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Spotlight

Germination changes can restructure communities through priority effects

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Priority effects caused by different species' arrival order can significantly influence community assembly and also plant community composition. Dawson-Glass *et al.* show for the first time in a multispecies setting, that warming-induced shifts in germination timing can restructure communities via seasonal priority effects that influence assembly and affect plant performance.

Community assembly theory often assumes that vegetation composition is mainly the result of seed dispersal and environmental filtering, modulated by biotic interactions such as competition, facilitation, grazing, or diseases. However, evidence is building that challenges this view and suggests that historical factors can have a substantial influence on community assembly. Under the umbrella term historical contingency, whereby the timing or sequence of ecological events significantly influence assembly outcomes – we are finding that it can matter who arrives first and what their traits are. Within historical contingency, the field of priority effects has been gaining traction and its relevance is found to apply across a wide range of organism types in biology as well as evolutionary ecology [1,2]. A number of greenhouse and field studies have shown that (stochastic) factors, such as arrival order, affect plant community composition or ecosystem functioning in a number of different ecosystems [3,4] and these can even lead to alternative vegetation states [5] or changes in ecosystem functioning and services [6]. Priority effects, if pervasive and persistent, could therefore play an important role in how ecosystems function and develop, as well in informing land management [7,8].

The main mechanisms put forward to explain how priority effects work relate to the extent that niches are filled by species and include niche preemption and niche modification [1]. Arrival history is deemed to be important because early arriving species can gain better access to resources than later arriving species and thereby increase their dominance (niche preemption). Early arriving species often manage to establish faster than other species, having a competitive advantage through being bigger than species that arrive or germinate later (asymmetric competition [1]). In niche modification, early arriving species actually alter the niche (via, e.g., changing nutrient availability or microbial diversity) and thus affect subsequent species (this can include facilitation, thus enabling later species to establish, an example of a positive priority effect). Such so-called priority effects have been confirmed in vegetation types ranging from riparian zones to dry prairies, to wood-decaying fungi or microbial communities, as well as for *Daphnia* invertebrates in rivers [2]. In applied ecology, priority effects receive a lot of attention in relation to how to manage and avoid the spread of invasive species, with the idea that filling available niches with desired native species can, through priority effect mechanisms, keep undesired species out [7–9]. By contrast, in environments where land use change is a key threat to diversity, such as temperate grasslands in Europe, priority effects created by sowing different plant functional groups before others suggest that this can alter ecosystem functions, including rooting depth [4,6]

Warming during climate change could also shift community assembly dynamics. Recent research has focused a clear spotlight on the role of germination sensitivity to warming, highlighting that earlier germination timing could vary strongly between plant species and hence alter dominance patterns in seasonal vegetation. Recent work by Dawson-Glass *et al.* [10] has shown that warming-induced shifts in germination timing in old-field plant communities (from abandoned agricultural land) can restructure communities via seasonal priority effects that influence assembly and affect plant performance. This is the first time such a finding has been reported for multispecies communities, with recent research on phenological sensitivity focusing mainly on single or paired species responses [11]. Dawson-Glass *et al.* first germinated 15 typical old-field species (both grasses and forbs, as well as native and non-native species) in growth chambers running at present day (hereafter ambient) or warmed (+3°C) spring conditions simulating expected warming trends in the Ohio region in the USA. They then assessed the day of maximum germination for both ambient and warmed seeds and used the sequence of germination timing to inform an assembly sequence in mesocosms in a common garden approach. They thus allowed the differential germination of different plant species in ambient or warmed conditions to create priority effect treatments with different arrival orders in a subsequent mesocosm experiment. Intriguingly, whether a species was native or non-native, a grass or a forb, did not affect the outcome, but whether a species germinated earlier during the warming or not did affect the outcome.

This approach is innovative and elegant, in that it pre-tests expected differences in germination under warming and uses the information to create experimental priority treatments. This kind of approach has not been taken before and it complements a rising number of publications focusing on the relationship between phenology and community assembly and structure [12]. As such the Dawson-Glass *et al*. study covers new ground in explicitly using germination sensitivity to help design a climate warming experiment that takes possible priority effects into account. Importantly, it underscores the need to increasingly consider germination phenology as a mechanism that can reshape communities, via assembly effects. Up until recently, phenological variation was not considered an important potential driver of community dynamics within one trophic level (in this case plants), but more as a driver of multitrophic interaction matches or mismatches during climate shifts.

This study [10] forms a great starting block for a whole suite of necessary follow-up experiments and research in the field of priority effects and phenology. In particular, the study has some weaknesses that do not allow one to make strong conclusions based on the data. One issue, is that the experimental design would have needed each of the 15 plant species to also be grown in monoculture in order to be able to distinguish effects of growing in an interspecific setting versus an intraspecific setting from biomass differences between species growing in the warming treatment mesocosms and the ambient mesocosms. To clearly attribute any change in biomass when grown in the warming sequence mesocosm to priority effects of early arrival, one would need to know how much growing in mixtures affects a species biomass compared with growing in monocultures (and strictly speaking ideally also know the biomass of a single plant growing alone without any competition). It would be enlightening to find out whether any priority effects found in follow-up experiments are driven by niche preemption or niche modification. Clearly separating these two mechanisms is no easy task, as I have personally experienced in experiments, because abiotic and biotic changes are often intricately intertwined. Another issue is that ideally (doing excellent science is such hard work) the warming-treatment mesocosms should also experience actual warming during the common garden experiment (as well as the treatments that actually occurred, where all species were grown at ambient temperatures), as this could change growth rates and senescence. I consider the latter issue not as important as the need for monocultures, because the study focuses on spring germination and seasonal priority effects probably generally play out during early phases of establishment. I find myself wondering whether such phenology-priority effect linkages may be stronger in systems that are more dynamic between years: grasslands (and maybe old-fields) exhibit strong changes in species dominance from growing season to growing season; this is part of the resilience of such systems compared with woodland or forests, where species are more static in abundance. Overall this study shines a spotlight on the previously underappreciated, yet likely increasingly important, phenological sensitivity of species as a shaper of plant communities during climate change.

Declaration of interests

The author declares no competing interests.

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