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Legacy effects in heathlands: Decoupling above- and belowground responses to subsequent drought events

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ABSTRACT

Climate change is intensifying droughts and disrupting ecosystem carbon cycles. A pivotal study reveals a critical insight: while chronic drought permanently alters the soil microbiome, these belowground legacies have a surprisingly minor effect on subsequent CO_2 fluxes. Instead, the primary driver of reduced carbon uptake is aboveground plant vulnerability, not soil microbial changes. This decoupling between resilient soils and vulnerable plants exposes a fundamental gap in climate models, which must now account for this plant-mediated risk to accurately project future climate-carbon feedbacks and inform conservation strategies.

Keywords: Carbon fluxes | Climate change | Heathlands | Microbial communities | Soil legacy

Climate change is dynamically modulating the structure and functioning of terrestrial ecosystems via shifts in temperature and precipitation regimes, with yet underexplored long-term implications for ecosystem carbon (C) fluxes [1-3]. Drought events cause a significant reduction in plant photosynthesis, constrain soil microbial metabolisms, and alter species composition, thereby impacting multiple ecosystem processes associated with C source-sink dynamics [4]. Figure 1 illustrates the conceptual pathway linking climate-driven drought to above- and belowground ecosystem responses. While the effects of short-term drought events have been studied extensively, our understanding of how subsequent events of drought cause legacy effects with implications for ecosystem responses remains elusive [5]. This knowledge gap is particularly relevant given the projected increase in frequency and intensity of drought events under global warming scenarios (IPCC 2023), raising concerns about ecosystem resilience and long-term stability of terrestrial carbon sinks. In this context, Heathlands (i.e., ecosystems dominated by the ericoid shrub *Calluna vulgaris*) are ecologically and culturally important landscapes in Europe, often vulnerable to nitrogen deposition and climate change [6]. In these ecosystems, the long-lived vegetation was recently used as an ideal system to explore the extent to which drought legacies alter above and belowground communities and the consequences for C cycling dynamics [7].

This study by Gliesch et al [7] presents findings from a long-term drought experiment in a Dutch heathland, where plots have experienced ca. 20 years of summer drought. By studying *Calluna vulgaris* at different growth stages in areas historically affected by long-term drought and combining manipulative experimentation, the authors provide important insights into the extent to which chronic drought reshapes plant and soil microbial communities, with consequences for ecosystem CO_2 fluxes. Specifically, Gliesch et al [7] demonstrated that long-term summer drought caused strong and persistent changes in both soil bacterial and fungal communities. These drought legacies were evident across multiple sampling years and mowing treatments, indicating that chronic water stress causes persistent shifts in belowground biodiversity. Notably, while bacterial communities were sensitive to both drought legacies and subsequent drought treatments, fungal communities exhibited greater resistance, consistent with fungal physiological adaptations that enable persistence under low soil moisture [8,9]. Importantly, the altered microbial community composition did not translate into significant changes in ecosystem respiration (ER) or net ecosystem exchange (NEE) under subsequent drought. As such, the authors highlight this mismatch between microbial shifts and carbon fluxes as a yet-unexplored decoupling between belowground diversity responses and ecosystem-level functioning.

In this study, the structure and biomass of plant communities had central roles in mediating ecosystem drought responses. For instance, drought legacy, especially in interaction with mowing treatments, promoted the dominance of fast-growing, opportunistic species (e.g., *Molinia caerulea* and *Rumex acetosella*) in younger *Calluna* plots (mown in 2020). These species likely exploited competitive release and increased nutrient availability following the *Calluna* decline. Yet, the most critical finding was that subsequent drought events reduced *Calluna* cover by ca. 15–20% in older, building-stage stands (mown in 2013), while younger plots showed no consistent reduction. Similarly, photosynthesis in younger plots declined by ca. 20–25% under drought relative to controls, and net ecosystem exchange (NEE) indicated approximately 25–30% reduction in carbon uptake, with fluxes becoming significantly less negative. Moreover, both photosynthesis and NEE in younger plots remained largely unaffected by the subsequent drought, despite their overall lower baseline values compared to older stands.

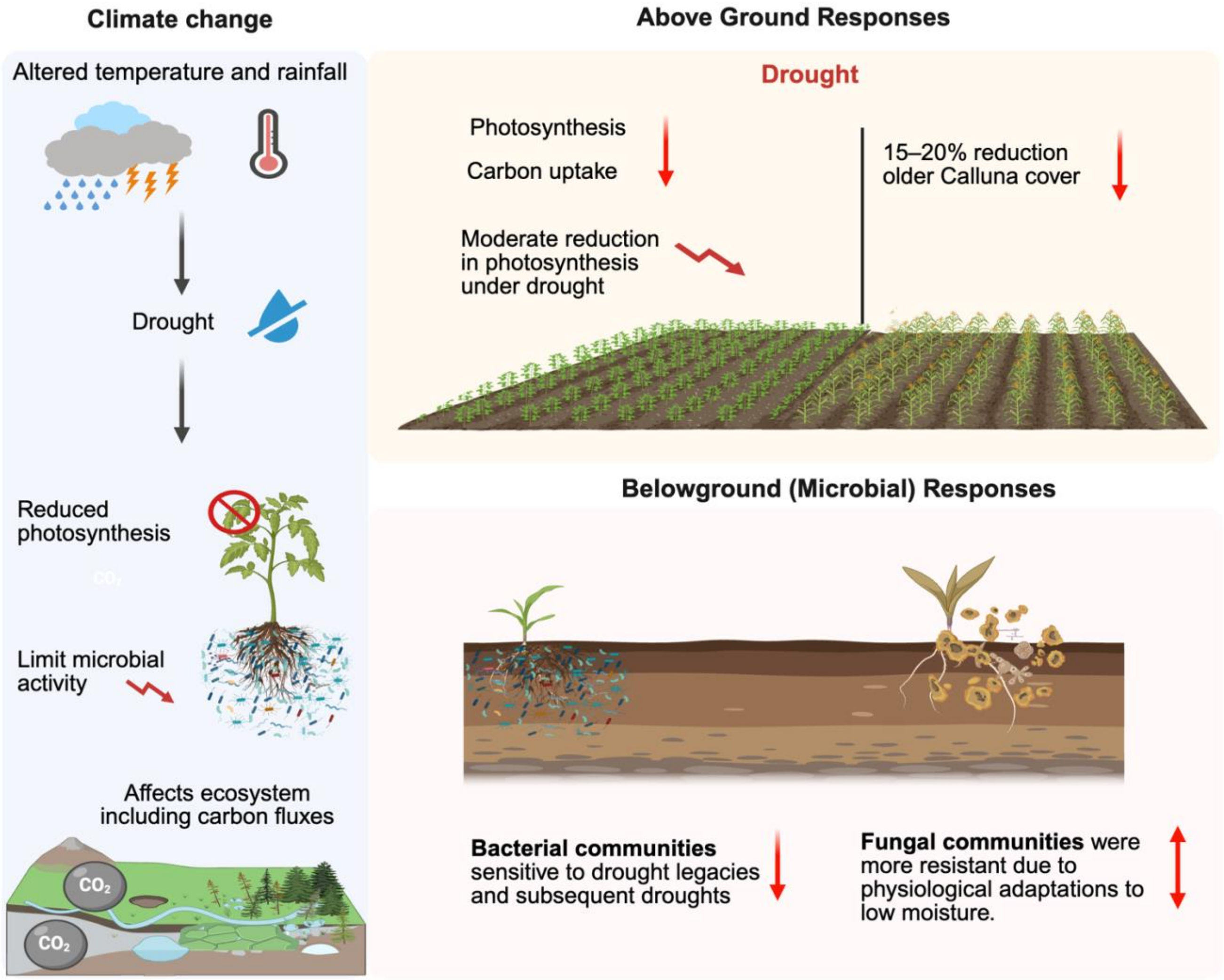

FIGURE 1 | Conceptual overview of drought-induced above- and belowground responses in heathland ecosystems.

Collectively, these results revealed that older *Calluna* is considerably more vulnerable to acute drought stress, possibly due to reduced physiological plasticity or cumulative tissue damage, despite displaying a greater capacity for C uptake. Thus, ecosystem C fluxes under subsequent drought were largely dictated by aboveground vegetation dynamics, especially the growth stage and biomass of *Calluna*, rather than by drought legacy effects observed in soil microbial communities.

The use of a long-term experimental system integrated with experimental manipulation constitutes a valuable aspect of the study reported by Gliesch et al [7]. This allowed the authors to disentangle multiple direct and indirect pathways associated with ecosystem responses. Specifically, the authors used structural equation modeling to show that plant community composition (i.e., *Calluna* cover) was the primary driver of both NEE and ER, whereas microbial community shifts did not significantly predict CO_2 fluxes. This modeling approach provided a mechanistic overview that highlights the overriding importance of vegetation in regulating ecosystem carbon balance, even in systems where microbial communities are persistently altered by the legacy of drought events. Furthermore, by examining plots at different vegetation stages (i.e., manipulated experimentally via mowing), the authors found that plant ontogeny is an important moderator of drought impacts on C fluxes, thus constituting a factor often overlooked in ecosystem-scale experiments.

Specifically, within ecosystem-scale experimentation, the use of decade-long field systems is of primary importance for capturing the sequential and often enduring effects imposed by drought legacies. For instance, in this study, the persistence of altered soil microbial communities years after the cessation of chronic drought suggests limited resilience or very slow recovery of soil biodiversity in heathlands. Yet, the absence of functional consequences for CO_2 fluxes raises important scientific questions with respect to metabolic redundancy and adaptation within the soil microbiota. For instance, one can argue that dynamic changes in soil microbial communities under drought do not affect CO_2 fluxes due to functional stability, where multiple taxa can perform similar functions. In contrast, less diverse plant communities in the system are more prone to drought impacts, leading to a reduction in photosynthesis, which cascades directly into a reduced C sink. This asymmetry between above- and belowground functional responses provides a crucial insight for advanced model prediction of diverse ecosystems to climate change vulnerability.

It is important to notice that a few limitations in this study also warrant careful consideration. First, the findings are derived from a single heathland (located in the Netherlands), which constrains the spatial generalizability of results. Distinct heathlands vary in management history, soil physicochemical and biological properties, and microclimates. Besides, the intensity and frequency of drought events are known to vary substantially across regions. Second, although microbial communities were sampled with high-resolution sequencing, their functional attributes (e.g., enzyme activities, metabolic potential) were not determined in the study, thus limiting interpretation of the apparent decoupling between community shifts and carbon fluxes. Third, plant and microbial communities were only sampled annually, not allowing for depicting potential shorter-term dynamics or lagged responses in these communities associated with fluctuations in CO_2 fluxes. Finally, while mowing treatments provided a clever proxy for *Calluna* life stage, they may not fully capture natural age structure or root system development, potentially influencing observed drought sensitivities in the experimental system. Collectively, these limitations highlight the need for replication across sites, higher temporal resolution of community sampling, and the necessity for quantifying functional soil microbial-mediated processes to advance mechanistic resolution of their findings.

Overall, the study by Gliesch et al [7] offers a landmark contribution that refines our understanding of the extent to which drought legacies alter ecosystem processes important for carbon cycling dynamics. Their long-term experiment reveals several pathways and variables that can now be explored and integrated with current Earth system models to refine model resolution in predictive accuracy. Moreover, future research could prioritize expanding the drought-legacy experimentation across ecosystems varying in vegetation structure, soil type, and climate regimes. Particularly, forests, grasslands, and peatlands may be expected to exhibit different balances of plant versus microbial control over carbon fluxes. Functional assays of microbial activity and metabolomics should complement community sequencing to resolve whether shifts in diversity translate into altered rates of microbial-mediated metabolic processes under stress. Moreover, integrating high-frequency measurements of CO_2 fluxes with continuous plant and microbial monitoring could uncover the temporal coupling or decoupling of above- and belowground responses. Finally, given that older *Calluna* stands proved most vulnerable to drought, there is a pressing need to examine how plant ontogeny interacts with climate extremes to determine ecosystem carbon budgets. These insights are vital for conservation and management of heathlands, which face simultaneous pressures from climate change, nitrogen deposition, and land-use conversion.

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AUTHOR CONTRIBUTIONS

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The author has nothing to report.

LINKED ARTICLE

This article is a Commentary on Gliesch et al. (2025) https://doi.org/10.1111/gcb.70441

REFERENCES

1. Reichstein M, Bahn M, Ciais P, Frank D, Mahecha MD, Seneviratne SI, Zscheischler J, Beer C, Buchmann N, Frank DC. **2013**. Climate extremes and the carbon cycle. *Nature* 500:287–295
2. Aldea J, Dahlgren J, Holmström E, Löf M. **2024**. Current and future drought vulnerability for three dominant boreal tree species. *Global Change Biology* 30:e17079
3. Abreha KB, Enyew M, Carlsson AS, Vetukuri RR, Feyissa T, Motlhaodi T, Ng'uni D, Geleta M. **2022**. Sorghum in dryland: morphological, physiological, and molecular responses of sorghum under drought stress. *Planta* 255:20
4. Fuchslueger L, Bahn M, Fritz K, Hasibeder R, Richter A. **2014**. Experimental drought reduces the transfer of recently fixed plant carbon to soil microbes and alters the bacterial community composition in a mountain meadow. *New Phytologist* 201:916–927
5. Anderegg W, Trugman A, Badgley G, Konings A, Shaw J. **2020**. Divergent forest sensitivity to repeated extreme droughts. *Nat Clim Chang* 10:1091–1095
6. Gliesch M, Sanchez LH, Jongepier E, Martin C, Hu Y, Tietema A, de Vries FT. **2024**. Heathland management affects soil response to drought. *Journal of Applied Ecology* 61:1372–1384
7. Gliesch M, Sanchez LH, Boreel K, Tietema A, de Vries FT. **2025**. Long-term drought persistently shifts plant and soil microbial communities but has limited impact on CO_2 fluxes under subsequent drought. *Global Change Biology* 31:e70441
8. Canarini A, Schmidt H, Fuchslueger L, Martin V, Herbold C, Zezula D, Gündler P, Hasibeder R, Jecmenica M, Bahn M. **2021**. Ecological memory of recurrent drought modifies soil processes via changes in soil microbial community. *Nat Commun* 12: 5308
9. Yang X, Zhang Y, Zhang X, Wang Y, Liu X, Liu M, Xiao Y, Wu J. **2025**. Soil microbiota from warmer and drier grasslands are more vulnerable to drought stress. *Global Change Biology* 31:e70507