THE UNIVERSITY OF CHICAGO

October 27, 2021

Dear Dr. Coulson,

Please find attached the manuscript, "No robust coexistence in a canonical model of plant-soil feedbacks," by Zachary R. Miller, Pablo Lechón-Alonso, 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 – have emerged as a leading mechanism to explain widespread coexistence in 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 communities.

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 lack of coexistence predicted by this model calls for critical reevaluation of model assumptions and urgent exploration of alternative theory.

Statement of novelty. 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. To our knowledge, this work is the first to characterize the dynamics of the Bever model in full generality, representing an advancement on recent efforts (e.g. Eppinga *et al.*, *Nature Ecology & Evolution 2018*; Mack *et al.*, *PLoS ONE* 2019). By demonstrating that this well-known PSF model is incompatible with multi-species coexistence, we believe our results will kickstart new interest and progress in the theory behind this rapidly advancing area of ecology. Publishing our 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 have not previously published research directly related to the Bever model for PSFs. In a recent manuscript (Miller & Allesina 2021, *in submission*), we introduce a mathematical model for a broad class of environmentally-mediated interactions, including PSFs as a typical example. This approach, which we cite in our present study, demonstrates how and when PSFs can facilitate the coexistence of many species, and represents an alternative framework for modeling these complex interactions.

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

Sincerely,

Zachary R. Miller