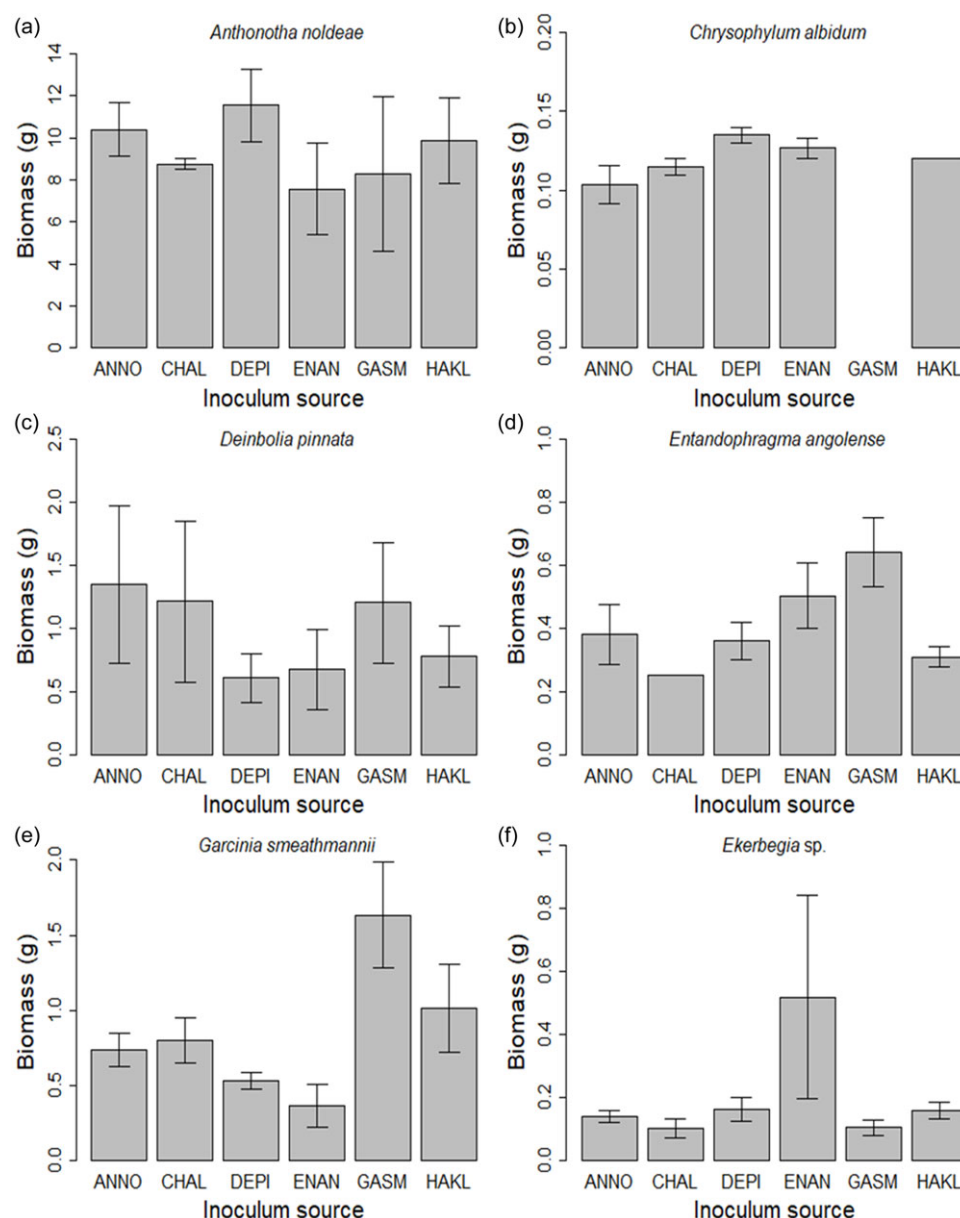


Figure 2. Mean ($\pm$ SE) biomass of (a.) *Anthonotha noldeae* (ANNO), (b.) *Chrysophyllum albidum* (CHAL), (c.) *Deinbolia pinnata* (DEPI), (d.) *Entandophragma angolense* (ENAN), (e.) *Garcinia smeathmannii* (GASM) and (f.) *Ekebergia sp.* (HAKL) estimated from shade house experiment comparing growth in response to six inoculum sources (one conspecific and five heterospecific). The ANOVA F and P values are reported in Table 2. (where error bars are absent, there was only one data point for the groups because the replicates died during the experiment).

Conclusions

This study showed that for a range of Afromontane species, negative plant-soil feedback does not influence seedling performance. While our results suggest that this mechanism may be present in some species, it is not sufficiently widespread to regulate plant populations and drive community dynamics. Further work on *G. smeathmannii* as well as more species is needed to confirm our interpretation of these results.

Acknowledgements. We wish to thank the management and staff of the Nigerian Montane Forest Project for helping with field work and logistics support. This study is a part of IA's PhD thesis that was funded by the University of Jos NEEDS assessment programme, Nigeria and a grant from the A. G. Leventis Foundation.

Financial Support. IA received a research grant from the Smithsonian Institute's Forest Global Earth Observatory (ForestGEO) for this project (Project ID 341243).

Competing interests. Authors declare none.

References

- Abiem I, Dickie I, Kenfack D and Chapman H (2021) Conspecific negative density dependence does not explain coexistence in a tropical Afromontane forest. *Journal of Vegetation Science* **32**, e12990.
- Bauer JT, Mack KM and Bever JD (2015) Plant-soil feedbacks as drivers of succession: evidence from remnant and restored tallgrass prairies. *Ecosphere* **6**, 1–12.
- Bennett JA and Klironomos J (2018) Climate, but not trait, effects on plant-soil feedback depend on mycorrhizal type in temperate forests. *Ecosphere* **9**, e02132.
- Bennett JA and Klironomos J (2019) Mechanisms of plant-soil feedback: interactions among biotic and abiotic drivers. *New Phytologist* **222**, 91–96.
- Berendse F (1990) Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. *The Journal of Ecology*, 413–427.

- Berendse F (1994) *Ecosystem stability, competition, and nutrient cycling*. In: *Biodiversity and Ecosystem Function*. Springer, pp 409–431.
- Bever JD (2003) Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New phytologist* **157**, 465–473.
- Bever JD, Mangan SA and Alexander HM (2015) Maintenance of plant species diversity by pathogens. *Annual Review of Ecology, Evolution, and Systematics* **46**, 305–325.
- Bezemer TM, Jing J, Bakx-Schotman JT, and Bijleveld EJ (2018) Plant competition alters the temporal dynamics of plant-soil feedbacks. *Journal of Ecology* **106**, 2287–2300.
- Chapman HM, Olson SM and Trumm D (2004) An assessment of changes in the montane forests of Taraba State, Nigeria, over the past 30 years. *Oryx* **38**, 282–290. [10.1017/s0030605304000511](https://doi.org/10.1017/s0030605304000511).
- Chapman J and Chapman H (2001) *The forests of Taraba and Adamawa States, Nigeria. An Ecological Account and Plant Species Checklist*. Christchurch, New Zealand.
- Chapman SK, Langley JA, Hart SC and Koch GW (2006) Plants actively control nitrogen cycling: uncorking the microbial bottleneck. *New Phytologist* **169**, 27–34.
- Chung YA and Rudgers JA (2016) Plant–soil feedbacks promote negative frequency dependence in the coexistence of two aridland grasses. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20160608.
- Comita LS and Engelbrecht BM (2014) Drought as a driver of tropical tree species regeneration dynamics and distribution patterns. *Forests and global change*, 261–308.
- Crawford KM and Knight TM (2017) Competition overwhelms the positive plant–soil feedback generated by an invasive plant. *Oecologia* **183**, 211–220.
- Delevich CA, Koch RA, Aime MC and Henkel TW (2021) Ectomycorrhizal fungal community assembly on seedlings of a Neotropical monodominant tree. *Biotropica* **53**, 1486–1497. <https://doi.org/10.1111/btp.12989>
- De Long JR, Fry EL, Veen G and Kardol P (2019) Why are plant–soil feedbacks so unpredictable, and what to do about it? *Functional Ecology* **33**, 118–128.
- Dickie IA, Koele N, Blum JD, Gleason JD and Mcglone MS (2014) Mycorrhizas in changing ecosystems. *Botany* **92**, 149–160.
- Goldenheim WM, Irving AD and Bertness MD (2008) Switching from negative to positive density-dependence among populations of a cobble beach plant. *Oecologia* **158**, 473–483. [10.1007/s00442-008-1157-0](https://doi.org/10.1007/s00442-008-1157-0).
- Inman-Narahari F, Ostertag R, Hubbell SP, Giardina CP, Cordell S and Sack L (2016) Density-dependent seedling mortality varies with light availability and species abundance in wet and dry Hawaiian forests. *Journal of Ecology* **104**, 773–780.
- Ke PJ, Miki T and Ding TS (2015) The soil microbial community predicts the importance of plant traits in plant–soil feedback. *New phytologist* **206**, 329–341.
- Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* **417**, 67–70.
- Kulmatiski A, Beard KH, Stevens JR and Cobbold SM (2008) Plant–soil feedbacks: a meta-analytical review. *Ecology letters* **11**, 980–992.
- Lamanna JA, Mangan SA, Alonso A, Bourg NA, Brockelman WY, Bunyavechewin S, Chang L-W, Chiang J-M, Chuyong GB and Clay K (2017) Plant diversity increases with the strength of negative density dependence at the global scale. *Science* **356**, 1389–1392.
- Liang M, Liu X, Etienne RS, Huang F, Wang Y and Yu S (2015). Arbuscular mycorrhizal fungi counteract the Janzen–Connell effect of soil pathogens. *Ecology* **96**, 562–574. [10.1890/14-0871.1](https://doi.org/10.1890/14-0871.1).
- Mangan SA, Schnitzer SA, Herre EA, Mack KM, Valencia MC, Sanchez EI & Bever JD (2010) Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466**, 752–755.
- Maron JL, Laney A, Ortega YK, Pearson DE and Callaway RM (2016) Negative plant-soil feedbacks increase with plant abundance, and are unchanged by competition. *Ecology* **97**(8), 2055–2063. <https://doi.org/10.1002/ecy.1431>
- Matthesius A, Chapman H and Kelly D (2011) Testing for Janzen–Connell effects in a west African montane forest. *Biotropica* **43**, 77–83.
- Reinhart KO, Bauer JT, McCarthy-Neumann S, MacDougall AS, Hierro JL, Chiuffo MC, Mangan SA, Heinze J, Bergmann J, Joshi J, Duncan RP, Diez JM, Kardol P, Rutten G, Fischer M van der Putten WH, Bezemer TM and Klironomos J (2021) Globally, plant-soil feedbacks are weak predictors of plant abundance. *Ecology and Evolution* **11**, 1756–1768. <https://doi.org/10.1002/ece3.7167>
- Schittko C, Runge C, Strupp M, Wolff S and Wurst S (2016) No evidence that plant–soil feedback effects of native and invasive plant species under glasshouse conditions are reflected in the field. *Journal of Ecology* **104**, 1243–1249.
- Smith-Ramesh LM and Reynolds HL (2017) The next frontier of plant–soil feedback research: unraveling context dependence across biotic and abiotic gradients. *Journal of Vegetation Science* **28**, 484–494.
- Smith LM and Reynolds HL (2015) Plant–soil feedbacks shift from negative to positive with decreasing light in forest understory species. *Ecology* **96**, 2523–2532.
- Tembe RP and Deodhar MA (2011) Clonal propagation and hydroxycitric acid production from in vitro shoot cultures of *Garcinia indica* using root suckers as explant. *In Vitro Cellular & Developmental Biology-Plant* **47**, 399–409.
- Teste FP, Kardol P, Turner BL, Wardle DA, Zemunik G, Renton M and Laliberté E (2017) Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science* **355**, 173–176. <https://doi.org/10.1126/science.aai8291>
- Thakur MP, Van Der Putten WH, Wilschut RA, Veen GC, Kardol P, Van Ruijven J, Allan E, Roscher C, Van Kleunen M and Bezemer TM (2021) Plant–soil feedbacks and temporal dynamics of plant diversity–productivity relationships. *Trends in Ecology & Evolution* **36**, 651–661.
- Van Der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A and Schweitzer JA (2013) Plant–soil feedbacks: the past, the present and future challenges. *Journal of Ecology* **101**, 265–276.
- Van Der Putten WH, Bradford MA, Pernilla Brinkman E, Van De Voorde TFJ and Veen GF (2016) Where, when and how plant–soil feedback matters in a changing world. *Functional Ecology* **30**(7), 1109–1121. <https://doi.org/10.1111/1365-2435.12657>
- Wardle DA (1999) How soil food webs make plants grow. *Trends in Ecology & Evolution* **14**, 418–420.
- Xi N, Adler PB, Chen D, Wu H, Catford JA, Van Bodegom PM, Bahn M, Crawford KM and Chu C (2021) Relationships between plant–soil feedbacks and functional traits. *Journal of Ecology* **109**, 3411–3423.
- Xi N, Bloor JM and Chu C (2020) Soil microbes alter seedling performance and biotic interactions under plant competition and contrasting light conditions. *Annals of Botany* **126**, 1089–1098.
- Xi N, McCarthy-Neumann S, Feng J, Wu H, Wang W and Semchenko M (2023) Light availability and plant shade tolerance modify plant–microbial interactions and feedbacks in subtropical trees. *New Phytologist* **238**, 393–404.
- Yadok BG, Forget P-M, Gerhard D and Chapman H (2019) Low fruit-crop years of *Carapa oreophila* drive increased seed removal and predation by scatterhoarding rodents in a West African forest. *Acta Oecologica* **99**, 103448.