Unravelling change in forest ground floras. A commentary on: 'Temporal patterns of seed germination in early springflowering temperate woodland geophytes are modified by warming'

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The simplistic assumption might be that if the spring is coming earlier with climate change, then plants will start to grow and flower earlier. In practice, while the flowering of some species has advanced, for others little change has been detected or they are even flowering later (Fitter and Fitter, 2002). Different phases of the plant growth cycle are influenced by seasonal temperature changes in different ways; only by understanding the combination of these effects can a final prediction of the effects of climate change be made. This issue is elegantly explored by Newton et al. (2020) in a study of the germination of two woodland geophytes: daffodils Narcissus pseudonarcissus and snowdrops Galanthus nivalis. Both of the species studied are more abundant further south in Europe than in the UK and so might be expected to benefit similarly from climate warming.

To test this, the authors set up an experiment to look at the effect that different seasonal warming (and cooling, to allow for possible weakening of the Atlantic Meridional Overturning Circulation) had on the dormancy of seeds of these species. Important messages from the study include that two ecologically similar species showed somewhat different responses to the same treatments. Warmer autumns and winters delayed the first autumn germination of N. pseudonarcissus but increased that of G. nivalis. There are potential effects of changes in germination rates on the soil seed bank. In most treatments, not all of the seeds germinated over the 2-year period,

but a higher proportion of ungerminated *G. nivalis* seeds proved not to be viable. The authors acknowledge that their work is based on study of a single population of each species, but they have results from other studies that suggest that the findings are valid more widely.

This study demonstrates why simple climate-niche models may fail to reflect how species actually respond to global warming. Changes to annual temperature means, even to a key seasonal mean, may not be enough to predict a response, if this depends, as with the species studied, on what happens to temperatures in the season before or after. The seasonality of temperature changes will also interact with other changes such as in precipitation. Increased summer temperatures that might be favourable for southern species may be accompanied by increased risk of drought, such that water availability becomes growth limiting, whereas, at least in the UK, winter-spring warming will generally coincide with relatively high water availability. In woodland there is also the complication that the measurements of temperature used in models are largely taken out in the open, whereas those experienced by the ground flora will be moderated by the sheltering effects of the tree canopy (De Frenne et al., 2013).

Why should this uncertainty about the response of woodland ground flora species to climate warming matter? The woody layers in a forest certainly contain the bulk of the biomass and hence the standing stock of carbon in the system. However, in many temperate forests, the ground flora typically has four to five times as many vascular plant species. The ground flora represents a fast cycling pool of carbon and nutrients, through its annual growth and dieback. The foliage (if not packed with toxins) is a major source of forage for herbivores, from leaf-mining moth caterpillars to mesofauna such as red deer Cervus elaphus. Tree regeneration may be facilitated by the protection given to seedlings by the surrounding vegetation or hindered by competition with it (Gilliam and Roberts, 2003). Massed displays of flowers in the ground flora, including the two species used in this study, are significant factors in attracting people to care about and to visit woods and forests, from which other benefits to society may flow.

The factorial experimental approach used in this study is to be commended,

but there are limits to how far it can be used to address interactions in the woodland ground flora more generally. Newton et al. (2020) demonstrate that the germination response can be temporally context dependent: what happens may depend on what has gone before. In the field, how species behave is also strongly spatially context dependent. A patch of daffodils may be growing better because it is under a gap (more heat, light and rainfall) created by a branch-fall than the patch a few metres away that is under closed canopy. or another that happens to be a favoured rutting area for deer.

Permanent plot studies, such as that established in 1974 in Wytham Woods by Colyear Dawkins (Kirby, 2010), are now being collated across Europe to look at change over environmental gradients, for example in atmospheric nitrogen levels, and over time scales that allow climate effects to be detected (Verheyen *et al.*, 2017). Experimental studies can then be targeted at the types of species or processes that emerge as most likely to yield interesting results.

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