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Comment

Plant-soil feedback as a driver of spatial structure in ecosystems

A commentary on “Belowground feedbacks as drivers of spatial self-organization and community assembly” by Inderjit, Ragan M. Callaway and Ehud Meron

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Analysis of spatial structure in ecosystems provides an opportunity to identify ecological processes and species interactions that are key to the system’s functioning [90,79,46,58,22]. In addition, the spatial structure of ecosystems may mediate their response to rapid environmental change, which becomes increasingly relevant during the Anthropocene ([84,74,72,3,5,68]). Within plant communities, spatial structure can emerge from the accumulation and concentration of abiotic resources. Established theory has shown that this accumulation of abiotic resources may lead to spatial self-organization of vegetation, expressed through regular spatial patterns that may have important consequences for the functioning of these ecosystems [41,88,69]. The driving mechanism of this kind of patterning has been described as scale-dependent feedback, which is positive at the local scale (e.g. within a vegetation patch), but becomes negative with increasing spatial distance (e.g. outside of a vegetation patch, [70]).

Alternatively, spatial structure can emerge from plant host-induced changes in the composition of the community of soil organisms, which subsequently feed back to the fitness of both the host- and competing plant species [12,85,31,55]. Importantly, as recently highlighted by Inderjit, Callaway and Meron in their review (Inderjit et al. [33]), these latter feedbacks between plant hosts and soil biota may thus comprise an alternative driver of spatial self-organization, complementing established theory on spatial self-organization through abiotic resource accumulation. We agree with

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the authors that this notion deserves attention in future research efforts, and in this commentary we will outline several specific avenues of interest within the context of plant-soil community interactions. We focus in particular on plant-soil pathogen interactions, but note that similar considerations may apply to interactions with symbiotic mutualists, and that plant-soil community interactions could be further mediated by higher tropic levels within the soil food web and by secondary plant metabolites, including allelopathic compounds.

Within our current focus, we first explore the potential role of plant-soil pathogen interactions in driving spatial self-organization. Subsequently, we discuss how the occurrence of multiple feedbacks within the same system may jointly drive plant community dynamics. We then discuss in more detail the role of soil moisture in mediating plant-soil feedbacks, before concluding with an outlook to future research.

Self-organization through plant-soil pathogen feedbacks and implications for biodiversity

Mathematical theory and a growing body of empirical evidence suggest that host-specific soil pathogens may enable the coexistence of strongly competing plant species, and the maintenance of highly diverse plant communities [8,66,10,82,19,45,63]. Considering the local scale at which these plant-soil interactions occur, we would expect that host-specific soil pathogens could drive spatial self-organization in the form of regular patterns if the average dispersal rate of soil pathogens would exceed the average dispersal rates of their host [59]. This notion is supported by simulations of a spatially explicit plant-soil feedback model [23] that considers two competing plant species, with both these species being suppressed by host-specific soil pathogens (Fig. 1). In these model simulations, local positive feedback is generated by aboveground competition coefficients, with the strengths of interspecific competition exceeding the strengths of intraspecific competition. In addition, when the average dispersal rate of host-specific pathogens exceeds the dispersal rate of the host plant, the spread of pathogens generates longer-range negative feedback.

Future models may describe the soil community composition in more detail, which could allow for different subsets of the soil community (including both pathogens and symbiotic mutualists) generating local positive and longer-range negative feedback. Nevertheless, these initial model explorations already suggest that both the relative strength of plant-soil feedback and the relative dispersal capability of soil pathogens may affect the type of spatial self-organization that emerges (Fig. 1). Specifically, when plant-soil feedback is relatively weak, and the dispersal capacity of soil organisms is relatively slow, emergent spatial structures are driven by competitive effects between hosts. In the case where the local, competition-driven positive feedback dominates, monospecific patches form, with eventually one plant species excluding the other (Fig. 1; [58]; [55]). With increasing strength of negative plant-soil feedback, traveling spiral wave patterns can be observed (Fig. 1). This type of self-organization was also shown by Inderjit et al. [33], for the case of an intransitive network of three host species.

Our observation of spiral wave patterns driven by plant-soil feedback complements results derived from a non-spatial plant-soil feedback model [8], which showed that a system of two plant hosts and strong negative plant-soil feedback can already exhibit intransitive dynamics [66]. Combining experimental data and a model extension to multi-species plant communities, recent research has highlighted the potential of plant-soil feedbacks to create intransitive networks within more diverse plant communities as well ([19,48]). Finally, under relatively high dispersal rates of soil pathogens, regular spatial patterns can be observed (Fig. 1), similar to the type of patterns observed in the arid ecosystem model simulations presented by Inderjit et al. [33]. Interestingly, the strength of plant-soil feedback may constrain the characteristic scale at which pattern formation occurs, with stronger negative feedback leading to pattern formation at smaller spatial scales (Fig. 1).

An important question to address is how these processes would manifest themselves in highly diverse communities characterized by species-specific plant-soil community interactions [49,10,19]. As higher species richness is maintained by stronger negative plant-soil feedback [19], these communities may no longer yield identifiable (i.e. spatially regular) patterns, but may exhibit mixed patterns in which for example conspecific trees become increasingly overdispersed [92]. Similarly, spatial patterns of expansion through travelling waves may become disrupted by adult trees that may be able to survive in spite of strong negative effects exerted by the local soil community (e.g. [58]). For example, adult trees of *Prunus serotina* may still survive in locations where high exposure to wilting disease prevents the survival of offspring [61,64,65]. Hence, the connections from spatial patterning of vegetation to process may be most relevant for systems where feedback operates between relatively small numbers of plant species or functional groups.

For such systems, our initial theoretical explorations highlight a critical need for measurement of plant-soil feedback strengths, and relative rates of dispersal of plant hosts and soil organisms. Approaches to empirically quantify

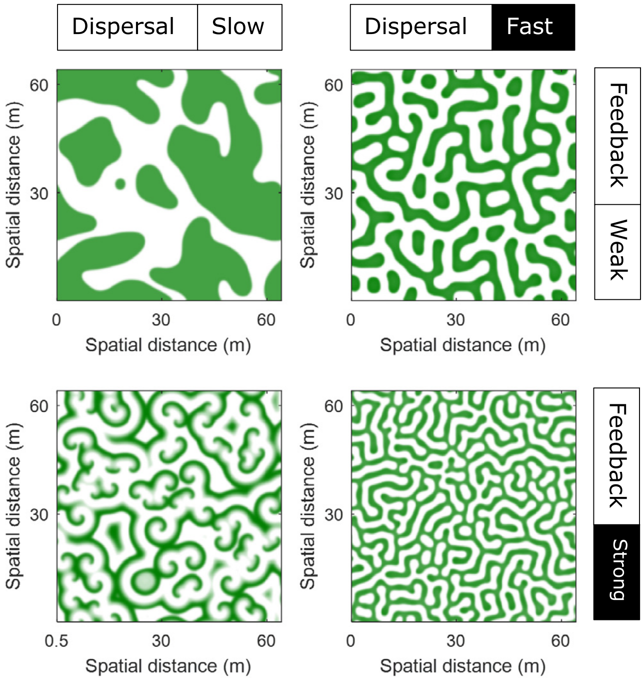

Fig. 1. Different types of spatial self-organization as observed in a spatially explicit plant-soil feedback (*adapted from [23]).a) Under weakly negative plant-soil feedback and the rate of dispersal of soil organisms being equal to the host plant's dispersal rate, two strongly competing plant species cannot coexist on the long term (here, plant species 1 (green) is slowly contracting to circular patches and excluded by plant species 2).b) Regular spatial patterns are observed when soil organisms' dispersal exceeds that of the plant. c) Travelling spiral waves are observed when feedback is strong and soil organismal dispersal is equal to that of the plant. d) Regular spatial patterns, as observed in b), form at a finer scale when the strength of negative plant-soil feedback is increased.*

Fig. 2. Within a scenario of two plant species experiencing strong negative plant-soil feedback, from relatively fast dispersing soil communities, variation in the relative growth rates of soil communities in space governs the self-organization process and the emerging vegetation patterns (*here, the abundance of plant species 1 is indicated in green*).

plant-soil feedback strengths have been well developed [86,6] and have been widely adopted [42,43,81,93,4,77,45,15]. This development has yielded a promising amount of empirical data that could be used to constrain parameters that quantify maximum plant-soil feedback strengths in spatial models. Within the spatially explicit model framework described above (Fig. 1), the rate at which the soil community composition differentiates, and hence plant-soil feedbacks build up, may affect the self-organization process and the type of patterning that is formed by the two competing plant host species (Fig. 2). In order to further develop our understanding of possible links between plant-soil feedbacks and spatial-self organization, we see two challenges for future empirical research: 1) quantification of the rates at which plant hosts can drive changes in soil microbial community composition, and 2) quantification of the rates of dispersal of (functional groups of) soil microbes that have differential impacts on plant fitness.

Empirical quantification of rates of differentiation and dispersal of root pathogens deserve attention, as these pathogens vary in their biology in interesting ways: some Oomycete pathogens including *Pythium* spp., for example, disperse through water, meaning that their dispersal capacity may be relatively limited, except with large precipitation events or in continuously saturated soils (e.g. [75]). In contrast, some Ascomycete pathogens including *Fusarium* spp., for example, can disperse farther and more rapidly through air (e.g. [83]). Dispersal of soil microbes may also interact with and depend on larger taxa functioning as vectors (e.g. [87]; [95]), highlighting an important consequence of soil biodiversity and even aboveground biota to consider when assessing pathogen dispersal rates.

Soil inoculation studies may provide empirical estimates for growth and dispersal rates, not only for root pathogens but also for other functional groups [60,37]. For example, it has been shown that the effects on plant growth of inoculation with native arbuscular mycorrhizal fungi in post agricultural environments can extend to several meters within a growing season ([57]), although these rates may also depend on the size of the plant hosts involved [91]. Environmental sequencing approaches could measure movement rates of microbial taxa more directly (e.g. [28]). Moreover, these latter approaches may also enable measurements of local relative growth rates of different functional groups of soil microbes (e.g. [16]).

In summary, considering this heterogeneity of local relative growth and dispersal rates of soil organisms may provide more insight into spatio-temporal development of plant-soil feedback within ecosystems. On the side of further theoretical development, corresponding modelling approaches would require a more detailed description of the soil community as well (e.g. [34]; [35]; [1]).

Self-organization through multiple, interacting feedbacks

As noted by Inderjit et al. [33], feedbacks involving abiotic resources and plant-soil community interactions may occur simultaneously within an ecosystem. Whether plant-soil feedbacks comprise a local feedback or a spatial, scale-dependent feedback may depend on the specific traits of the organisms involved. Similarly, feedbacks involving abiotic resources may be local or scale-dependent as well ([24,21,40]). How these two types of feedback jointly drive system dynamics may thus depend on whether they are both scale-dependent feedbacks, both local feedbacks, or whether one type is local while the other type is scale-dependent (Fig. 3). In their review, Inderjit et al. [33] describe the interesting case where two feedbacks are both scale-dependent, with environmental conditions determining which of the two feedbacks is dominant in driving the spatial patterns in resources ([27,33]). Related to this case, interactions between scale-dependent feedbacks may also be reflected in novel pattern morphologies, or they may be antagonistic and prevent self-organization in the form of regular spatial patterns ([20]).

In cases where two types of scale-dependent feedbacks differ in their characteristic spatial scale, self-organization may also emerge in the form of multi-scale patterns, for example a pattern of regularly spaced patches with each patch containing regular spatial patterns within [47,76]. Previous research has also shown that in systems where pattern formation occurs through one scale-dependent feedback, an additional local positive feedback may sharpen ecotones, and may create a larger region of hysteresis between ecosystem thresholds marking transition points between patterned and spatially homogeneous states ([24]). Finally, while systems with only local positive feedbacks may not exhibit spatial self-organization in the form of regular spatial patterns, the relative strength of each feedback may determine critical patch sizes above which a particular type of vegetation is able to expand, for example [55,56]. Thus, in cases where multiple feedbacks occur simultaneously within a system (e.g. abiotic resource-related feedbacks and plant-soil feedbacks), it is important to understand whether these are local or scale-dependent feedbacks. In fact, whether these feedbacks are local or scale-dependent may depend on ecosystem characteristics and environmental conditions, which in turn may constrain the possibilities for self-organization within the ecosystem (Fig. 3). Further theoretical research could focus on cataloguing the range of possibilities (Fig. 3) more completely, while empirical research may determine the feedback types (i.e. local or scale-dependent) and their relative strengths for particular ecosystems.

Soil moisture dynamics mediating plant-soil feedbacks and self-organization

In addition to the possibility of co-occurring feedbacks described above, Inderjit et al. [33] also highlight a case where plant-water dynamics and plant-soil interactions would be mechanistically linked, which may mediate or modify plant-soil feedbacks. One potential mechanism, as explained by Inderjit et al. [33] and highlighted above for the case of some Oomycetes, is that water transport may also redistribute soil organisms. In line with this notion are observations of increased motility of microbes in soils with higher water content [95]. Recent research has also emphasized another type of mechanism, in that plant hosts' influence on soil community composition may depend on local soil moisture content (reviewed in [82]). In general, the abundance of soil biota is expected to decrease with decreasing soil moisture (e.g. [38]). In addition, the changes in bacteria may become more pronounced with decreasing soil

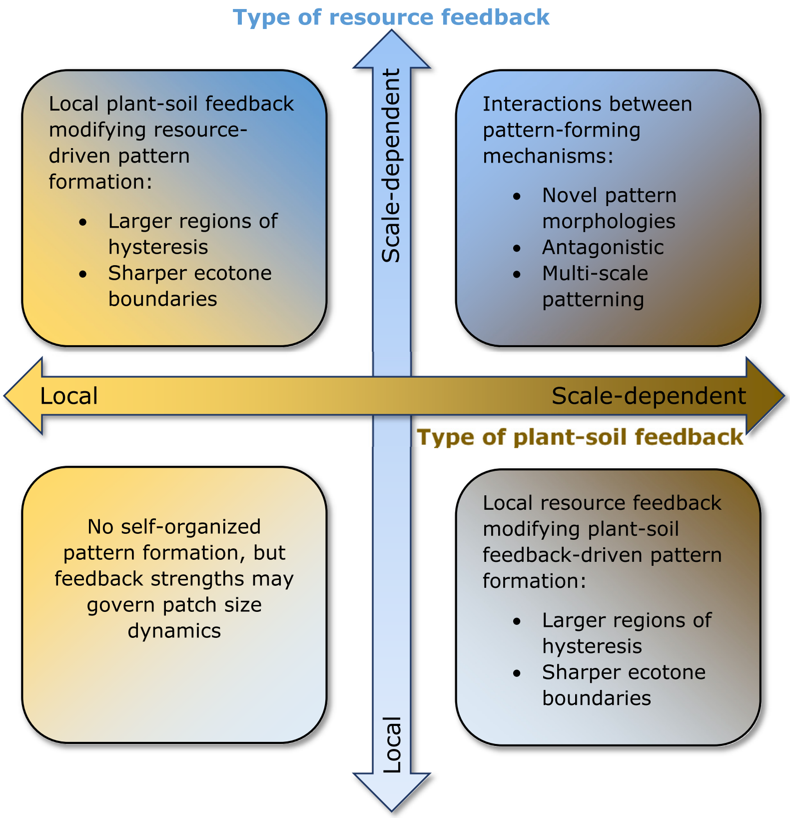

Fig. 3. In systems where plant-soil feedback and feedbacks involving abiotic resource accumulation and concentration occur simultaneously, the effects of these feedbacks will depend on whether they comprise a local or scale-dependent feedback. Hence, when two feedbacks occur simultaneously, four scenarios can be distinguished that differ in the potential of the feedbacks driving spatial self-organization within the ecosystem.

moisture, as compared to fungi [18,17]. As a result, spatial variation in soil moisture, driven by resource concentration mechanisms, may induce spatial variation in soil community composition and therefore the strength or even the sign (i.e. positive or negative) of plant-soil feedback [53,54].

It has been hypothesized that these effects of moisture and plant-soil feedbacks may be stronger in forest than in grassland ecosystems [25,82]. For eastern US deciduous forests, it has been suggested that higher tree diversity in wetter climatic regions may result from the moister soils increasing the growth rate and abundance of host-specific pathogens [9,10,36]. The same mechanism may also partly explain the higher diversity of tropical forests as compared to deciduous forests [14,49,10]. While these previous studies have focused on soil moisture variation over time, or variation along climatic gradients, it would be interesting to explore how spatial variation in soil moisture conditions at the landscape scale, as driven by resource concentration feedbacks, would modify strengths of plant-soil feedbacks. In turn, it would be of interest to explore whether these modified plant-soil feedbacks would amplify or dampen spatial self-organization processes.

Outlook: key components of plant-soil systems and their spatio-temporal fingerprints

Focusing mostly on belowground feedbacks emerging from interactions between plant hosts and soil biota, our commentary has highlighted the importance of understanding the spatial and temporal scales involved in these interactions and their potential contribution to spatial self-organization processes. Focusing on active dispersal rates of soil biota, these rates seem to be comparable to soil water transport and vegetation dispersal rates, i.e. on the order of 10^{-3} – 10^{-2} m day^{-1} [96,89,2,44,57,95], although it is unclear how these short-term observations relate to longer-term expansion patterns [80,23]. Even in these short-term estimates, the indicated ranges of uncertainty (i.e. the upper estimate of the range typically being 5-7 times larger than the lower estimate) suggest that differences between functional groups, or individual species within functional groups, could be large enough to create divergent local- and scale-dependent feedback dynamics [78,96,89,2,44,95]. However, as mentioned earlier, passive dispersal of soil organisms, through water, wind (e.g. saltation of soil particles) or dispersal vectors, may lead to higher dispersal rates. The latter form of dispersal may be a function of soil biodiversity itself, and hence may vary depending on internal ecosystem dynamics.

Such divergent feedback dynamics could also be driven by differential dispersal abilities of host-specific and generalist soil organisms that may exert either positive or negative effects on plant growth, which would create spatially variable effects on plant host fitness. For example, we focused mostly on the role of root pathogens in this commentary, but plant-soil feedback may involve or be driven by symbiotic mutualists as well [7,67,52]. Explicit modelling of mutualists that disperse more slowly than pathogens could generate local positive feedback, providing an alternative pathway to the local positive feedback generated by competitive interactions in the presented model framework (Fig. 1, 2). Moreover, such belowground spatial structuring in soil community composition may mediate plant-soil feedback effects [11]. Furthermore, empirical observations suggest that soil community dynamics may operate on timescales of weeks to months [39,13,94,15,30], meaning an intermediate scale between the fast and slow processes occurring in ecosystems in which spatial self-organization occurs ([29,24,70,26]).

We propose that future modelling efforts may consider building on recent approaches separating multiple spatio-temporal scales involved in spatial self-organization and pattern formation [62,47,73,71,26]. In addition, future modelling studies could not only address the simultaneous accumulation of both pathogenic and mutualistic soil organisms [35,1], but also the higher trophic interactions affecting the composition and structuring of the belowground food web [32]. Apart from expanding this biotic dimension, consideration of the effects of abiotic changes in soil conditions by plant secondary metabolites, including allelopathic compounds, on plant-soil feedbacks would call for additional expansions of current model frameworks as well [51,50].

In conclusion, we agree with Inderjit et al. [33] that it is of interest to further investigate to what extent aboveground spatial structure in ecosystems can be explained by belowground processes. Previous modelling approaches considering spatial self-organization in (semi-)arid ecosystems may indeed provide a useful entry point for these endeavors. In addition, the development of spatially explicit models that capture the unique features of belowground processes, and plant-soil feedbacks in particular, may yield new insights in spatial self-organization and contribute to novel theory on the origin and dynamics of ecosystem pattern formation, and their consequences for ecosystem functioning in a changing world.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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