

Letters

Multiple routes underground? Frost alone cannot explain the evolution of underground trees

Introduction

Finckh *et al.* (2016; this issue of *New Phytologist*, pp. 904–909) query our inferences drawn from a recent study (Maurin *et al.*, 2014) on the evolutionary origins of the geoxylic suffrutex life form in southern Africa. Geoxylic suffrutices, or more informally ‘underground trees’ represent a distinct growth form characterized by a long-lived woody xylopodia underground with often short lived aerial shoots (White, 1979; Simon & Pennington, 2012). Described in detail by White (1979), ‘geoxyles’ are common in fire-dependent savanna ecosystems. Using a time calibrated phylogenetic tree for the woody taxa of southern Africa, sampling 1400 taxa, we showed that the geoxylic suffrutex life form evolved independently multiple times, suggesting a selective advantage to going ‘underground’ (Maurin *et al.*, 2014). We reviewed four putative drivers of the geoxyle habit: (1) winter frost on the South African Highveld, proposed by Burt Davy (1922); (2) mammal herbivory; (3) edaphic factors, particularly seasonal waterlogging; and (4) fire. We discussed evidence in support of each, and found that escape from fire is the most general explanation. We noted that ‘poor growing conditions that reduce growth rates of juvenile trees would also result in reduced probabilities of reaching fire-proof sizes and transitioning to tall mature trees’ and that ‘geoxyles are common where site conditions reduce growth rates, such as on seasonally waterlogged and/or low-nutrient soils, or, . . . at high-altitude sites with cold winters’ (Maurin *et al.*, 2014). Finckh *et al.* (2016) suggest we may have overestimated the link with fire, and overlooked the importance of frost; we revisit their arguments.

Evidence of fire as an evolutionary driver

Finckh *et al.* (2016) argue against the importance of fire in driving the evolution of the geoxyle life form on three accounts.

First, the current fire regime is largely anthropic, and Finckh *et al.* (2016) suggest that fire-return rates were likely much lower in the absence of people, when the geoxyle life form evolved. Fire-return interval provides a major selective pressure because a too-frequent fire-return can inhibit regeneration by trapping saplings in a regeneration bottleneck (Bond & Keeley, 2005). Finckh *et al.* (2016) suggest that, without humans, fire-return intervals were far enough apart for species to escape the fire-trap. However, as

Finckh *et al.* (2016) note themselves, we do not have accurate data on paleo-fire regimes. In their wide-ranging analysis of human impacts on African savanna fire regimes, Archibald *et al.* (2012) suggested that the first impact of humans would have been to *reduce* fire frequencies by altering fuel continuity. Further, Finckh *et al.* (2016) assume that the selection pressure exerted by fire needs to be constant. This assumption is erroneous. A short and regular fire-return might completely exclude trees; however, even irregular fires spaced far apart would exert a major selective force by causing stem mortality of a whole cohort of younger trees. Any species that was less impacted by such events, even if rare, would be favoured by natural selection. In addition, growth rates vary immensely among trees species, a faster growth rate might allow quick escape from the fire-trap, but at the cost of reduced lifespan, whereas a slow growing species might be exposed to fire for longer, but have longer lifespan (Wright, 2002; Leigh *et al.*, 2004). The geoxyle life form might thus represent an alternative, slow-growing, life-history strategy, and anecdotal evidence does suggest that some geoxyle individuals are surprisingly long-lived, with some individuals living to an estimated 13 000 yr or more (Sussman *et al.*, 2014).

Finckh *et al.* (2016) assert that a 5 yr fire-free interval is sufficient for saplings to grow into (relatively fire-proof) trees so that a shorter fire cycle is needed to favour the evolution of a geoxyle life form. They do not reference the source of the ‘5 yr’ interval. However the length of the fire-free interval is critical to our arguments. Intrinsically slow growth rates, and/or environmental conditions that prolong juvenile growth out of the flame zone, would select for growth forms that live and reproduce within the flame zone. The understandably sparse data available for African savanna trees indicate wide variation in (and slower) growth rates to fire-proof sizes (e.g. Chidumayo & Frost, 1996; Wakeling *et al.*, 2011; February *et al.*, 2013). Comparative data on trees, shrubs and geoxyles under different environmental conditions would contribute greatly to better understanding of woody plant life history evolution in savanna fire regimes.

Second, vegetation patterns on the Angolan plateau, which is rich in geoxylic suffrutices, shows opposite patterns to those that would be predicted from a fire-driven landscape: hills are forested, but slopes are dominated by geoxylic grasslands. This high-elevation plateau has many unique characteristics, and whether observations from this can be extrapolated across southern Africa may be debated. Nonetheless, it is important to note that, contrary to the conclusions drawn by Finckh *et al.* (2016), fire is still a major component of this landscape. Airy Shaw (1947) refers to the extensive herbaceous communities, including the ‘Parkland’ and ‘Orchard’ vegetation types, within which up to 50% of the vegetation represents savanna grasses, and which are subject to annual fires before the first rains. Forest/grassland mosaics are common in savanna landscapes in

Africa with grass-fuelled fires seldom penetrating more than a few metres into closed forest, which tends to be wetter and cooler. Nonetheless, these frequent, but low intensity fires could easily have provided sufficient selection pressure to favour the underground growth of geoxyles.

Third, Finckh *et al.* (2016) suggest that our arguments that geoxyles minimize resource input into vegetative growth to the benefit of reproductive output are unsupported and would only allow geoxyles to outcompete trees if fire-return intervals were < 5 yr. As we have shown earlier, the requirement for a minimal fire-return interval of 5 yr is fallacious. We acknowledge that we do not have accurate estimates of resource investment into growth vs reproduction, collecting such data across many species is challenging, particularly so for trees. Anecdotally, we observe, however, that because fruit sizes do not differ significantly between geoxyle and trees sister species (Table 1 from Maurin *et al.*, 2014), it would seem that the proportional investment in reproductive output must be large for geoxyles, even given that large trees have more fruits. Further, we cannot see how this argument would favour frost over fire as an evolutionary driver (see later).

Evidence of frost as an evolutionary driver

Finckh *et al.* (2016) propose frost as a more probable evolutionary driver of the geoxyle lifeform, citing evidence that the Angolan Plateau is subject to frost, they observe frost burns on trees in the ecotone between forests and grasslands at their study site in Cussequ Angola (Revermann & Finckh, 2013), and that tropical trees are, in general, sensitive to frost. We do not dispute this evidence, nor, however, do we find it compelling as a general explanation for the evolution of geoxylic suffrutices. Observational data, which we cited, support Finckh *et al.* (2016) in that some geoxyles occur in regions subject to occasional frost; however, geoxyles are also common where frost is absent. Notably the distribution of vegetation types in Angola, such as ‘ngoti’ and ‘anharas de borracha’ – where geoxyles are most abundant and diverse – extend far beyond the areas in which the ‘frost trap’ may operate, and the vast chanas de borracha (*Landolphia*) of the Lundas receive no frosts at all, but severe fires. Importantly, our original analysis encompassed the entirety of southern Africa, from the Zambezi region between 8°5'S and 34°5'S and 11°7'W and 40°9'E, and searched for macro-evolutionary trends across many hundreds of lineages. It is not, therefore, a meaningful comparison to contrast these results with data from a single case study. Further, evidence for the importance of frost in the Brazilian cerrado cited by Finckh *et al.* (e.g. Filgueiras & Peña, 1989), comes from the far south (Sao Paulo state) or from relatively high altitude, where occasional frosts occur, whereas most of the two million square kilometres of the cerrado is frost free. While hard frost is more common in seasonally dry chaco woodlands of Argentina and Paraguay, geoxyles are rare or absent (e.g. Prado, 1993a,b). We agree that frost (as well as other factors, such as nutrient poor soils and seasonal waterlogging) is most likely locally important, a point we

made in our original manuscript, but we argue that it is not the key driver.

Summary

We appreciate the thoughtful commentary by Finckh *et al.* (2016) and we welcome more work on these fascinating plants. Their biology, morphology and population ecology is poorly known. Indeed life history evolution in woody plants in savannas generally is far less studied than in other flammable ecosystems (Bond & Keeley, 2005). The coincidence in the timing of the emergence of flammable savanna in Africa and the appearance of woody fire-maintained cerrado plants in Brazil is striking. Our dates on the origin of the geoxyle lifeform are consistent with marine charcoal records of increased fire activity in the Atlantic as savannas spread (Morley & Richards, 1993; Hoetzel *et al.*, 2013). If the geoxyle lifeform arose in response to frost, it is not clear why we should observe such a marked signature in the timing of their evolutionary origins. Nevertheless there remain many unanswered questions on phylogenetic inferences on the origin of Africa's flammable grasslands. For example, in some genera, such as *Fadogia*, there appear to have been reversals back to a ‘tree’ lifeform, but our phylogenetic sampling is not yet sufficient to generate hypotheses as to what might have favoured this reversal. In addition, the evolutionary age of some suffrutices appear unusually old (> 10 million yr), much older than the rise to ecological dominance of fire-dependent savanna. It is possible that savanna persisted much further back in geological time than current estimates suggest, perhaps as geographically restricted or marginal habitats, and these taxa reflect this earlier vegetation history. Alternatively, we might simply be missing the recent relatives of these older taxa; our taxonomic sampling of lineages may have been insufficient, or their nearest relatives could be found elsewhere or may have become recently (in evolutionary terms) extinct, pulling back perceived divergence time to the most recent extant common ancestor. Unravelling these complexities may reveal new insights into the evolutionary history of the geoxyle life form and the major vegetation shifts that reshaped the flora of much of southern Africa over the past several millions years.

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