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Comment

Spatial pattern formation, community assembly and resilience

Comment on "Belowground feedbacks as drivers of spatial self-organization and community assembly" by Inderjit, Ragan M. Callaway, Ehud Meron

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In their inspiring review, Inderjit et al. propose how two types of spatial vegetation pattern formation in ecosystems, global and local, may affect plant community assembly through belowground feedbacks [1]. Global spatial pattern formation leads to large-scale self-organized periodic patterns of different shapes (including stripes, spots and rings), while local spatial pattern formation results in small-scale self-organized ecotones, both types consisting of biota, 'allelochemicals' and resources. Such ecotones are spatial fronts or boundaries separating domains of alternative ecosystem states [1].

This is a very interesting contribution, because it links spatial vegetation pattern formation in ecosystems to community assembly at different spatial scales; a connection that is largely overlooked until now, and that is important in the context of climate change. It is also important, because it considers the integration of different mechanisms: belowground resources feedbacks, soil biota and 'allelopathy'. Moreover, it raises an imperative question: how does this spatial pattern formation and its effects on community assembly contribute to ecosystem resilience with climate change?

Spatial pattern formation largely determines intra- and interspecific competition and facilitation between plants through scale-dependent effects on belowground resources, soil biota and 'allelopathy' [2–4]. This, in turn, shapes plant community assembly, consisting of community composition and functional diversity. Functional diversity is the diversity of functional traits in a community quantified by the abundance of groups of species (so-called functional groups) that share given values of selected functional traits. In this way, spatial pattern formation is important for its effects on shifting community composition and changing functional diversity in the context of climate change [5]. Once again, two scales dominate in this framework of spatial pattern formation and climate change: shifting niches with particular groups of species at ecosystem (global) scale, and moving ecotones consisting of desertification and plant invasion fronts at local scale [1]. Desertification fronts are moving boundaries between spatial domains separating dysfunctional and functional ecosystem states (f.i. bare soil and vegetated soil, or shrubland and grassland), and the dynamics of these fronts determine whether desertification is reversible or not. Invasion fronts separate ecosystems states of native and invasive plant communities. Interestingly, the direction of movement of invasion fronts can

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be predicted by a single 'snapshot' in time of the spatial plant distributions within those boundaries [6]. How these two types of spatial pattern formation, global and local, affects community assembly with climate change in the future Anthropocene is largely unknown, and an important area of future research.

Many studies emphasize scale-dependent feedbacks between plants and resources as main driving mechanisms of spatial pattern formation, where positive feedback dominates nearby, and negative feedback prevails further away [7]. However, soil biota and 'allelopathy' typically intermingle with these processes, and current review elegantly addresses this complex interaction [1]. Especially noteworthy are the so-called 'allelopathic' self-inhibitory effects on individuals of the same species. One main mechanism that is largely unnoticed in this context and that should be highlighted, is the inhibitory and toxic effects of extracellular self-DNA fragments in decomposing plant litter [8]. This effect of self-DNA may be a mechanism that is of more general importance than currently realized, because it is found to be applicable to many organisms other than plants, including bacteria, fungi, algae, protozoa and insects [9]. Therefore, this is a universal mechanism that can only be classified as 'allelopathy' if one also includes those other organisms, and not only plants, as being potentially 'allelopathic', or self-inhibitory. It is noteworthy that the effects of extracellular self-DNA on plants are very much intermingled with the decomposition process involving soil biota, which makes it difficult or even impossible to separate those effects of self-DNA and soil biota under natural circumstances. For plants, such 'allelopathic' self-inhibitory mechanisms drive ring formation and species coexistence, thereby largely affecting community assembly in ecosystems [2,10]; a very clear example of the link addressed by Inderjit et al. [1].

It has recently been discovered that spatial vegetation pattern formation can be an indicator of multi-stability and resilience [11,12]. Multi-stability constitutes that many different spatial patterns can be found at one point in time in the same area under similar environmental circumstances, while each of those patterns can remain stable during a substantial period of time (decades) and changing environmental conditions [11]. In this manner, spatial pattern formation can be considered as a pathway of resilience, as changing environmental conditions such as climate change are likely to involve spatial pattern formation, re-patterning and re-re-patterning in the longer term (decades or more) [1,12]. The fascinating link between spatial pattern formation and community assembly addressed by Inderjit et al. [1] may constitute an additional pathway that increases resilience with climate change, in the following way. Spatial pattern formation can interact with community assembly responses, by locally releasing the imposed global stress through resource redistribution [7,13]. For instance, and in other words, if spatial pattern formation, re-patterning and re-re-patterning occurs with drier climates in water-limited systems, increased water availability in local vegetation patches may maintain community assembly largely unchanged, as compared to situations without spatial pattern formation. Local stress release through spatial pattern formation is a general phenomenon in many ecosystems, resulting from various scale-dependent feedback mechanisms [7,13]. It could therefore likely be expected that these two pathways of responses, spatial pattern formation and community assembly, act in concert in ecosystems in general, with emerging resilience as a consequence. However, this link between spatial pattern formation, community assembly and resilience remains largely unknown and is an important question for future research. The theory of spatial pattern formation is very promising and urgently needed to further unravel this link. Once again, it can be expected that this will reveal that many ecosystems are much more resilient than currently thought, because of spatial pattern formation.

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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