THE UNIVERSITY OF
CHICAGO

October 26, 2021

Dear Editor,

Please find attached the manuscript, "No robust coexistence in a canonical model of plant-soil feedbacks," by Zachary R. Miller, Pablo Lechón, and Stefano Allesina, which we would like to submit to *Ecology Letters* as a Letter.

In recent decades, plant-soil feedbacks (PSFs) – indirect interactions between plants mediated by changes to local soil microbiota and chemistry – have emerged as a leading mechanism to explain widespread coexistence in natural plant communities. The study of PSFs, both in theory and in the field, has been guided by a modeling framework introduced by Bever, Westover, and Antonovics in a landmark 1997 paper. However, the now-canonical "Bever model" is formulated for only two species, while natural communities may contain tens or hundreds of co-occurring plants. Bridging this gap has been a crucial ongoing challenge for the field.

Here, we extend the Bever model to include an arbitrary number of species and use results from evolutionary game theory to thoroughly characterize coexistence in this extended model. Our central finding is that coexistence of more than two species is virtually impossible within this framework. We show that multi-species coexistence can only arise under highly artificial parameter combinations, and collapses when these conditions are violated even slightly. Such fine-tuned conditions never arise by chance, are not robust to inevitable biological variation, and cannot explain coexistence in real-world systems.

These surprising results have significant implications for plant community ecology. The Bever model undergirds the analysis and interpretation of PSF experiments across a wide array of systems, and our findings suggest that applying two-species predictions to richer communities will yield incorrect inference about plant coexistence. Abundant empirical evidence indicates that PSFs do play an important role in maintaining diversity in plant communities; the apparent contradiction between these observations and the model predictions calls for critical reevaluation of model assumptions and urgent exploration of alternative theoretical frameworks.

Our analysis illuminates a long-standing disconnect between the low diversity of a simple, but widely utilized, PSF model, and the high diversity of real-world ecosystems. By demonstrating that this well-known model is incompatible with multi-species coexistence mediated by PSFs, we believe our results will kickstart new interest and progress in the theory behind this rapidly advancing area of ecology. Publishing these findings in Ecology Letters will allow us to reach the broad range of theoreticians and experimentalists across community, plant, and soil ecology who work with and rely on PSF models.

We thank you for your time, and we look forward to hearing from you.

Sincerely,

Zachary R. Miller