

Plant-soil interactions in global biodiversity hotspots

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This Special Issue explores plant-soil interactions in global biodiversity hotspots and highlights the extent to which these interactions may play a role in explaining the megadiversity of these hotspots. On a global scale, biodiversity hotspots are mainly located where high relief (mountains) and high geodiversity (variety in geology and soils) intersect, especially in tropical and Mediterranean climate regions. Factors causing spatial heterogeneity of temperature and precipitation often further increase the number of plant species per unit area. Meta-analyses indicate about twenty global biodiversity hotspots with >3000 plant species per 10,000 km² (Mutke and Barthlott 2005; Barthlott et al. 2007). The top five localities with >5000 species per 10,000 km², covering just 0.2 % of the Earth's land area surface, but harbouring 6.2 % of total plant diversity, are: i) Costa Rica-Chocó; ii) Atlantic Brazil; iii) Tropical Eastern Andes; iv) Northern Borneo; and v) New Guinea (Barthlott et al. 2005). Although most biodiversity hotspots are in moist tropical regions, there are also regions with a Mediterranean climate that are extremely species-rich: the South African Cape (*fynbos*), California (*chaparral*) in the United States,

and the sandplains (*kwongkan*) of south-western Australia. Some islands are also global centres of diversity and endemism, notably New Caledonia, Madagascar and the islands of the Malesian archipelago.

Soil fertility has been posited as a key driver for plant diversification through resource competition to access limiting nutrients, and there is abundant evidence for increasing plant diversity with decreasing soil nutrient status, especially in the case of phosphorus (Huston 1979, 1980; Lambers et al. 2010; Blanck et al. 2011; Olde Venterink 2011; Pekin et al. 2012). The 'biogeochemical niche' hypothesis proposes that plants competing in the same habitat with co-existing plant species use essential elements differently (Garten 1978; Peñuelas et al. 2009, 2013; Sulpice et al. 2014; Chimphango et al. 2015; Lambers et al. 2015). Such resource partitioning relates to evolved efficiency in uptake, symbiotic relationships and specialised metabolic functioning, as well as opportunistic use of micro-scale habitat and soil chemical gradients. Different nutrient-acquisition strategies as a consequence could promote niche differentiation and hence reduce competition for limiting resources (Fyllas et al. 2009). A recent study conducted in the *kwongkan* of south-western Australia showed, however, that variation in plant diversity is not explained by local resource heterogeneity/partitioning and soil fertility along a gradient, but rather determined by environmental filtering driven by decreasing phosphorus availability and soil acidification during long-term pedogenesis, and this highlights that long-term evolutionary processes shape present-day species pools (Laliberté et al. 2014).

An example in case of nutrient-limited soils are those derived from ultramafic geology, characterised by an

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unusual geochemistry with low calcium/magnesium quotients, limited phosphorus and potassium availability and concomitantly high concentrations of nickel (Van der Ent et al. 2016a). These soils can impose edaphic stresses that may favour the evolution of plant species by promoting divergence, as a result of the insular occurrence of these soils, ultimately leading to adapted specialistic plants and endemism (Whittaker 1954; Rajakaruna 2004; O'Dell and Rajakaruna 2011). In many hotspots, such as in California and New Caledonia, the presence of ultramafic soils contributes disproportionately to concentrating the local levels of plant diversity (Harrison et al. 2006; Isnard et al. 2016). This is reflected in this Special issue, with four articles focussing on ultramafic ecosystem in the biodiversity hotspots of New Caledonia, Northern Borneo and the Mediterranean Basin. Elsewhere, other types of geodiversity have also provided evolutionary forces driving plant diversification, for example in Brazil, in the rock outcrops of the Brazilian Atlantic Rainforest (do Carmo and Jacobi 2016) and in the *campos rupestres* (Silveira et al. (2016).

Patterns of biodiversity are highly scale-dependent, and particularly high levels of diversity often coincide with habitat patchiness and species turnover (β -diversity) along gradients (Harrison and Inouye 2002). This is exemplified by the case of Mount Kinabalu in Northern Borneo, which has more than 5000 vascular plant species in less than 1200 km² (Beaman 2005). A large-scale ecological study shows that within climatic zones on this mountain the distribution of plant species is linked to soil chemistry with stunted vegetation and elevational floristic compression on chemically-adverse ultramafic soils (van der Ent et al. 2016b). Where the effects of high-altitude and nutrient-poor soil combine in tropical rainforest, gymnosperms may compete with angiosperm trees facilitated through high insolation (Sawada et al. 2016). Elsewhere in Southeast Asia, on Hainan Island (China), a large-scale plot study by Jianga et al. (2016) emphasised the importance of soil and microclimatic factors for driving diversity in lowland and montane (semi-deciduous) forests. In the Brazilian Atlantic rainforest, outcrops of a different geological origin also enhance the plant megadiversity through promoting edaphic and topographic gradients, resulting in high α - and especially β -diversity (do Carmo and Jacobi 2016). In Brazil, such local fine-scale variation in soil nutrient and/or moisture availability influences radial growth of the dominant tree species, *Dalbergia*

nigra (Pontara et al. 2016). However, ostensibly homogeneous habitats, notably old climatically-buffered infertile landscapes (OCBILs), are also exceptionally species-rich, the *fynbos* of the Cape Floristic Region and the *kwongkan* of south-western Australia are famous examples (Allsopp et al. 2014; Lambers 2014), but *campos rupestres* fall in the same category (Silveira et al. 2016; Oliveira et al. 2015, 2016).

The role of cluster roots and functionally similar root structures and of root architecture in severely phosphorus-impooverished landscapes is explored in two articles focussing on *Eucalyptus* and a Proteaceae from Australia and Brazil, respectively. Experimental evidence shows that the root architecture and biomass allocation of *Eucalyptus* species reflects that of edaphic adaptations of specialised species, even when grown under common conditions (Hamer et al. 2016). This may have implications for the ability of edaphic specialists to acclimate to changes in their environment, especially climate change. Another edaphic root adaptation is the formation of cluster roots, which are generally associated with a burst of carboxylate exudation to enhance phosphorus uptake in phosphorus-limited environments (Shane and Lambers 2005). Cluster roots are best known from the sandplains of south-western Australia; their formation is suppressed at elevated phosphorus supply, in response to elevated leaf phosphorus concentration (Shane et al. 2003). However, studies with a Brazilian Proteaceae demonstrated that, unusually, cluster-root formation and foliar phosphorus concentration do not depend on the amount of phosphorus supplied under experimental conditions (de Britto et al. 2016). Root mycorrhizal associations are another adaptation of plants growing on nutrient-impooverished soils, and their effect on legume trees in French Guiana is the subject of the work presented by Brearley et al. (2016). Rhizobacterial communities were also investigated in an extreme microhabitat: the roots of nickel-hyperaccumulating plants (Álvarez-López et al. 2016). The results of that study exhibit that even under toxic conditions the diversity of microbes associated with hyperaccumulating roots may be high with selective enrichment of nickel-tolerant bacteria. One especially intriguing example of edaphic specialisation is the evolution of carnivorous plants in the genus *Nepenthes* from the pitcher-plant family (Nepenthaceae). In the Old World this genus is known for its many narrow endemics, restricted to severely nutrient-limited soils, often on isolated mountain peaks and ultramafic outcrops

(van der Ent et al. 2016c). The roles of climate, soils and vicariance in shaping the diversity and distribution of *Nepenthes* in Southeast Asia are reviewed in an article by Clarke and Moran (2016).

Perhaps the most extreme example of plant-soil interactions occurs on metalliferous soils (Baker et al. 2010). The copper-cobalt outcrops of the Katangan Province in the Democratic Republic of the Congo are the richest location for metallophytes (plants growing in metalliferous soils) in the world, with over 600 species described to date (Faucon et al. 2010; Ilunga et al. 2013). The levels of endemism are especially remarkable and illustrate how challenging soil conditions can favour the evolution of edaphic endemics (Faucon et al. 2016). These mineralised outcrops are, however, under enormous pressure from the mining industry, which extract the resources contained in this region. Several articles in this Special Issue stress concerns for continued existence of highly-diverse edaphic floras, due to resource extraction, climate change, and land clearing. Priority setting is necessary to respond to global biodiversity threats, and there have been concerted efforts to shortlist major biodiversity hotspots, defined as biogeographic regions with >1500 endemic vascular plant species and less than 30 % of original primary habitat remaining (Myers et al. 2000). This ultimately led to a compilation of 35 hotspots that combined cover 17.3 % of the global land surface but contain 44 % of all known species of vascular plants and 77 % of all endemic plant species (Myers 2003; Myers et al. 2000; Mittermeier et al. 2004, 2011; Williams et al. 2011). In many hotspots, the strong link with geodiversity, epitomised by the occurrence of (edaphic) endemics, makes the local diversity especially threatened by habitat destruction and disturbances, as specialised species may be unable to survive under other conditions (Jacobi et al. 2011). Another threat may arise from limited investment in sexual reproduction in some endangered plants that are adapted to phosphorus-impoverished conditions which makes them more vulnerable to extinction (Fujita et al. 2014).

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