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Short Communication

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Investigating plant-soil feedbacks in tropical montane forest trees

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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

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

 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

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

Species	<i>F</i> -value	P-value
Anthonotha noldeae	0.539	0.743
Chrysophyllum albidum	1.803	0.233
Deinbolia pinnata	0.264	0.925
Entandophragma angolense	1.780	0.198
Garcinia smeathamannii	4.387	0.013
Ekebergia 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 Afromontane 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 smeathmanii* (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. smeathmanii* 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 *Entandophragma angolense* (Meliaceae), *Chrysophyllum albidum* (Sapotaceae), *Deinbolia pinnata* (Sapindaceae), *Anthonotha noldeae* (Fabaceae), *Ekerbergia* sp (Meliaceae) and *Garcinia smeathmannii* (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 \times 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_{t+1} and size t_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 contextdependent (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 (±SE) biomass of (a.) Anthonotha noldeae (ANNO), (b.) Chrysophyllum albidum (CHAL), (c.) Deinbolia pinnata (DEPI), Entandophragma angolense (ENAN), (d.) (e.) Garcinia smeathamannii (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. smeathmanii* as well as more species is needed to confirm our interpretation of these results.

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Competing interests. Authors declare none.

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