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INVITED COMMENTARY

Why Andromeda is no goddess for the sustainability of bogs

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In Greek mythology, the beautiful goddess Andromeda is freed from the ravages of Cetus, a terrible sea monster, by Perseus who has fallen in love with her. The two love-birds eventually wed and Andromeda produces six sons, and lives a fulsome life. But what has this cheery tale got to do with bogs? Back on planet Earth, *Andromeda polifolia*, and many related ericaceous shrub species, are also reproducing effectively, spreading their seed, and encroaching into new environments. This so-called 'shrubification' is occurring in northern latitude peatlands (Breeuwer et al., 2009) and at high altitudes through the loss of alpine grassland (Broadbent et al., 2022). Despite such observations, shrubification of peatlands by evergreen ericaceous species is far less well studied than, for example, arctic tundra, where expansion is driven largely by deciduous shrubs (Mekonnen et al., 2021).

The success of *Andromeda* and other ericaceous shrubs seems to be related to their ability to respond positively to climate change, particularly to warmer, drier conditions. In peatlands, the dramatic shifts in vegetation induced by climate change are a pressing concern given the amount of carbon captured and stored in these habitats. Moreover, the conversion of slow-growing vegetation dominated by *Sphagnum* and other bryophytes, where vascular root systems are absent, to more productive shrubs with well-developed root systems, has potential to substantially change the amount and dynamics of energy (carbon) flow into soils, and strongly influence rates of biogeochemical cycling (Trinder et al., 2008). Thus, while the phenomenon of shrubification is comprehensively documented and described across multiple ecosystems, changes in the linkages between above-ground and below-ground processes because of shrub encroachment are generally less well understood.

So what are the proximate mechanisms above- and below-ground that underpin shrubification in peatlands, and what is the relative importance of the two key components of climate change—increased temperature and reduced rainfall—in facilitating such shifts? These questions were the focus of a paper published in this issue by Buttler et al. (2023). An important feature of the study relates to the experimental design, which combined field manipulations of climate change factors (water table depth and air temperature) with observational measurements along a natural gradient, thus combining the benefits of both approaches. While such an approach is not in itself novel, the application has rarely, if ever, been applied to address shrubification in peatlands. Moreover, the effort to establish and maintain such an experiment in the field is vast. The value of this dual approach was borne-out in the interpretation of the data: the authors concluded that the combined effect of warming and rainfall reduction provided a more robust explanation of findings. This important outcome would not have been possible without a combined experimental and observational approach.

A key novelty of the work was the impressive combination of analyses that included quantification of vegetation biomass and litter chemistry, chemistry of pore water, soil microbial and faunal communities, soil enzyme activities and environmental parameters. This suite of analyses recognises the vital role of interactions between above-ground and below-ground components of ecosystems, including among trophic levels, and between biotic and abiotic components. By doing so, rigorous insight of the mechanisms underpinning how warming and rainfall reduction drives peatland functioning is possible. Here, warmer, drier conditions stimulate the biomass and cover of *Andromeda* and increases leaf phenolic concentrations, which then negatively affects enzyme multifunctionality both directly and indirectly, via soil fungal and faunal communities. *Andromeda* therefore has the capacity to substantially modify peatland biogeochemical cycling, including key pools of organic matter.

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As is the case with many elegant field-based studies, additional questions and complexities are raised. One potential piece of the jigsaw that was not the focus of Buttler et al. (2023) was a role of ericoid mycorrhizal fungi, specifically how these fungi may influence interactions among plants and soil processes in response to climate manipulations. Ericaceous roots are often highly branched and very fine, sometimes with diameters of only 15 microns, and the cortical cells are heavily colonised by coils of ericoid mycorrhizal fungal hyphae, which grow into the rhizosphere and proliferate along root surfaces. Fuelled by recent assimilate from host plants (Stribley & Read, 1974), ericoid mycorrhizal fungi can suppress the growth of saprotrophic fungi and thus decomposition of organic matter (Fanin et al., 2022), and themselves contribute to the pool of organic matter in soil by producing necromass (Clemmensen et al., 2015). In contrast, the fungi may also simultaneously accelerate soil organic matter degradation through the priming effect, whereby inputs of recent plant photosynthate can stimulate microbial breakdown of older, more recalcitrant organic matter (Talbot et al., 2008). Indeed, past work in bogs has shown that modest increases in temperature can disrupt ericoid mycorrhizal colonisation of *A. polifolia* via interactions with phenolics produced by *Sphagnum* (Binet et al., 2017). Thus, the 'below-ground components' element of the structural equation model produced by Buttler et al. (2023; their figure 8) may be even more complex than can be deduced from their analyses.

Despite these possible gaps, Buttler et al. (2023) is a timely and important reminder of the need for multi-disciplinary approaches to tackle grand challenges such as climate change impacts and underlies the importance of considering multiple factors as drivers of change. Nonetheless, our ability to concurrently manipulate several factors of change is poor (Rillig et al., 2019), and it remains to be tested how peatland functioning and shrub expansion responds to additional factors of nitrogen deposition and elevated atmospheric CO_2 concentrations alongside increased temporal variability of climate. One suspects an ability to slow the onward march of *Andromeda* is little better than myth.

CONFLICT OF INTEREST STATEMENT

The author has no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed for the current article.

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