

Opinion

Temporal Dynamism of Resource Capture:
A Missing Factor in Ecology?Emily J. Schofield,^{1,2,*} Jennifer K. Rowntree,² Eric Paterson,¹ and Rob W. Brooker¹

Temporal dynamism of plant resource capture, and its impacts on plant–plant interactions, can have important regulatory roles in multispecies communities. For example, by modifying resource acquisition timing, plants might reduce competition and promote their coexistence. However, despite the potential wide ecological relevance of this topic, short-term (within growing season) temporal dynamism has been overlooked. This is partially a consequence of historic reliance on measures made at single points in time. We propose that with current technological advances this is a golden opportunity to study within growing season temporal dynamism of resource capture by plants in highly informative ways. We set out here an agenda for future developments in this research field, and explore how new technologies can deliver this agenda.

What is Temporal Dynamism and Why Is It Important?

Understanding plant community composition and functioning are fundamental challenges in ecology. It is not yet fully understood why specific communities exist at particular points in space and time, why some communities are more diverse than others, and how diversity impacts on ecosystem function. In plant communities, many theories have been proposed to explain plant coexistence, including cyclical disturbance [1,2], different individual responses to species interactions [3], multiple limiting resources [4,5], intraspecific trait variation [6], and facilitative plant–plant interactions, particularly in extreme environments [7,8].

We argue that short-term (i.e., within growing season) **temporal dynamism** (see [Glossary](#)) in resource acquisition might be central to addressing these fundamental challenges. Temporal dynamism can be described as a form of **heterochrony** that is controlled by intrinsic gene expression but also influenced by external environmental factors such as climatic conditions [9]. However, apart from a few cases, **within growing season temporal dynamism** in resource acquisition is rarely considered as a topic in its own right, in part because it has historically proven hard to measure. This contrasts, for example, with our knowledge of other temporally dynamic processes such as plant phenology, about which much more is known.

Phenological studies have shown the importance of the timing of key events in the structure and functioning of plant communities [10]. Therefore, similar important consequences for temporal dynamism in **resource capture** might reasonably be expected. For example, if different species **temporally segregate** the capture of common resources to avoid competition, increased complementarity can promote plant coexistence [11], with profound implications for fundamental processes such as biodiversity–ecosystem function relationships. Importantly, we propose that, owing to the wealth of new analytical approaches that are currently available, now is the time to address the historical oversight of within growing season temporal dynamism.

Highlights

Temporal dynamism has previously been studied in a range of specific habitats and generally over long time-scales, but short-term within growing season temporal dynamics of resource capture and plant–plant interactions have so far been over looked.

Temporal dynamics have been overlooked due to reliance on traditional proxy methods to study plant–plant interactions such as biomass, and to measuring at only a single timepoint.

However, a suite of new non-destructive techniques are now available, including stable isotope-labelling systems, soil zymography, DNA and RNA technology, and X-ray computed tomography scanning of root growth to study the temporal dynamics of resource capture. These will allow us to identify and then understand the role of temporal dynamism in the structure and function of multispecies plant communities.

¹The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH, UK

²Manchester Metropolitan University, School of Science and the Environment, John Dalton Building, Chester Street, Manchester M1 5GD, UK

*Correspondence: emily.schofield@hutton.ac.uk (E.J. Schofield).

Before considering these new opportunities, we examine previous studies of temporal dynamism, with a focus on resource capture. We discuss the limitations of, and lessons learned from, previous studies and how they can form the basis of a future research agenda. We then focus on new experimental approaches, considering how these can address current knowledge gaps, and discuss the wider relevance of this subject area to ecology.

Past Studies of Temporal Dynamism in Plant Communities

Previous research provides clear examples of how temporal dynamism of ecological processes can regulate the structure and functioning of plant communities. Arguably, one of the best-studied examples is plant–pollinator interaction dynamics. Pollinators vary the plant species visited interannually, which promotes coexistence in species-rich communities [12,13]. Other examples involve temporally dynamic resource capture; in arid environments, temporal dynamism has been found in the growth response of plants to erratic inputs of water [14], depending on both the timing of the water input in the growing season and the time since the previous water input [15]. In alpine systems, nutrient turnover is temporally dynamic, with mineralisation occurring throughout winter [16], and spring microbial turnover then providing nutrients to plants [17].

Such temporal dynamics are not only of academic interest – they can play a central role in regulating the impacts of key environmental change drivers. For example, one way non-native species can become invasive is by occupying a vacant niche [18]. Occupying a temporal niche left vacant by the native plant community could allow the invasive species to capture nutrients at a time of reduced competition. It may appear that in some cases invasive species take over a niche from native species. However, it is unclear whether invasive species establishment depends on the exploitation of a temporal niche gap. Although phenological differences between native and invasive species have been shown [16], the underlying role of within growing season temporal dynamism in nutrient capture has yet to be demonstrated (probably for the reasons we discuss below). A similar example is the phenology of hemiparasitic plants. The life cycle of many hemiparasites is shortened relative to its hosts, influencing nitrogen cycling with earlier leaf fall than the host community [19,20]. Early leaf fall provides an input of nitrogen to the host community when it becomes limited [21]. Here the rate of water and nitrogen uptake by *R. minor* parasitizing *Hordeum vulgare* (barley) has received attention [22], but the temporal dynamics of this interaction have yet to be explored.

These examples, only a selection from the many that could be listed, demonstrate the likely importance of temporal dynamism of resource capture by plants. Far fewer studies have sought to measure this process directly. An important example is the work by Trinder *et al.* which used a series of destructive harvests to examine the temporal dynamics of nitrogen capture and biomass accumulation of *Dactylis glomerata* (cock's foot) and *Plantago lanceolata* (ribwort plantain). Trinder *et al.* found that, in response to interspecific competition, both species shifted the timing of the maximum rate of biomass accumulation and nitrogen capture by up to 17 days [23]. The species diverged the timing of these resource capture processes in ways that possibly reduce direct competition. However, it is notable that this type of study, looking explicitly at the temporal dynamism of resource capture, is to the best of our knowledge extremely rare.

Why Does It Matter that Temporal Dynamism Has Been Overlooked?

Many of the fundamental processes and properties of terrestrial communities are governed by the outcome of plant–plant interactions [24]. However, despite a huge amount of work on plant–plant interactions, especially competition, there are still unanswered questions about the role of plant–plant interactions in governing plant community composition.

Glossary

Heterochrony: a change in the timing and rate of a developmental process within an organism compared to an ancestral species, including the onset and duration of flowering, leaf production, and internodal length [9].

Resource capture: the acquisition of resources, including nutrient, water, and light, by a plant. This is commonly expressed as a rate, namely units of resource capture over a period of time.

Soil zymography: non-destructive method to measure chitinase, cellulase, or nitrogen mineralisation hotspots at a fine spatial resolution in the soil. Useful for studying changes in the location and intensity of enzymatic activity over time.

Temporal dynamism: variation through time in the rate or effect of a particular process. For example, this could be variation in the per unit biomass capture by a plant of soil nutrients or water, or the extent to which neighbouring plants compete with each other (which might itself result from temporal dynamism in resource capture by individuals). Such temporal dynamism can be driven by external factors (changes through time in climate or resource availability) or intrinsic factors (e.g., plant developmental stage).

Temporal segregation: a shift in the timing of a process in response to a neighbouring individual. Commonly observed in animal feeding, it limits niche overlap and promotes coexistence. Some niche overlap is still to be expected, but direct resource competition is reduced.

Within growing season temporal dynamism: variation through time, but within a given growing season, in the rate or effect of a particular process. Such variation is distinct from interannual variation, which might be caused by factors such as variation in climate between growing seasons.

Box 1. Theory of Temporal Dynamism of Nutrient Capture

Plants do not uniformly take up nutrients throughout the growing season. Instead, nutrient capture is regulated based on the nutrient requirements and growth stage of the plant [56]. When plants are grown in isolation, nutrients are taken up at the optimum time (Figure I; panels A and B show two individuals grown in isolation). However, when plants are grown together the timing of nutrient capture might change, perhaps to minimise competition (panel C shows the two individuals grown together). This can then promote the coexistence of competing individuals [11], and might be an important factor in communities such as tropical rainforests and grasslands, with multiple species timing key processes differently to minimise competition (panel D shows a hypothetical multispecies community, with each line representing a different species).

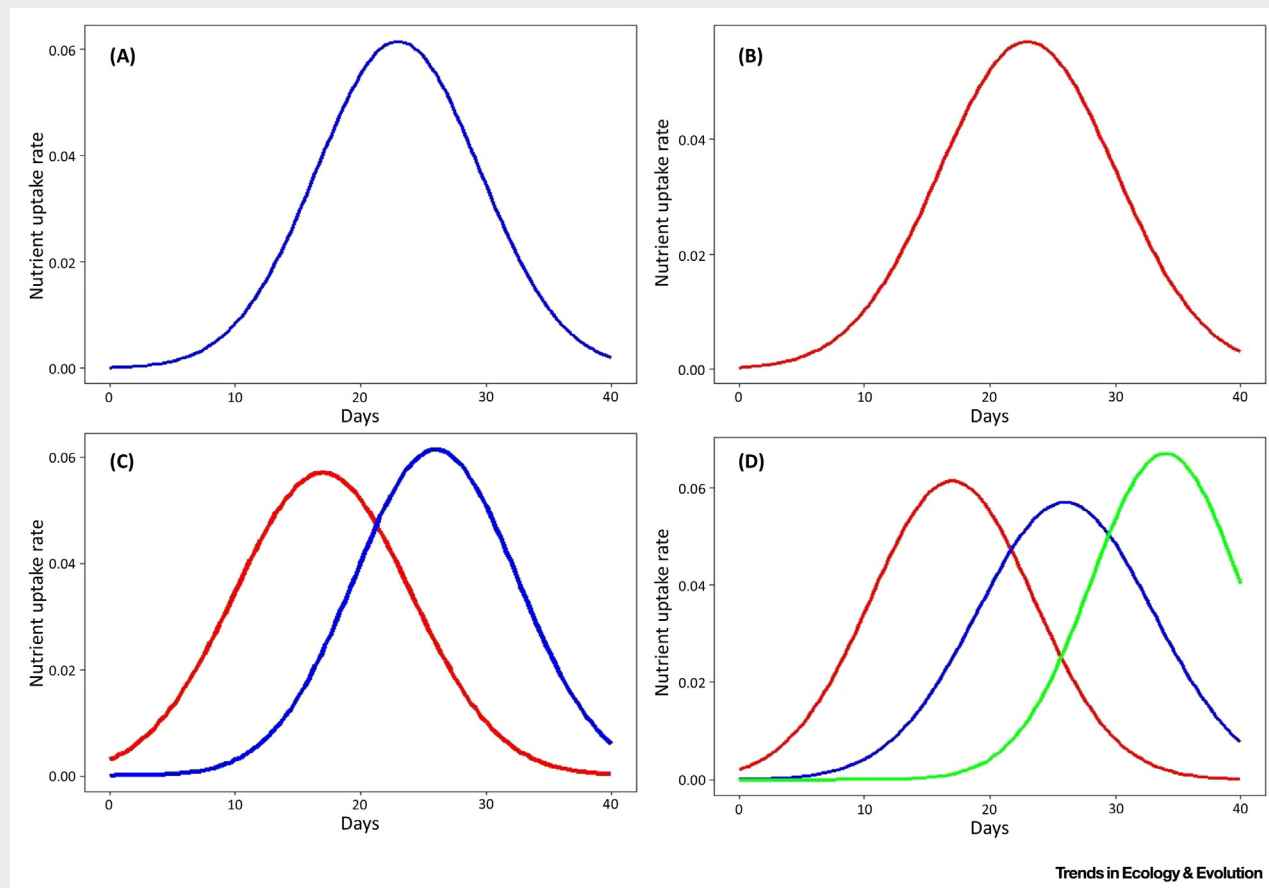


Figure I. Theoretical Role of Temporal Dynamism in Plant Coexistence. In isolation (A,B) plants take up nutrients in a specific profile over the growing season. By contrast, when grown together (C) the two plants offset the period of maximum nutrient capture to limit competition. In a multispecies community (D) this could lead to species occupying distinct temporal niches, leading to coexistence.

For example, our current understanding of the niches available within plant communities, which strongly regulate plant–plant interactions, cannot explain the level of observed coexistence [25]. A better understanding of short-term temporal dynamism in resource capture, and its consequences for plant–plant interactions, might help to explain this apparent paradox. Temporally dynamic resource-capture processes, and the temporal niche segregation which this could enable, could alter crucial plant–plant interactions so as to have a stabilising effect on communities. This would allow a higher diversity than would otherwise be the case to be supported [26], at potentially both a species [27] and genotypic level [28], with the community using a greater proportion of the available resources [29]. In this example, temporal dynamism in resource capture can be considered as an unmeasured trait (Box 1).

Why Has Temporal Dynamism in Resource Capture Been Overlooked?

Given the general importance of the temporal dynamism of ecological processes, and the likelihood that in many cases this is related also to temporally dynamic resource capture within a growing season, why have so few studies explicitly addressed this latter topic?

Plant ecology has traditionally relied on one final biomass measurement to assess the consequences of plant–plant interactions. Biomass is a relatively cheap and easy measure of plant response, making large-scale greenhouse and field studies possible [26]. However, there are some drawbacks to using single timepoint measurements of biomass to assess plant–plant interactions, and especially the short-term temporal dynamism of these processes. First, owing to the influence of other external environmental factors, the accumulation of biomass is rarely influenced by competition alone [23]. This makes it an unreliable direct measure of the outcome of competition. The use of only single harvesting to assess the outcome of plant–plant interactions is clearly inappropriate for measuring short-term temporal dynamism in resource capture. In addition, the precise timing of biomass harvest and measurement within a growing season can influence the perceived outcome of the plant–plant interaction because plants grow and develop at different times throughout the year [26]. The same criticisms can also be made of other common annual, single timepoint measurements, for example, flower production and seed set. To understand the role of temporal dynamism of resource capture in regulating community dynamics, repeated measures of resource capture are required. However, to take this step we need first to realise and accept the limitations of single timepoint studies, and move to more detailed studies of the competitive process itself.

Traditional approaches, for example plant biomass and tissue nutrient-content analysis, can be used to explore issues of temporal dynamism in plant–plant interactions. However, they need to be coupled to multiple harvesting points through time, as used by Trinder *et al.* to examine the temporal dynamics of resource capture in *Plantago lanceolata* and *Dactylis glomerata* [23]. Although the multiple-harvest approach is a valuable tool, it is destructive and requires large-scale and labour-intensive studies. The inclusion in a study of multiple harvests to track temporal dynamism of resource capture and plant–plant interactions through time increases the size and complexity of an experiment, and therefore reduces the complexity of the questions that can be asked [11,29]. In addition, multiple harvesting means that responses are averaged over many plants, potentially masking subtle dynamic individual-level responses in resource capture and growth. Non-destructive methods would instead allow the responses of an individual plant to be studied over time.

Such drivers of the historical oversight support a case for the use of innovative new technologies, particularly non-destructive and direct measures of resource capture, such that temporal dynamism of resource capture can be given the attention it deserves.

Setting and Addressing a New Research Agenda

From the above discussions, and consideration of well-known ecological concepts, a series of questions can be presented (see Outstanding Questions) in a clear research agenda. If addressed, this agenda could advance the study of temporal dynamism of resource capture. Importantly, this research agenda is not only of relevance to plant ecophysiologists or community ecologists. By influencing, for example, the temporal availability of resources to other groups such as soil organisms, pollinators, and herbivores, the study of temporal dynamism in plant resource capture will likely have wide-reaching consequences for ecological research.

As discussed, although temporal dynamism in resource capture can itself be detected using destructive harvesting techniques [23], new technological approaches will be necessary to look at the complex series of processes involved in the dynamics of plant nutrient capture and its role in community composition. Below, we provide examples of how these advances might enable some of the key questions of the research agenda to be addressed.

What Is the Interaction Between Temporal Dynamism of Resource Capture with Plant Physiology and Morphology?

The plasticity of plant root traits may facilitate the temporal dynamics of resource capture, while at the same time root physiology and morphology could be influenced by changes in the temporal dynamics of nutrient uptake. Therefore, the relationship between temporal dynamism of resource capture and root traits is a key topic because roots are the organs of nutrient uptake.

Microrhizotrons – small cameras inserted into the soil to record root foraging and fine root developing [30,31] – allow the study of root foraging activity. However, they are limited in not giving a view of the whole root system. Whole root system growth dynamics can be studied with automated root phenotyping facilities, using high-definition cameras to photograph root development of plants grown in Perspex boxes [32]. Changes in root morphology and foraging can then be related to the location of soil microbial activity (**soil zymography**, see below) and plant nutrient capture.

For a 3D view of root growth dynamics, X-ray computed tomography (CT) scanning can be used to visualise plant roots grown in soil. Root architectural development can then be related to resource capture. The development of specialist root-tracking software and facilities [33] will allow much larger and more complex experiments to be carried out on dynamic competition for soil resources between the roots of multiple individuals. This approach has already been used to study root growth in response to competition between *Populus tremuloides* (quaking aspen) and *Picea mariana* (black spruce) seedlings. Both species increased rooting depth and altered root architecture in response to a competitor [34], but this study did not simultaneously assess soil resource capture. By combining successive scanning of root growth and successive destructive harvesting to look at the temporal dynamics of nutrient uptake, the relationship between root growth and nutrient uptake can begin to be addressed.

Is Temporal Dynamism in Nutrient Capture Moderated in Response to Neighbours Simply by Overlapping Depletion Zones or by More Complex Signalling Pathways?

Traditionally plant competitive responses to a neighbour have been thought to occur when the zones of nutrient depletion in the soil overlap [35]. As the complexities of plant–plant communication are revealed [36], it is becoming clear that plant–plant competitive interactions might not occur solely based on nutrient availability. RNA sequencing, which enables us to examine the genes upregulated in specific circumstances in tissue samples, is one way to look at dynamic plant responses to the presence of a neighbour.

Studies in *Arabidopsis thaliana* have identified that common stress-response pathways such as jasmonate production are activated in response to a competitor [37]. Detection of the upregulation of stress-associated genes can indicate when a target plant detects the presence of a neighbour, whether the response differs depending on the identity of the neighbour, and the length of time between neighbour detection and any form of additional physiological response by the target plant (e.g., priming of soil microbes; see below).

A key question is whether upregulation of gene expression occurs before the nutrient-depletion zones of neighbouring plants overlap. Such an effect would indicate that responses to neighbouring plants are more complex than simply a response to the overlap of soil depletion zones as a consequence of developing root systems. The question of whether plants start responding to neighbours and to the threat of potential competition long before they come into close physical contact can then be addressed. This approach, therefore, provides a unique opportunity to understand temporal dynamism and competition at a molecular level, and to determine how temporal dynamism of resource capture is moderated in response to competition through a cascade of molecular responses in the target plant.

How Does the Activity of the Soil Microbial Community Influence Temporal Dynamism in Resource Capture?

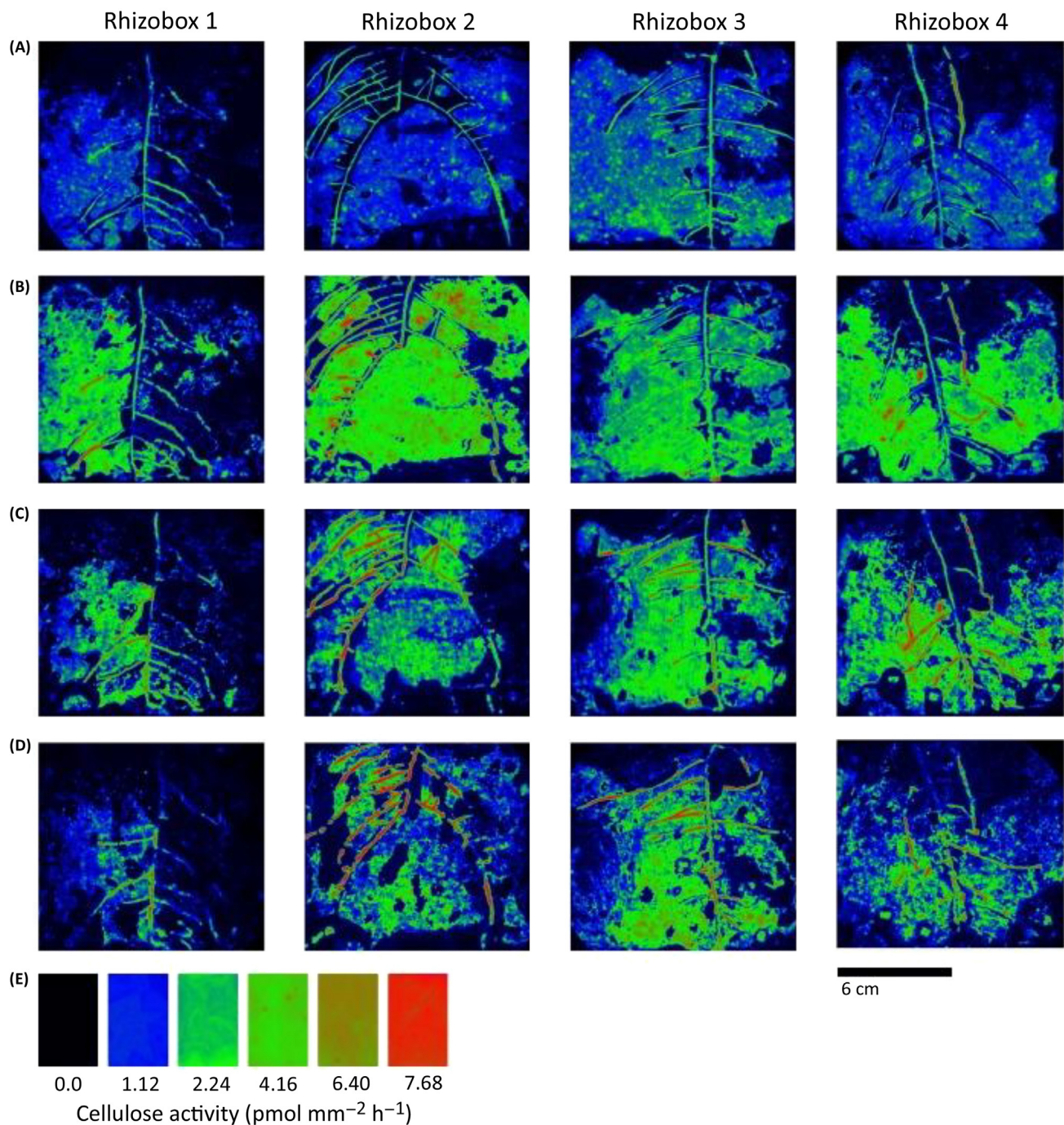
Throughout the year, soil microbial communities mineralise and immobilise nutrients from soil organic matter (SOM), driving nutrient cycles that mobilise organic nutrient stocks into plant-available forms during the growing season [38,39]. Plants can influence these processes through the rhizodeposition of labile carbon and amino acids to influence microbial process rates (rhizosphere priming effects, RPE [40,41]), with rhizodeposition varying with plant development, species, and genotype [42–44].

One method to examine the influence of plants on the dynamics of SOM mineralisation is to study the timing of rhizosphere priming effects for plants in competition versus isolated plants. Stable-isotope labelling ($^{15}\text{N}/^{13}\text{C}$) can allow plant impacts on soil nutrient cycles to be quantified [45]. This can be done non-destructively and dynamically through isotopic partitioning of soil CO_2 efflux into plant and SOM-derived components [46], or tracing ^{15}N fluxes (derived from labelled organic matter) in soil solution [47–49]. This approach allows the timing and magnitude of soil community priming to be measured over time, and compared relative to other temporally dynamic measurements including RNA expression (see above) and resource capture (Figure 1).

Further information about specific soil microbial activities can then be provided through soil zymography, allowing the location and intensity of enzyme activity in soil to be quantified over time [50]. This methodology has already been used to identify ‘hot moments’ when microbial activity is higher than background levels [51]. Such ‘moments’ can be occasional or occur periodically with events such as spring growth and autumn leaf fall [52]. Using these techniques, it can be assessed, for example, whether periods of greater microbial activity precede plant nutrient capture or whether they are themselves dependent on priming activities by the plant.

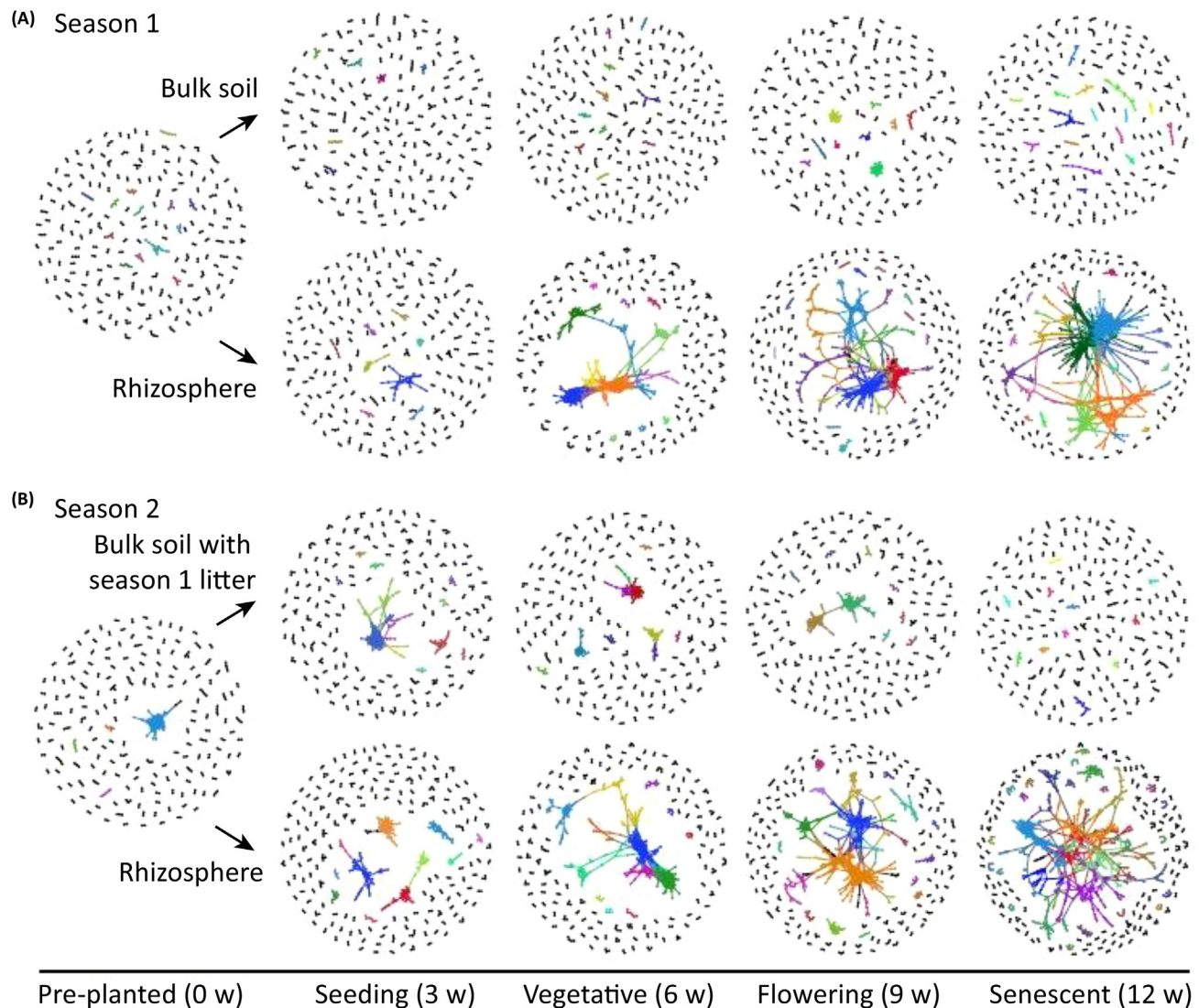
How Are the Temporal Dynamics of Soil Microbial Community Composition Influenced by Plant Temporal Dynamics?

A crucial factor regulating the functional capacity of soil communities to mediate nutrient cycling is their composition. The soil community is known to be temporally dynamic seasonally and with plant developmental stage [24]. Shi *et al.* used a 16S ribosomal RNA approach to produce a network representation of microbial diversity over two growing seasons, comparing bulk and rhizosphere soil (Figure 2) [53]. The decreasing cost, increasing throughput capacity, and analysis speed of genomics creates an opportunity to study temporal dynamism in the soil community over the growing season [54]. When compositional studies are combined with studies of soil microbial activity (e.g., using metatranscriptomics), it can be assessed how changes in the dynamism of plant resource capture are associated with either short-term (i.e., more activity-based) or long-term (i.e., more community-composition based) changes in the soil community.



Trends in Ecology & Evolution

Figure 1. The Potential Role of Soil Zymography in Studying Temporal Dynamism in Soil Community Activity. The potential role that soil zymography analysis can play in studying the temporal dynamics of soil functions. The cellulase activity surrounding roots of *Lupinus polyphyllus* (large-leaved lupin) was analysed 18 days after sowing (A), and 10 days (B), 20 days (C), and 30 days (D) after cutting shoots. Adapted, with permission, from [50].



Trends in Ecology & Evolution

Figure 2. Temporal Dynamics of the Plant-Associated Soil Community. The figure shows the potential role of soil community characterisation and network analysis in studying the temporal dynamics of the soil community associated with resource capture. (A,B) Differences in the rhizosphere and bulk soil community of *Avena fatua* were compared over two growing seasons. Samples were taken every 3 weeks (w) for two seasons. Shi *et al.* looked at the difference in the diversity and level of interconnection between bulk and rhizosphere soil. Nodes represent operational taxonomic units (OTUs), and lines represent the linkages between them. The rhizosphere soil becomes more interconnected but less diverse over time because the plant exerted a selection pressure on the soil community. Adapted, with permission, from [53].

What Is the Future Strategy To Study Temporal Dynamism?

Temporal dynamism is an overlooked factor in ecology and could be a vital central mechanism by which plants coexist in complex communities. Although studying temporal dynamism of resource capture will not be straightforward, the potential benefit to the understanding of ecosystem functioning is likely to be considerable. There is now an ideal opportunity to understand the within growing season temporal dynamics of resource capture as part of broader ecological system dynamics.

To understand the role of temporal dynamism of resource capture in plant coexistence it needs to be understood how plants coordinate temporally dynamic responses, the intermediary role of the soil microbial community, and the consequences at the individual plant and plant community level. Therefore, to study these distinct but interconnected processes, an integrated approach is required [55]. From the examples we have discussed above it is clear that a vast amount of knowledge can be gained about temporal dynamism in resource capture from using these cutting-edge technologies. Once the fundamental questions about temporal dynamism of resource capture have been addressed, the wider community-level consequences can then be considered, building upon these fundamental studies.

The ultimate goal of this research should be to integrate temporal dynamism as a factor into existing models, to define new niche space, and aid the explanation of coexistence in complex communities. Only then can the question of whether temporal dynamism in resource capture leads to coexistence of neighbouring plants can begin to be addressed. This approach can then be applied to other temporally dynamic processes, answering other fundamental questions about ecosystem functioning.

Acknowledgments

We thank Elizabeth Price and Francis Brearley for their valuable comments on the draft manuscript. E.J.S. was funded by Manchester Metropolitan University and the James Hutton Institute, R.W.B. and E.P. were funded by the Rural and Environment Science and Analytical Services Division of the Scottish Government through the Strategic Research Programme 2016–2021.

References

1. Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory on JSTOR. *Am. Nat.* 111, 1169–1194
2. Bongers, F. *et al.* (2009) The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecol. Lett.* 12, 798–805
3. Rowntree, J.K. *et al.* (2011) Genetic variation changes the interactions between the parasitic plant–ecosystem engineer *Rhinanthus* and its hosts. *Philos. Trans. R. Soc. B Biol. Sci.* 366, 1380–1388
4. Tilman, D. (1982) *Resource Competition and Community Structure*, Princeton University Press
5. Valladares, F. *et al.* (2015) Species coexistence in a changing world. *Front. Plant Sci.* 6, 1–16
6. Mitchell, R.M. and Bakker, J.D. (2014) Quantifying and comparing intraspecific functional trait variability: a case study with *Hypochaeris radicata*. *Funct. Ecol.* 28, 258–269
7. Brooker, R.W. *et al.* (2007) Facilitation in plant communities: the past, the present, and the future. *J. Ecol.* 96, 18–34
8. Butterfield, B.J. *et al.* (2013) Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecol. Lett.* 16, 478–486
9. Geuten, K. and Coenen, H. (2013) Heterochronic genes in plant evolution and development. *Front. Plant Sci.* 4, 381
10. Tang, J. *et al.* (2016) Special feature: international LTER emerging opportunities and challenges in phenology: a review. *Ecosphere* 7, e01436
11. Li, C. *et al.* (2014) The dynamic process of interspecific interactions of competitive nitrogen capture between intercropped wheat (*Triticum aestivum* L.) and Faba bean (*Vicia faba* L.). *PLoS One* 9, e115804
12. MacLeod, M. *et al.* (2016) Measuring partner choice in plant–pollinator networks: using null models to separate rewiring and fidelity from chance. *Ecology* 97, 2925–2931
13. Kipling, R.P. and Warren, J. (2014) An investigation of temporal flowering segregation in species-rich grasslands. *Ecol. Res.* 29, 213–224
14. Thompson, K. and Gilbert, F. (2014) Spatiotemporal variation in the endangered *Thymus decussatus* in a hyper-arid environment. *J. Plant Ecol.* 8, 79–90
15. Schwinning, S. *et al.* (2004) Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* 141, 191–193
16. Jaeger, C.H. *et al.* (1999) Seasonal partitioning of nitrogen by plants and soil microorganisms in an alpine ecosystem. *America* 80, 1883–1891
17. Bardgett, R.D. *et al.* (2005) A temporal approach to linking aboveground and belowground ecology. *Trends Ecol. Evol.* 20, 634–641
18. Volkovich, E.M. and Cleland, E.E. (2014) Phenological niches and the future of invaded ecosystems with climate change. *AoB Plants* 6, 1–16
19. Mudrák, O. *et al.* (2016) Changes in the functional trait composition and diversity of meadow communities induced by *Rhinanthus minor* L. *Folia Geobot.* 51, 1–11
20. March, W.A. and Watson, D.M. (2007) Parasites boost productivity: effects of mistletoe on litterfall dynamics in a temperate Australian forest. *Oecologia* 154, 339–347
21. Quested, H.M. (2008) Parasitic plants – impacts on nutrient cycling. *Plant Soil* 311, 269–272
22. Jiang, F. *et al.* (2010) Interactions between *Rhinanthus minor* and its hosts: a review of water, mineral nutrient and hormone flows and exchanges in the hemiparasitic association. *Folia Geobot.* 45, 369–385
23. Trinder, C. *et al.* (2012) Dynamic trajectories of growth and nitrogen capture by competing plants. *New Phytol.* 193, 948–958
24. Lortie, C.J. *et al.* (2004) Rethinking plant community theory. *Oikos* 107, 433–438
25. Clark, J.S. (2010) Individuals and the variation needed for high species diversity in forest trees. *Science* 327, 1129–1132
26. Trinder, C.J. *et al.* (2013) Plant ecology's guilty little secret: understanding the dynamics of plant competition. *Funct. Ecol.* 27, 918–929

Outstanding Questions

A Research Agenda for Temporal Dynamism in Plant Resource Capture

The following are key research questions which set out a clear research agenda for linking the issue of temporal dynamism in resource capture to central aspects of plant ecophysiology, plant community ecology, and community ecology more widely. We have ordered them such that they run from studies which might be conducted on individual plants to studies with increasing complexity in terms of biotic interactions – initially interactions with other plants, then with soil organisms, then with other elements of the wider community (for example pollinators and herbivores).

(i) What is the interaction of temporal dynamism of resource capture with plant physiology and morphology?

(ii) Is temporal dynamism in phenology matched by patterns of temporal dynamism in nutrient uptake?

(iii) Is temporal dynamism in nutrient uptake moderated in response to neighbours simply by overlapping depletion zones or by more complex signalling pathways?

(iv) How do interactions with soil organisms influence temporal dynamism in resource capture?

(v) Is temporal dynamism in resource capture widespread, or is it associated with particular plant strategy types?

(vi) Does temporal dynamism in resource capture lead to a reduction in competition, and contribute to plant coexistence and the development of multispecies plant communities?

(vii) What are the wider consequences of temporal dynamism for community structure and function at other trophic levels?

27. Proulx, R. *et al.* (2010) Diversity promotes temporal stability across levels of ecosystem organization in experimental grasslands. *PLoS One* 5, 1–8
28. Fridley, J.D. *et al.* (2007) Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. *J. Ecol.* 95, 908–915
29. Allan, E. *et al.* (2011) More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proc. Natl. Acad. Sci. U. S. A.* 108, 17034–17039
30. Warren, J.M. *et al.* (2015) Root structural and functional dynamics in terrestrial biosphere models – evaluation and recommendations. *New Phytol.* 205, 59–78
31. McCormack, M.L. *et al.* (2015) Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytol.* 207, 505–518
32. Marshall, A.H. *et al.* (2016) A new emphasis on root traits for perennial grass and legume varieties with environmental and ecological benefits. *Food Energy Secur.* 5, 26–39
33. Mairhofer, S. *et al.* (2015) Extracting multiple interacting root systems using X-ray microcomputed tomography. *Plant J.* 84, 1034–1043
34. Dutilleul, P. *et al.* (2015) X-ray computed tomography uncovers root–root interactions: quantifying spatial relationships between interacting root systems in three dimensions. *Front. Plant Sci.* 6
35. Ge, Z. *et al.* (2000) The importance of root gravitropism for inter-root competition and phosphorus acquisition efficiency: results from a geometric simulation model. *Plant Soil* 218, 159–171
36. Babikova, Z. *et al.* (2013) Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. *Ecol. Lett.* 16, 835–843
37. Masclaux, F.G. *et al.* (2012) Transcriptome analysis of intraspecific competition in *Arabidopsis thaliana* reveals organ-specific signatures related to nutrient acquisition and general stress response pathways. *BMC Plant Biol.* 12, 227
38. Laliberté, E. (2016) Below-ground frontiers in trait-based plant ecology. *New Phytol.* 213, 1597–1603
39. de Vries, F.T. and Caruso, T. (2016) Eating from the same plate? Revisiting the role of labile carbon inputs in the soil food web. *Soil. Biol. Biochem.* 102, 4–9
40. Kuzyakov, Y. (2010) Priming effects: interactions between living and dead organic matter. *Soil. Biol. Biochem.* 42, 1363–1371
41. Mommer, L. *et al.* (2016) Root–root interactions: towards a rhizosphere framework. *Trends Plant Sci.* 21, 209–217
42. Chaparro, J.M. *et al.* (2013) Root exudation of phytochemicals in *Arabidopsis* follows specific patterns that are developmentally programmed and correlate with soil microbial functions. *PLoS One* 8, e55731
43. Bardgett, R.D. *et al.* (2014) Going underground: root traits as drivers of ecosystem processes. *Trends Ecol. Evol.* 29, 692–699
44. Mwafurirwa, L. *et al.* (2016) Barley genotype influences stabilization of rhizodeposition-derived C and soil organic matter mineralization. *Soil Biol. Biochem.* 95, 60–69
45. McKane, R.B. *et al.* (1990) Spatiotemporal differences in ¹⁵N uptake and the organization of an old-field plant community. *Ecology* 71, 1126–1132
46. Lloyd, D.A. *et al.* (2016) Effects of soil type and composition of rhizodeposits on rhizosphere priming phenomena. *Soil Biol. Biochem.* 103, 512–521
47. Yang, H. *et al.* (2013) Plant neighbor effects mediated by rhizosphere factors along a simulated aridity gradient. *Plant Soil* 369, 165–176
48. Studer, M.S. *et al.* (2014) Carbon transfer, partitioning and residence time in the plant–soil system: a comparison of two ¹³CO₂ labelling techniques. *Biogeosciences* 11, 1637–1648
49. Zambrosi, F.C.B. *et al.* (2012) Contribution of phosphorus (³²P) absorption and remobilization for citrus growth. *Plant Soil* 355, 353–362
50. Spohn, M. and Kuzyakov, Y. (2014) Spatial and temporal dynamics of hotspots of enzyme activity in soil as affected by living and dead roots – a soil zymography analysis. *Plant Soil* 379, 67–77
51. Kuzyakov, Y. and Blagodatskaya, E. (2015) Microbial hotspots and hot moments in soil: concept & review. *Soil Biol. Biochem.* 83, 184–199
52. Philippot, L. *et al.* (2009) Biochemical cycling in the rhizosphere having an impact on global change. *Plant Soil* 321, 61–81
53. Shi, S. *et al.* (2016) The interconnected rhizosphere: high network complexity dominates rhizosphere assemblages. *Ecol. Lett.* 19, 926–936
54. Prosser, J.I. (2015) Dispersing misconceptions and identifying opportunities for the use of “omics” in soil microbial ecology. *Nat. Rev. Microbiol.* 13, 439–446
55. Harris, G.A. (1967) Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecol. Monogr.* 37, 89–111
56. Herrera Paredes, S. *et al.* (2016) Giving back to the community: microbial mechanisms of plant–soil interactions. *Funct. Ecol.* 30, 1043–1052