



## Tansley review

# Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands

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## Summary

Hyperdiverse forests occur in the lowland tropics, whereas the most species-rich shrublands are found in regions such as south-western Australia (kwongan) and South Africa (fynbos). Despite large differences, these ecosystems share an important characteristic: their soils are strongly weathered and phosphorus (P) is a key growth-limiting nutrient. Soil-borne pathogens are increasingly being recognized as drivers of plant diversity in lowland tropical rainforests, but have received little attention in species-rich shrublands. We suggest a trade-off in which the species most proficient at acquiring P have ephemeral roots that are particularly susceptible to soil-borne pathogens. This could equalize out the differences in competitive ability among co-occurring species in these ecosystems, thus contributing to coexistence. Moreover, effective protection against soil-borne pathogens by ectomycorrhizal (ECM) fungi might explain the occurrence of monodominant stands of ECM trees and shrubs amongst otherwise species-rich communities. We identify gaps in our knowledge which need to be filled in order to evaluate a possible link between P limitation, fine root traits, soil-borne pathogens and local plant species diversity. Such a link may help to explain how numerous plant species can coexist in hyperdiverse rainforests and shrublands, and, conversely, how monodominant stands can develop in these ecosystems.

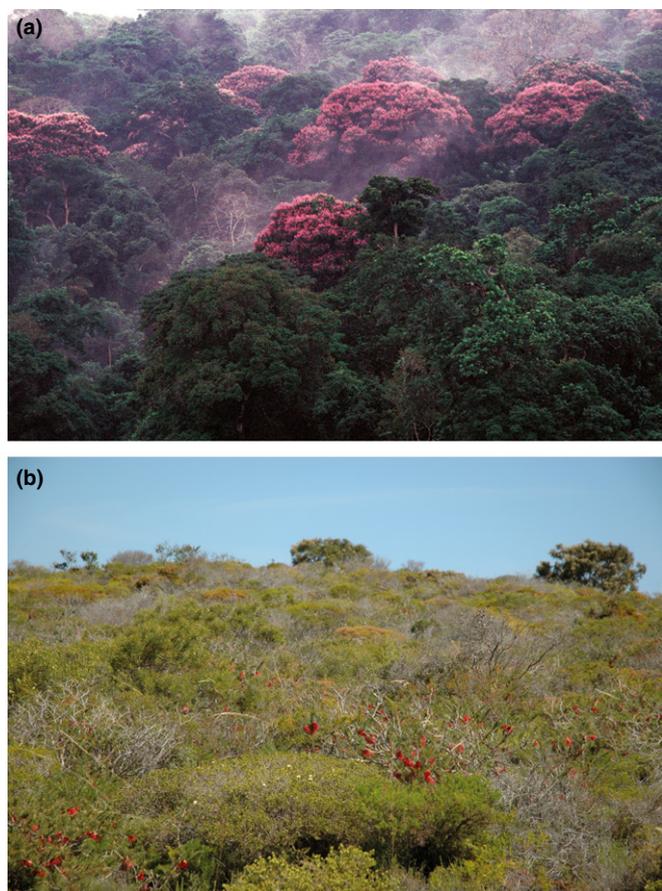
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**Key words:** alpha diversity, Janzen–Connell hypothesis, kwongan, monodominance, mycorrhizal fungi, negative density dependence (NDD), plant–soil feedback, tropical rainforest.

## I. Hyperdiverse forests and shrublands

Some terrestrial ecosystems support an exceptionally large number of coexisting plant species at the local scale. This is especially true

for lowland tropical rainforests (Fig. 1a), which contain the most species-rich plant communities in the world (Wilson *et al.*, 2012). For example, 307 tree species with a diameter at breast height  $\geq 10$  cm have been recorded within 1 ha in Amazonian Ecuador



**Fig. 1** Species-rich lowland tropical rainforests and seasonally dry shrublands. (a) Lowland tropical rainforest on Barro Colorado Island, Panamá. (b) Kwongan shrublands in Lesueur National Park, Western Australia. Photo credits: (a) S. Joseph Wright; (b) Etienne Laliberté.

(Valencia *et al.*, 1994). High woody plant diversity at local scales (i.e. alpha diversity), however, is not restricted to lowland tropical rainforests. Some seasonally dry shrubland ecosystems, such as kwongan in south-western Australia (Fig. 1b) and fynbos in South Africa, are also exceptionally diverse (Cowling *et al.*, 1996). In kwongan, species evenness is exceptionally high (Lamont *et al.*, 1977) and a single 10 m × 10 m (0.01 ha) plot can contain *c.* 40 shrub species as mature individuals (G. Zemunik, unpublished). What allows so many tree or shrub species to coexist in these hyperdiverse communities? Do similar mechanisms underlying plant species coexistence operate across these two different ecosystem types?

At first glance, hyperdiverse lowland tropical rainforests and seasonally dry shrublands have little in common, apart from their high levels of local plant diversity. Nevertheless, hyperdiverse lowland tropical rainforests and seasonally dry shrublands share one important characteristic: their soils are old, strongly weathered and thus nutrient impoverished, and phosphorus (P) availability, in particular, limits plant productivity (Cleveland *et al.*, 2011; Huston, 2012; Laliberté *et al.*, 2013). Other regions supporting less diverse Mediterranean shrublands (California, Chile, Mediterranean Basin) have more fertile soils (Cowling *et al.*, 1996).

Could P limitation contribute to plant species coexistence in hyperdiverse tropical rainforests and seasonally dry shrublands?

One reason why local plant diversity is exceptionally high in hyperdiverse rainforests and shrublands on P-impoorished soils is that the same factors leading to P depletion in soils (i.e. absence of large-scale geological disturbances over tens of thousands of years) also lead to large plant species pools over evolutionary timescales (Terborgh, 1973; Hopper, 2009). Species pool size is an important determinant of local plant diversity (Grace *et al.*, 2011; Laliberté *et al.*, 2014) and, consequently, not all P-limited ecosystems necessarily have high plant diversity. For example, seasonally dry shrublands similar to those found in south-western Australia also occur in south-eastern Australia, but plant diversity in that region is much lower because of climate-driven extinctions during the Pleistocene (Sniderman *et al.*, 2013). That said, although species pool size helps to explain variation in local plant diversity (Laliberté *et al.*, 2014), it does not identify the actual mechanisms contributing to plant species coexistence. Many different mechanisms have been proposed to explain how a large number of plant species can coexist in hyperdiverse rainforests (Wright, 2002) or shrublands (e.g. Lamont *et al.*, 1984). For example, a number of proposed mechanisms have addressed how plant species compete for, or partition, limiting resources, such as soil nutrients (see reviews by Wright, 2002; Laliberté *et al.*, 2013). Our aim, in this review, is not to provide an exhaustive list of the different mechanisms underlying plant species coexistence in hyperdiverse forests and shrublands, but rather to focus on one in particular. In tropical rainforests, the role of natural enemies (e.g. pathogens) in generating distance- or density-dependent mortality of juveniles (Gillett, 1962; Janzen, 1970; Connell, 1971) is increasingly being recognized as a key driver of plant species coexistence (Gilbert, 2002; Wright, 2002; Freckleton & Lewis, 2006; Terborgh, 2012; Bagchi *et al.*, 2014), but this has received comparatively little attention in hyperdiverse shrublands. Our focus on negative density dependence (NDD) mediated via soil-borne pathogens does not invalidate other proposed mechanisms underlying plant species coexistence, because many of these mechanisms are mutually compatible (Wright, 2002; Laliberté *et al.*, 2013). We also discuss the occurrence of monodominant stands (i.e. > 50% of canopy trees or shrubs from one species) amongst otherwise species-rich rainforests and shrublands. We propose a hypothesis linking P limitation, root traits and susceptibility to soil-borne pathogens that may help to explain how a large number of plant species can coexist in hyperdiverse rainforests and shrublands, and, conversely, how monodominant stands can develop.

Our review is divided into five sections. First, we review evidence for P limitation of plant productivity in hyperdiverse lowland tropical rainforests and seasonally dry shrublands. Second, we show how poor recruitment close to conspecific mature individuals and/or at high seedling densities is common in these two ecosystem types. Third, we discuss the importance of soil-borne pathogens in causing NDD. Fourth, we discuss root traits that enable the efficient acquisition of P in P-impoorished soils, and hypothesize a trade-off between efficient P acquisition and resistance to soil-borne pathogens. Such a mechanism would tend to equalize differences in competitive ability among co-occurring species,

thereby enhancing opportunities for coexistence and increasing local species diversity. Finally, we propose avenues for further research to explore a possible link between P limitation, root traits and pathogen-mediated NDD in hyperdiverse rainforests and shrublands. Although our hypothesis should apply equally well to species-rich shrublands, such as south-western Australian kwongan and South African fynbos, given the climatic, edaphic and floristic similarities between these two regions (Cowling *et al.*, 1996), our review focuses on the former. Our hypothesis should also be relevant to other seasonally dry ecosystems with high woody plant diversity and P-poor soils, such as the Brazilian cerrado (Furley & Ratter, 1988). By presenting this hypothesis, our aim is to stimulate new research on the role of soil-borne pathogens in promoting plant species coexistence in hyperdiverse plant communities, especially in seasonally dry shrublands, where far less research on mechanisms driving plant species coexistence has been conducted than in lowland tropical rainforests.

## II. Evidence for P limitation

In addition to climate and temperature, nutrient supply is a major constraint to terrestrial primary productivity. Of all plant nutrients, nitrogen (N) and P most commonly limit or co-limit plant growth (Elser *et al.*, 2007). In temperate, boreal and arctic ecosystems, N is generally considered to be the key limiting nutrient (Vitousek & Howarth, 1991), although co-limitation by N and P is also widespread (Elser *et al.*, 2007). However, P is the nutrient thought to most strongly limit plant growth in lowland tropical rainforests (Vitousek, 1984) and many seasonally dry shrublands. This is because their soils are old and generally strongly weathered (Sánchez, 1976), which leads to P depletion from the soil profile (Walker & Syers, 1976; Turner & Laliberté, 2014).

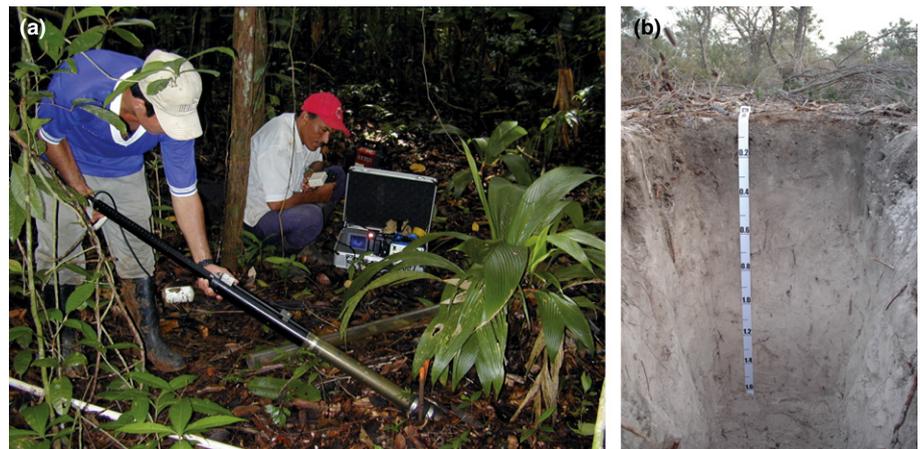
### 1. Lowland tropical rainforests

The contention that P rather than N limits the productivity of lowland tropical rainforests is supported by several indirect proxies, such as high foliar N : P ratios (Townsend *et al.*, 2007), high foliar and soil  $\delta^{15}\text{N}$  values (Martinelli *et al.*, 1999) and large N losses (Hedin *et al.*, 2009). Although there is considerable

biogeochemical heterogeneity within the tropical forest biome (Townsend *et al.*, 2008), recent analyses have suggested that soil P concentration is the strongest predictor of aboveground net primary production (ANPP) and other ecosystem processes in lowland tropical rainforests (Aragão *et al.*, 2009; Cleveland *et al.*, 2011).

Direct evidence for P limitation comes from long-term fertilization experiments (Fig. 2a). However, as a result of the difficulties in establishing and maintaining these experiments, only four have ever been conducted in mature lowland tropical rainforests (Mirmanto *et al.*, 1999; Wright *et al.*, 2011; Alvarez-Clare *et al.*, 2013; Fisher *et al.*, 2013). In a lowland dipterocarp forest in Indonesia, P and N were found to co-limit litter fall production, although the study was relatively short term (*c.* 1.5 yr after fertilization; Mirmanto *et al.*, 1999). In a lowland Ecuadorian rainforest, foliar N : P ratios (*c.* 25) pointed towards P limitation, although tree growth was co-limited by P and N availability (Fisher *et al.*, 2013). In Costa Rica, a higher proportion of canopy trees had increased in basal area, small subcanopy trees had doubled in stem growth and seedlings had more leaves, 2.7 yr after P addition (Alvarez-Clare *et al.*, 2013). In Panamá, litter fall was greater in P-fertilized plots, whereas potassium (K) reduced allocation to fine roots, and N and K together increased the diameter growth of saplings and poles (Wright *et al.*, 2011). The growth of shaded tree seedlings was also nutrient limited, as height growth increased with K addition and with the addition of P and N in combination (Santiago *et al.*, 2012). However, the biomass and activity of soil microbes were strictly limited by P availability (Turner & Wright, 2014).

Collectively, the results from long-term fertilization experiments point towards an important role of P in regulating ecosystem processes in lowland tropical rainforests, although other nutrients (especially K and N) have been shown to determine certain aspects of tropical forest productivity. The importance of P in the long-term fertilization experiment from Panamá is significant, given the relative fertility of the site (Wright *et al.*, 2011), which has total soil P concentrations > 90% of 63 Amazonian sites (Fyllas *et al.*, 2009). On this basis, we propose that P limitation of productivity and other ecosystem processes is probably even stronger in most lowland tropical rainforests.



**Fig. 2** (a) Minirhizotron measurements in a long-term field fertilization experiment in a lowland tropical rainforest, Barro Colorado Nature Monument, Panamá (Yavitt *et al.*, 2011). (b) Soil profile in species-rich kwongan showing a strongly weathered sandy soil with a very thick (> 1 m), pale bleached eluvial horizon, Lesueur National Park, Western Australia. Photo credits: (a) S. Joseph Wright; (b) Etienne Laliberté.

## 2. Kwongan shrublands

Despite an absence of long-term field fertilization experiments, evidence for P limitation of plant productivity in kwongan is compelling. This is in large part because the soil total P concentrations found in these strongly weathered soils (Fig. 2b) are among the lowest ever recorded. For example, total P in surface (0–20 cm) soils in species-rich kwongan is  $< 7 \text{ mg P kg}^{-1}$  soil (Hayes *et al.*, 2014), or  $c. 6 \text{ g P m}^{-2}$  over 1 m depth (Turner & Laliberté, 2014). By contrast, total P over the first 50 cm is  $c. 400 \text{ g P m}^{-2}$  (or  $c. 800 \text{ g P m}^{-2}$  over 1 m) in the oldest (4100 ka) soil of the well-studied Hawaiian chronosequence (Crews *et al.*, 1995), where plant growth is P limited (Vitousek & Farrington, 1997). In addition, the growth of phytometer plants on low-P soils in kwongan has been shown experimentally to be strongly P limited (Laliberté *et al.*, 2012). Moreover, native kwongan plant species found on these low-P soils have very high ( $> 40$ ) foliar N : P ratios, as well as some of the lowest foliar P concentrations and highest P resorption proficiency and efficiency values ever reported (Hayes *et al.*, 2014). Finally, the soil total carbon (C) : organic P ratio in surface soils from kwongan sites averages  $c. 1000$  (Turner & Laliberté, 2014), whereas it ranges between 44 and 287 in soils from around the world (Kirkby *et al.*, 2011). Although the importance of P in controlling plant growth and species distributions in Australian ecosystems has long been recognized (Beadle, 1954; Heddle & Specht, 1975), kwongan appears to be one of the most extreme cases of P-impooverished ecosystems in Australia and, possibly, the world.

## III. Negative density dependence

NDD is the process by which plant performance (i.e. survival, growth, reproduction) declines with greater density of conspecific neighbours. NDD promotes species coexistence by keeping dominant species in check, thereby freeing up resources for subordinate species. Many mechanisms can cause NDD, including intraspecific resource competition (Tilman, 1988), host-specific enemies whose impact increases with the density of the host (Gillett, 1962) and temporal variation in environmental attributes that affect regeneration, coupled with a long-lived stage that survives through good and bad times (Chesson, 2000).

NDD has now been widely documented for all life stages of tropical forest plants. Seed production, seed survival, seedling regeneration and the growth and survival of saplings and adults all provide evidence for NDD (Alvarez-Buylla, 1994; Harms *et al.*, 2000; Hubbell *et al.*, 2001; Comita *et al.*, 2010). As such, NDD is an important process that contributes to local plant species coexistence in lowland tropical rainforests (Wright, 2002; Terborgh, 2012).

In contrast with lowland tropical rainforests, NDD has rarely been evaluated in hyperdiverse shrublands. In kwongan, seedling recruitment occurs almost exclusively after fire from seeds either stored in the canopy or as a persistent soil seed bank (Bell *et al.*, 1993). In addition, many species also resprout vigorously after fire (Bell *et al.*, 1993). Lamont *et al.* (1993) evaluated the effect of post-fire microsites (i.e. bare sand vs litter patches) on seed and seedling

distribution of *Banksia* and *Hakea* species (Proteaceae), as well as seedling survival and growth. After a fire, most seeds and dead leaves fall directly beneath the canopy of the parent plant (Lamont *et al.*, 1993). As a result, seed and seedling density is much greater in litter patches accumulated under canopies, compared with exposed bare sand between mature plants (Lamont *et al.*, 1993). Despite 2–10-fold greater nutrient concentrations in litter patches, seedling survival was two to three times less, and surviving seedlings were 35% smaller, in litter patches compared with exposed bare sand (Lamont *et al.*, 1993). There was no marked herbivory on any of the seedlings, and little to no shading in litter patches. The authors attributed such NDD to competition for water among neighbouring seedlings (and resprouting plants in some cases) in litter patches. A potential role of soil-borne pathogens, however, was not explored.

The potential importance of NDD for plant species coexistence in kwongan has been highlighted recently through a simulation model (Groeneveld *et al.*, 2013), although the cause of NDD was not explicitly modelled. The model was parameterized using data on population dynamics of resprouting and nonresprouting (i.e. ‘seeders’) shrubs in the genus *Banksia*. In the model, plant species richness was maintained, and realistic rank-abundance distributions were obtained (based on Lamont *et al.*, 1977), only in the presence of local conspecific NDD (Groeneveld *et al.*, 2013). The results from this modelling exercise suggest that NDD might be important in driving plant diversity in kwongan, but additional field observations and experiments are needed to support this hypothesis.

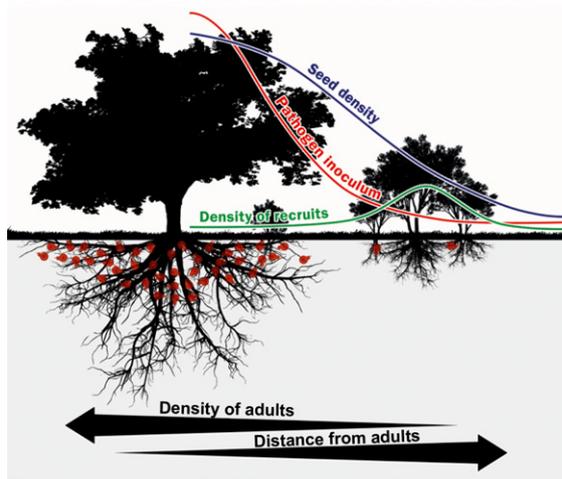
## IV. The importance of soil-borne pathogens

Gillett (1962) first proposed that host-specific pests and pathogens could cause NDD and thereby regulate plant diversity. Janzen (1970) and Connell (1971) independently proposed a spatially explicit variant of this general hypothesis in which seed dispersal limits potential recruitment in areas of low adult density far from seed-bearing plants, whereas natural enemies limit realized recruitment in areas of high adult density close to seed-bearing plants (Fig. 3a). This Janzen–Connell mechanism will facilitate plant species coexistence when the natural enemy has limited dispersal potential (Adler & Muller-Landau, 2005) and some degree of host specialization (Sedio & Ostling, 2013). Many soil-borne pathogens fulfil these requirements, as do many insect and vertebrate seed predators and herbivores (Gilbert *et al.*, 2012).

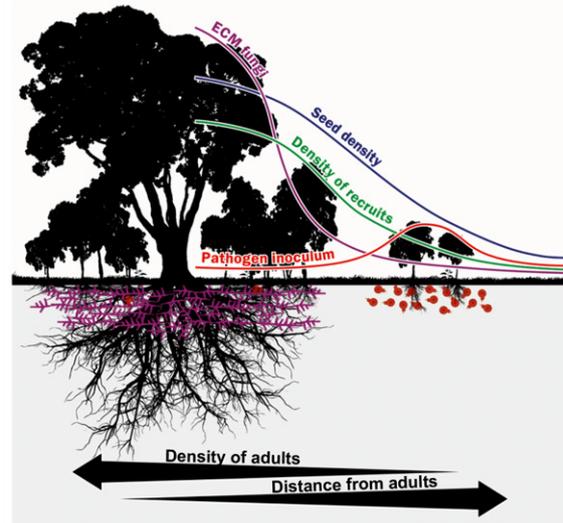
### 1. Soil-borne pathogens in lowland tropical rainforests

Soil-borne pathogens appear to be particularly important agents of NDD in tropical rainforests. An early meta-analysis discounted forest vertebrates as causal agents of distance and density dependence among seeds and seedlings (Hammond & Brown, 1998). In a recent series of experiments in Belize, fungal or oomycete soil-borne pathogens caused strong density-dependent seedling recruitment failure (Bell *et al.*, 2006; Bagchi *et al.*, 2010); by contrast, insect herbivores reduced overall seedling abundance, but did so indiscriminately, such that their effect on seedling species diversity

(a) Negative density dependence



(b) Monodominance



**Fig. 3** Plant–soil interactions leading to (a) negative density dependence and (b) monodominance. In (a), inoculum of soil-borne pathogens builds up in the root zone of mature plants, leading to poor conspecific seedling survival and growth. Recruits perform better (and reach higher densities) away from conspecific mature individuals where pathogen inoculum is lower. Such negative density dependence promotes local plant species coexistence by preventing dominance by one species. In (b), seedlings of an ectomycorrhizal (ECM) plant species show higher survival and growth (and reach higher densities) near a conspecific mature plant because they recruit into an established ECM fungal network that provides resistance against soil-borne pathogens, whilst also enhancing phosphorus acquisition. Moreover, ECM fungi can directly suppress the activity of soil-borne pathogens. This can eventually lead to monodominance by the ECM species.

was small (Bagchi *et al.*, 2014). Additional experiments have shown that the growth of tree seedlings is suppressed in soils collected under mature conspecific trees, relative to soils collected under heterospecifics, in tropical rainforests (Mangan *et al.*, 2010; McCarthy-Neumann & Kobe, 2010). Damping-off pathogens were the most important agents of mortality of shaded seedlings for six of nine tree species studied in a Panamanian forest (Augspurger, 1984), and these damping-off pathogens acted in a distance- and density-dependent manner, consistent with the Janzen–Connell hypothesis (Augspurger & Kelly, 1984). Similar effects of soil-borne pathogens have also been found in temperate (Packer & Clay, 2000) and subtropical (Liu *et al.*, 2012) forests.

## 2. Soil-borne pathogens as agents of NDD

Pathogens most likely to lead to Janzen–Connell effects have relatively narrow host ranges (i.e. high host specificity), infect mature plants and juveniles (including germinating seeds), but cause greater damage on juveniles, have persistent propagules that enable the local build-up of pathogen inoculum around hosts, and show limited dispersal ability (Gilbert, 2002; Adler & Muller-Landau, 2005). In particular, one group of soil-borne pathogens that fits these criteria and causes strong NDD in tropical trees is the oomycetes (Gilbert, 2002; Bell *et al.*, 2006; Freckleton & Lewis, 2006; Bagchi *et al.*, 2010). However, the potential importance of oomycetes as agents of NDD might reflect the ease with which they are manipulated in the field through the use of specific fungicides (e.g. Bell *et al.*, 2006; Bagchi *et al.*, 2010, 2014), and other groups of soil-borne pathogens whose effects are more difficult to elucidate might also be important.

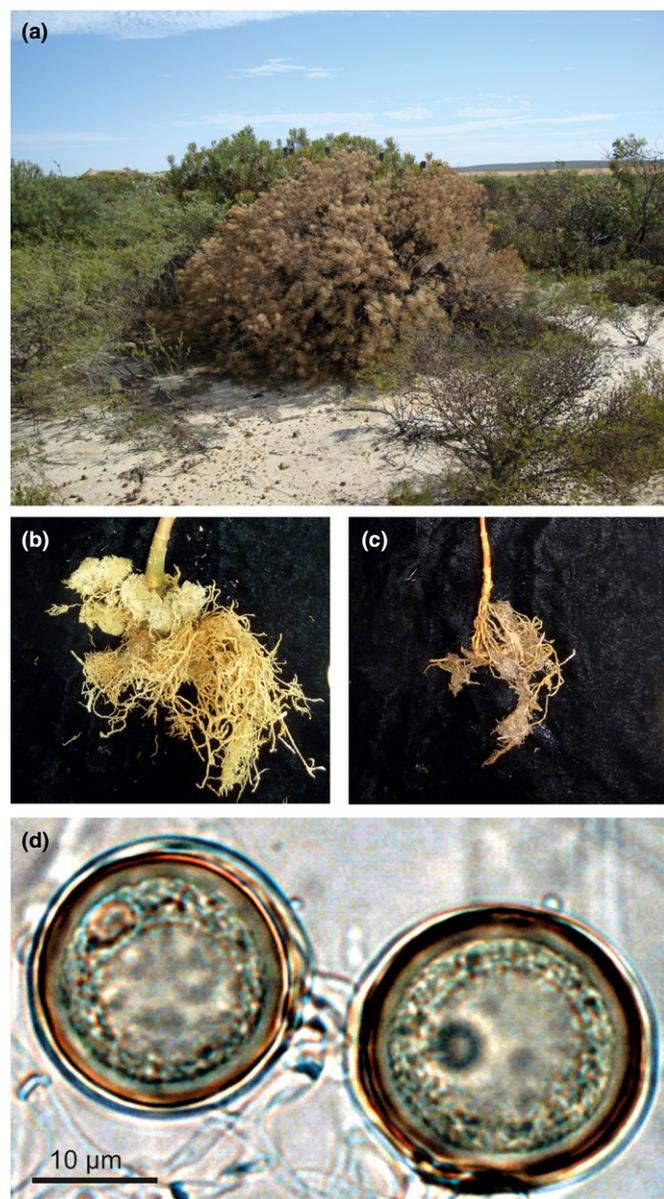
Oomycetes (e.g. *Pythium*, *Phytophthora*) cause damping-off diseases in seedlings (but also dieback in adults, particularly well

documented for *Phytophthora*), produce persistent long-lived oospores and have relatively limited natural dispersal (Ristaino & Gumpertz, 2000). However, some oomycetes (as well as other soil-borne fungal pathogens) have broad host ranges (e.g. Grünwald *et al.*, 2008), although a recent analysis has shown that microbial pathogens (including oomycetes) are more specialized than invertebrate pests (e.g. insects, nematodes) and viruses (Gilbert *et al.*, 2012). Oomycetes with a broad host range include species of economic importance as pathogens of crop plants, but many of the newly described *Phytophthora* species from natural ecosystems appear to have narrow host ranges (Scott *et al.*, 2013). For example, two pathogens introduced to south-western Australia, *Phytophthora cinnamomi* and *P. multivora*, have broad host ranges (Shearer *et al.*, 2004; Burgess *et al.*, 2009), yet related and geographically restricted *Phytophthora* species recently recovered from kwongan appear to have much narrower host ranges (Rea *et al.*, 2011; A. Simamora & T. I. Burgess, unpublished). In either case, pathogens need not be host specific to cause Janzen–Connell effects (Sedio & Ostling, 2013); many pathogens have broad host ranges, but hosts vary in their susceptibility (Gilbert, 2002). Co-infection by generalist pathogens can also lead to differential effects on hosts (Hersh *et al.*, 2012). Pathogens with broad host ranges can still promote species coexistence if plant species with higher competitive ability tend to be most susceptible, as discussed further later.

## 3. Soil-borne pathogens in kwongan

Most research on soil-borne pathogens in kwongan has focused on the introduced oomycete *P. cinnamomi*. This introduced pathogen is a serious threat to plant biodiversity in south-western Australia, because c. 40% of plant species from this global biodiversity hotspot

(including hyperdiverse kwongan shrublands) are susceptible (Shearer *et al.*, 2004). However, native and endemic *Phytophthora* species thought to have coevolved with the flora have recently been isolated from species-rich kwongan (Burgess *et al.*, 2009; Rea *et al.*, 2011; A. Simamora & T. I. Burgess, unpublished). Contrary to the introduced *P. cinnamomi*, which leads to local extinctions of plant species and thus decreases plant diversity (Shearer *et al.*, 2007), these native *Phytophthora* species only kill mature plants following extreme rainfall events (Rea *et al.*, 2011), but could affect juveniles and generate Janzen–Connell effects (Fig. 4). For example, in



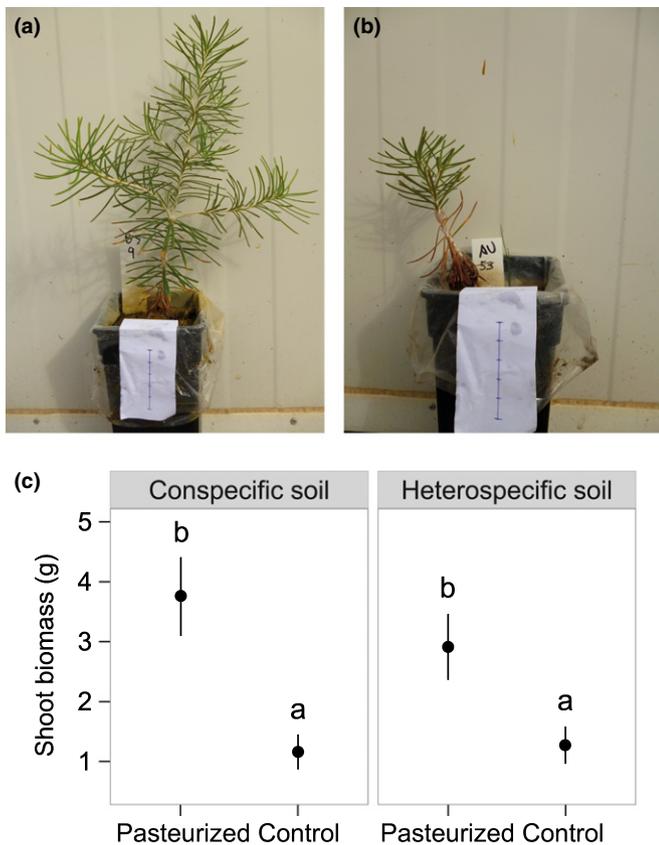
**Fig. 4** Effects of *Phytophthora arenaria* in kwongan. (a) Wilted *Banksia grossa* near Eneabba, Western Australia, killed by root and collar rot caused by *P. arenaria*. (b) Healthy root system of a *Banksia occidentalis* seedling, showing dense cluster roots near the base of the stem. (c) Diseased root system of a *B. occidentalis* seedling inoculated with *P. arenaria*. (d) The thick-walled oospores of *P. arenaria* are thought to favour survival in the seasonally dry climate of kwongan (Rea *et al.*, 2011). Photo credits: (a) G. Hardy; (b–d) A. Simamora.

recent trials using an endemic *Phytophthora* species, inoculation before germination prevented emergence, whereas inoculation after seedling emergence reduced survival and growth (A. Simamora & T. I. Burgess, unpublished). This provides evidence for their role as emergence pathogens.

As a first step towards the determination of the potential importance of soil-borne pathogens on seedling recruitment in kwongan, we grew seedlings of *Banksia leptophylla* (Proteaceae), a locally abundant species, in soils that were collected either under conspecific mature plants or below the co-occurring shrub *Acacia spathulifolia* (Fabaceae). Soils were either triple pasteurized or not. After 7 months in the glasshouse, aboveground biomass was three times greater in pasteurized soils than in unpasteurized soils, although soil origin (conspecific or *A. spathulifolia*) had no effect (Fig. 5; E. Laliberté, T. I. Burgess & P. Quévieux, unpublished). This suggests that native soil-borne pathogens can strongly reduce seedling performance in kwongan, but not necessarily in the distance-dependent manner predicted by the Janzen–Connell hypothesis. We do not attribute the greater biomass gain in pasteurized soils to potential increases in soil nutrient availability, as P is the key limiting nutrient in these soils (Laliberté *et al.*, 2012; Hayes *et al.*, 2014) and Bray P was similarly low (*c.* 2 mg P kg<sup>-1</sup> soil) in pasteurized and unpasteurized soils collected below *A. spathulifolia*, and only slightly increased after pasteurization (1.2 vs 1.5 mg P kg<sup>-1</sup> soil) in soils collected under *B. leptophylla* (E. Laliberté & P. Quévieux, unpublished). We recovered the damping-off oomycete pathogen *Pythium irregulare* from > 60% of root and soil samples from the unpasteurized soils, but no oomycetes were recovered from any sample from the pasteurized soils (E. Laliberté, T. I. Burgess & P. Quévieux, unpublished). These preliminary results should be treated with caution, as follow-up experiments are required to determine whether this effect holds across other species, and to confirm whether *P. irregulare* is the causal agent underlying the reduced growth. Nevertheless, the apparent high susceptibility to soil-borne pathogens of *B. leptophylla* – a locally abundant plant species – is noteworthy. This species, like virtually all Proteaceae from south-western Australia, is nonmycorrhizal and produces short-lived cluster roots highly specialized for efficient P acquisition (Lambers *et al.*, 2006). In the next section, we ask whether traits enabling the efficient acquisition of P in hyperdiverse, P-limited ecosystems, such as lowland tropical rainforests and kwongan, could lead to a trade-off, whereby plant susceptibility to soil-borne pathogens is increased. Such a mechanism would enhance coexistence by reducing differences in competitive ability among species.

## V. A trade-off between efficient P acquisition and fine root defence?

Newsham *et al.* (1995) proposed that fine root traits allowing efficient P acquisition might lead to greater susceptibility to soil-borne pathogens; here, we develop this hypothesis further, focusing on P-limited hyperdiverse forests and shrublands. Although a trade-off between efficient P acquisition and defence against pathogens could occur in other ecosystems, and could involve



**Fig. 5** Growth of *Banksia leptophylla* is impaired by soil pathogens in species-rich kwongan, Western Australia. Seedlings were grown in soil collected either under conspecific mature shrubs or under co-occurring *Acacia spathulifolia* ('heterospecific'), and these soils were either triple pasteurized (three cycles at 80°C for 30 min, with 24 h between each cycle) or not (P. Quévieux, E. Laliberté & T. I. Burgess, unpublished). Representative seedlings are shown that grew for 7 months in (a) triple-pasteurized soil or (b) control (i.e. unpasteurized) soil. All seedlings from all treatments survived, but there were large differences in shoot biomass between the triple-pasteurized and control soils. (c) Shoot biomass in the different soil treatments. Values are means ± 95% confidence intervals. Different letters indicate significant differences based on 95% confidence intervals. The damping-off oomycete pathogen *Pythium irregulare* was isolated from > 60% of root or bulk soil samples from the control soils, but was never recovered in samples from the triple-pasteurized soils.  $n = 15$ . Photo credits: (a, b) Pierre Quévieux.

nutrients other than P, we focus on P and hyperdiverse forests and shrublands because the mechanisms contributing to plant species coexistence are of particular interest in hyperdiverse systems, there is evidence for an important role of soil-borne pathogens in generating NDD in these systems (see previous section) and, as we discuss later, a trade-off between efficient nutrient acquisition and defence against pathogens should be particularly strong for a poorly mobile nutrient, such as P, given the nature of efficient P acquisition mechanisms involving short-lived roots.

Why would low P availability and P limitation of plant growth be associated with relatively poorly defended fine roots? A cost–benefit 'economic' approach (Eissenstat & Yanai, 1997; Lynch & Ho, 2005) that considers P dynamics in soils is useful. A key aspect of P cycling in soils is its movement towards plant roots predominantly through diffusion along concentration gradients, rather than via

transpiration-induced mass flow (Barber, 1962). The diffusion of P is very slow in soils, especially in dry soils, and diffusion is the rate-limiting step to plant P uptake (Bhadoria *et al.*, 1991). The diffusion of P is particularly slow in strongly weathered tropical soils, because low pH and high concentrations of aluminium (Al) and iron (Fe) oxides and hydroxides lead to strong P sorption (Fontes & Weed, 1996). Consequently, the diffusion shells (i.e. nutrient-depleted cylinders of soil around roots) for P have very small (< 1 mm) radii (Gahoonia & Nielsen, 1992), and a strategy used by plants to enhance P acquisition is to increase root (hair) length and thus the volume of soil explored (Lynch & Ho, 2005). Because root maintenance respiration costs can be high, relative to the cost of making fine new roots (Eissenstat & Yanai, 1997), there would be little advantage in maintaining fine roots for a long period if these fine roots rapidly deplete P in their rhizosphere. By contrast, in ecosystems in which N limits productivity, investing C into longer lived, better defended fine roots might be a viable strategy, because mass flow can make a significant contribution to N acquisition (Oyewole *et al.*, 2014). This may explain the coordinated syndromes of long-lived leaves and long-lived fine roots found in species from infertile habitats in temperate and high-latitude ecosystems (Ryser & Lambers, 1995; Schläpfer & Ryser, 1996; Craine & Lee, 2003; Tjoelker *et al.*, 2005; Freschet *et al.*, 2010), where N rather than P limits productivity (Elser *et al.*, 2007).

### 1. Tough leaves, but weak roots?

Many of the predictions about root lifespan and investment in defence against root herbivores or pathogens extend from studies on leaf defence (Eissenstat & Yanai, 1997). Under nutrient-limited conditions, slow-growing species with better defended leaves are favoured, because the precious nutrient capital invested in leaves is preserved for a longer period, thereby maximizing long-term leaf nutrient-use efficiency (Coley *et al.*, 1985; Herms & Mattson, 1992; Lambers & Poorter, 1992). As a general rule, shade-tolerant tree species in lowland tropical rainforests tend to have well-defended leaves with long lifespans (Coley & Barone, 1996). Most damage to leaves occurs during early leaf development when leaves are most vulnerable, and many species show delayed greening of leaves, which minimizes their nutritional value until structural defences are established (Coley & Barone, 1996). Likewise, most plant species in kwongan have tough, scleromorphic leaves (Pate *et al.*, 1984) with a long lifespan (Veneklaas & Poot, 2003) (Fig. 6a, b). Delayed greening also features in kwongan, particularly in Proteaceae (Fig. 6a), and is possibly a strategy to reduce herbivory and use P more efficiently (Sulpice *et al.*, 2014).

Most studies exploring covariation among leaf and root traits have found synchronous trait syndromes above and below ground (Ryser & Lambers, 1995; Schläpfer & Ryser, 1996; Craine & Lee, 2003; Tjoelker *et al.*, 2005; Freschet *et al.*, 2010). As a result, the prevailing view is that leaf and root traits tend to be coordinated, such that nutrient-poor, unproductive conditions should favour species with long-lived leaves and long-lived roots (Grime *et al.*, 1986; Schläpfer & Ryser, 1996; Eissenstat & Yanai, 1997; Reich, 2014). Because biotic agents (e.g. root herbivores, pathogens) are



**Fig. 6** Contrasting longevity of leaves and roots of *Hakea prostrata* (Proteaceae) in a phosphorus-impoorished habitat in south-western Australia. (a) Young expanding leaves, showing delayed greening, and older green scleromorphic leaves that live for several years. (b) Cross-section of a mature 1-yr-old leaf, with photosynthetic cells fluorescing red and epidermal cells and fibrous tissue shown in blue. (c) Proteoid roots develop a bottlebrush-like morphology; the main root is perennial and proteoid-rootlet initiation (far left) to senescence (far right) occurs over c. 21 d in this species, grown in hydroponics at extremely low [Pi]  $\leq 1 \mu\text{M}$ . Photo credits: (a) Shayanna Crouch; (b) John Kuo; (c) Michael W. Shane.

the primary causes of fine root death (Eissenstat & Yanai, 1997), longer lived fine roots must be better protected against herbivores and pathogens. The available evidence from tropical rainforests, however, suggests that fine roots in these ecosystems are, in fact, short lived compared with those in temperate forests (Gill & Jackson, 2000).

Measurement of the turnover of the smallest roots (i.e. first- and second-lowest orders), which are most dynamic and responsible for the majority of nutrient acquisition, is inherently challenging. Long-term direct *in situ* observations of the finest roots using minirhizotrons are arguably best suited to this task, as opposed to comparisons of fine root productivity (i.e. using sequential coring or ingrowth cores) against fine root standing biomass (e.g. Aragão *et al.*, 2009) or isotopic methods (e.g. Trumbore *et al.*, 2006), both of which underestimate fine root turnover (Strand *et al.*, 2008). In a low-P tropical lowland rainforest in Malaysia, minirhizotron observations (Fig. 2a) showed that 50% of individual fine roots only lived between 25 and 125 d (Green *et al.*, 2005). In another minirhizotron study in a lowland tropical rainforest in Panamá, average fine root lifespan was c. 120 d (Yavitt *et al.*, 2011); median lifespan would be significantly lower, as root lifespan distributions are positively skewed (Strand *et al.*, 2008). By contrast, the median lifespan of first- and second-order fine roots of several temperate tree species was > 200 d (McCormack *et al.*, 2012). To our knowledge, there are no published minirhizotron studies with fine root lifespan data in kwongan or fynbos. However, we know from glasshouse experiments that *Hakea prostrata* (Proteaceae), a common species in P-impoorished kwongan shrublands, produces very short-lived (< 3 wk), dense clusters of fine roots that are specialized for efficient P acquisition (Fig. 6c; Shane *et al.*, 2004). Some Cyperaceae produce specialized short-lived (< 10 d) dauciform roots with very long and dense root hairs (Shane *et al.*, 2006). Other species from these ecosystems are expected to function similarly, producing ephemeral, but physiologically active, fine roots to 'mine' P (Lambers *et al.*, 2006, 2008).

The prevailing view of nutrient limitation favouring long root lifespan (Grime *et al.*, 1986; Eissenstat & Yanai, 1997) is partly based on the assumption of little nutrient resorption from fine roots (e.g. Nambiar, 1987), with their death being a significant pathway for nutrient loss. However, this assumption needs to be revisited for P, as P resorption from fine roots can be substantial (Shane *et al.*, 2004; Freschet *et al.*, 2010).

Higher temperature has been proposed as an explanation for the more rapid fine root turnover in tropical rainforests relative to higher latitude ecosystems (Gill & Jackson, 2000), and to explain the higher fine root turnover at lower elevations among tropical rainforest sites (Girardin *et al.*, 2013). The two main temperature-related hypotheses are an increase in root maintenance respiration with rising temperature, which shortens the optimal lifespan of roots, and greater root herbivore or pathogen pressure in warmer climates, which leads to higher fine root mortality (Eissenstat & Yanai, 1997; Gill & Jackson, 2000). We propose an alternative hypothesis: low P availability and P limitation of plant growth favour fine roots that are associated with a short root lifespan; the highly seasonal water availability (e.g. Mediterranean climate in kwongan) would accentuate this. Consistent with our hypothesis, the cluster root lifespan of *Embothrium coccineum* (Proteaceae) from soils high in total P, but low in 'available' P, in southern South America is also short, despite relatively low temperatures (Delgado *et al.*, 2014). Nevertheless, we recognize the difficulty of disentangling a temperature effect from a P availability effect using these observational data, as increases in temperature at lower latitudes correlate with the lower P availability of more strongly weathered low-latitude soils (Huston, 2012).

## 2. Root traits that enhance P acquisition

Root morphological and architectural traits are important for P acquisition. For example, a high specific root length (SRL; i.e. fine root length per unit dry mass) enhances P acquisition (Ho *et al.*,

2005) by allowing a greater soil volume to be explored per unit C invested, yet roots with high SRL tend to be less well defended against biotic stresses (Eissenstat, 1992). A second strategy is root hairs (i.e. extensions of epidermal cells), which are induced by low P supply (Ma *et al.*, 2001) and extend the zone of P depletion around roots (Föhse *et al.*, 1991). Given that root hairs entail minor maintenance respiration costs (Bates & Lynch, 2000), the high variation in root hair formation observed within species suggests potential negative side-effects, such as higher susceptibility to pathogens (Lynch & Ho, 2005). As in high SRL, root hairs greatly increase the surface area through which pathogens can enter roots (e.g. Kraft *et al.*, 1967). Another adaptation to enhance P acquisition under P-limited conditions is the preferential allocation of fine roots to surface soil layers (e.g. Lynch & Brown, 2001), where P availability, but also inoculum density of most soil-borne pathogens, are highest. Therefore, the fine root morphological and architectural adaptations leading to efficient P acquisition might increase susceptibility to soil-borne pathogens.

Symbiotic associations with mycorrhizal fungi are an important strategy to enhance P acquisition (Smith & Read, 2008). The two main types are arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi. The primary mechanism by which AM fungi enhance plant P acquisition is by extending the volume of soil explored by AM hyphae. The diameter of extraradical hyphae is about one order of magnitude smaller than that of fine roots, and hyphae can enter soil pores that are inaccessible to roots. Extraradical hyphae of AM fungi are very short lived (5–6 d; Staddon *et al.*, 2003). The hyphae of ECM fungi also greatly increase the P-absorbing surface (Rousseau *et al.*, 1994), and ECM fungi can also mobilize some sorbed P through the release of organic anions and hydrolyse organic P using extracellular phosphatases (Plassard & Dell, 2010).

Arbuscular mycorrhizas are widespread among tree species from lowland tropical forests (Alexander, 1989; McGuire *et al.*, 2008). By contrast, ectomycorrhizas are restricted to fewer tropical forest taxa, albeit from ecologically important families such as the Dipterocarpaceae, Fagaceae, Myrtaceae and Caesalpinioideae (Alexander & Lee, 2005). In kwongan, nonmycorrhizal plant species (e.g. Proteaceae) feature prominently (Lamont, 1993), although AM plant species are also found in large number and together comprise a large fraction of total canopy cover (Lamont, 1982). ECM plant species (mostly Myrtaceae, Fabaceae and Casuarinaceae) are also relatively important, but tend to be less abundant than nonmycorrhizal or AM species (G. Zemunik, unpublished).

### 3. Mycorrhizas and protection against root pathogens

Symbioses with AM fungi can provide multiple benefits to plants beyond improved P nutrition, such as protection against root pathogens (Newsham *et al.*, 1995), in particular pathogenic fungi, such as *Rhizoctonia*, *Fusarium* or *Verticillium*, and oomycetes, such as *Phytophthora* and *Pythium* species (Pozo & Azcón-Aguilar, 2007). Potential modes of action are direct competition between AM fungi and pathogens for C or infection sites, enhanced plant nutrition, induced plant resistance and changes in soil

microbiota in the mycorrhizosphere (Azcón-Aguilar & Barea, 1997; Whipps, 2004). Induced resistance linked to the priming of jasmonate-based plant defences following AM fungal colonization has been suggested as the most important mode of action (Pozo & Azcón-Aguilar, 2007). However, to our knowledge, enhanced pathogen resistance through AM fungal colonization has been reported primarily for herbaceous species (mostly crop plants), but has not been studied in woody plants in natural ecosystems, such as hyperdiverse forests and shrublands.

Contrary to AM fungi, ECM fungi have long been known to offer effective protection to woody plants against root pathogens (Garrett, 1956; Marx, 1972), and there are at least three reasons to believe that the level of protection provided by ECM fungi is greater than that provided by AM fungi (Connell & Lowman, 1989). First, ECM colonization does not only induce resistance (Strobel & Sinclair, 1991), but many ECM fungal species also release antibiotic compounds (Marx, 1972). For example, colonization of pine roots by the ECM fungus *Paxillus involutus* led to a five-fold increase in antibiotic activity in the mycorrhizosphere and was associated with a six-fold decline in sporulation of the fungal root pathogen *Fusarium oxysporum* (Duchesne *et al.*, 1988). Second, the fungal mantle surrounding fine roots and the Hartig net can act as important physical barriers to the entry or spread of pathogens into roots (Marx, 1972). Finally, there has been some evidence from temperate forests of the fine roots of ECM hardwood tree species living considerably longer than roots of co-occurring AM hardwood tree species (Aber *et al.*, 1985; Eissenstat & Yanai, 1997), suggesting that they may be better protected against root pathogens. However, this requires further investigation, as more recent studies found little difference in fine root lifespan among co-occurring AM and ECM trees in temperate forests (Withington *et al.*, 2006; McCormack *et al.*, 2012). To our knowledge, no study has ever compared fine root lifespan among AM and ECM plants in species-rich rainforests or shrublands.

### 4. Ectomycorrhizas and monodominance

The greater resistance against pathogens provided by ECM fungi, relative to species that associate with AM or nonmycorrhizal plants, could have important consequences for plant species coexistence and local plant diversity (Fig. 3b). Although lowland tropical rainforests are renowned for their high local plant diversity (Wilson *et al.*, 2012), monodominant forests also occur in similar climatic and soil conditions, often adjacent to species-rich stands (Connell & Lowman, 1989; Torti *et al.*, 2001; Peh *et al.*, 2011b; McGuire, 2014). In south-eastern Asia, dominance by one family (primarily Dipterocarpaceae) rather than one species can also occur (Connell & Lowman, 1989). In many (but not all; Peh *et al.*, 2011a) cases, these dominant tree species form ectomycorrhizas, and it has been suggested that associations with ECM fungi contribute to monodominance (Connell & Lowman, 1989; Hart *et al.*, 1989; McGuire, 2014). One mechanism could be enhanced conspecific seedling survival and growth (e.g. Newbery *et al.*, 2000) because of the presence of established host-specific ECM networks, leading to a positive feedback that promotes dominance (Fig. 3b). For example, seedlings of the ECM species *Dicymbe corymbosa*, which



**Fig. 7** Examples of ectomycorrhizal monodominant stands amongst species-rich forests and shrublands. (a) Monodominant (> 75% basal area) stand of the ectomycorrhizal tree *Dicycme corymbosa* in central Guyana. (b) Monodominant stand of the ectomycorrhizal shrub *Melaleuca systena* in Lesueur National Park, Western Australia. Photo credits: (a) Krista McGuire; (b) Etienne Laliberté.

forms monodominant stands in central Guyana (Fig. 7a), showed greater survival under conspecific mature trees, and ECM fungal networks in particular led to 47% greater seedling survival and 73% greater height growth (McGuire, 2007b). Future experiments should test whether this benefit is caused by ECM networks conferring greater resistance against root pathogens. Such an effect could be very important as germinating seeds of monodominant tropical ECM tree species can become colonized by ECM fungi very rapidly (McGuire, 2007b), and the seed-to-seedling transition is a critical period during which strong NDD caused by soil-borne pathogens (particularly oomycetes) occurs in tropical rainforests (Bagchi *et al.*, 2010, 2014).

Monodominant stands also occur amongst otherwise species-rich kwongan, although this has received comparatively little attention. On sandplain, dense ‘thickets’ dominated by *Acacia*, *Melaleuca* or *Allocasuarina* species can be found (Hnatiuk & Hopkins, 1981; Beard, 1984). Species from these three genera form

ectomycorrhizas (Brundrett, 2009). Although these thickets are often associated with particular edaphic conditions (e.g. winter-wet depressions; Hnatiuk & Hopkins, 1981), this is not always the case (Fig. 7b). It would be worth exploring whether a positive feedback involving ectomycorrhizas and soil-borne pathogens contributes to the formation of monodominant thickets in kwongan, notwithstanding a possible role of edaphic conditions (e.g. higher soil moisture or P availability).

## VI. Perspectives

### 1. Is efficient P acquisition associated with high susceptibility to root pathogens?

The hypothesis that efficient P acquisition might trade off against susceptibility to soil-borne pathogens has been around for some time (Newsham *et al.*, 1995), but has yet to receive much experimental attention. To our knowledge, it has not been explored in hyperdiverse rainforests or shrublands, despite these ecosystems being strongly P limited and (at least for lowland tropical rainforests) plant recruitment dynamics being significantly impacted by soil-borne pathogens. In kwongan, there is circumstantial evidence of efficient P acquisition trading off against resistance to pathogens. In these P-impooverished soils, nonmycorrhizal plants (particularly Proteaceae) are common (Lamont, 1993), and their success in these environments is partly linked to their short-lived, specialized cluster roots that ‘mine’ P by releasing large amounts of carboxylates (Lambers *et al.*, 2006). However, many Proteaceae are highly susceptible to both the introduced *P. cinnamomi* (Shearer *et al.*, 2004) and native *Phytophthora* species (Rea *et al.*, 2011). This is consistent with our hypothesis that roots that are highly efficient at acquiring P are poorly defended against soil-borne pathogens.

In lowland tropical rainforests, most tree species form mycorrhizal associations (Alexander, 1989; Alexander & Lee, 2005; McGuire *et al.*, 2008), but there can still be considerable variation in fine root morphology and AM colonization amongst coexisting species (John, 1980). In an examination of 89 tropical tree species from a species-rich lowland tropical rainforest on nutrient-poor soils (i.e. oxisol, podzol) near Manaus, Brazil, John (1980) found that the relationship between fine root morphology and AM colonization largely agreed with Baylis’ (1970) predictions about root architecture and mycorrhizal dependence. Some species with thicker magnolioid fine roots were heavily colonized, some with thin roots with root hairs were lightly colonized, yet most species had roots of ‘intermediate’ size and were either nonmycorrhizal or only lightly colonized. Although this suggests that the necessary variation needed for trade-offs to operate between efficient P acquisition and susceptibility to pathogens does exist, we still know too little about the functional aspects of mycorrhizal associations in lowland tropical rainforests (but see Moyersoen *et al.*, 1998). There is a need for studies comparing seedling performance of co-occurring species with contrasting belowground strategies and fine root morphologies for P acquisition, in the presence or absence of native soil-borne pathogens. It is expected that species with high SRL, highly branched root systems and/or high root hair density

would be best at acquiring P, but most susceptible to pathogens (Newsham *et al.*, 1995). By contrast, species with thicker, denser and less branched fine roots that strongly depend on AM fungi for P acquisition should be less susceptible to pathogens, whereas ECM species with high root colonization should be least susceptible.

## 2. How does low irradiance influence fine root defence?

In kwongan shrublands, light availability is unlikely to ever constrain photosynthesis, even of recruits, because of the open canopy and post-fire recruitment. The situation in lowland tropical rainforests is very different, where recruits persist in deep shade for many years. Tropical rainforest tree seedlings are much more likely to succumb to damping-off pathogens in the shade than in light gaps, especially near conspecific mature trees (Augsburger, 1984; Hood *et al.*, 2004), and susceptibility to pathogens is greater for less shade-tolerant species (McCarthy-Neumann & Kobe, 2008). Moreover, seedlings often show reduced AM colonization and are generally less responsive (in terms of growth) to AM colonization at low irradiance (Bureau *et al.*, 2000; Gehring, 2003). AM fungi can even reduce seedling survival and growth of shade-tolerant tropical tree species (McCarthy-Neumann & Kobe, 2008).

Further studies on the interactions between light availability, C allocation to fine roots and mycorrhizal fungi, and susceptibility to soil-root-borne pathogens are clearly needed to improve our mechanistic understanding of pathogen-mediated NDD in hyperdiverse tropical rainforests. This is important, because seedling mortality in the shade before the formation of light gaps in these forests can strongly impact future tree composition and diversity. With that in mind, the potential benefit of ECM seedlings rapidly recruiting into an already established, extensive ECM fungal network whose growth has been maintained by C from sunlight-exposed conspecific canopy trees (without implying C transfer to seedlings from mature plants via the network) might be particularly significant in terms of enhancing seedling protection against soil-borne pathogens, and thereby promoting monodominance.

## 3. Why are ECM monodominant stands not more common?

Given the potential benefit of ECM fungal networks in protecting recruits from soil-borne pathogens, thus negating Janzen–Connell effects (Fig. 3b), an intriguing question is why ECM monodominant stands do not take over hyperdiverse rainforests and shrublands (McGuire, 2014). One possibility is that the ECM symbiosis entails greater C costs to the host than does the AM symbiosis (Leake *et al.*, 2004; Phillips & Fahey, 2006). Another possibility is that recruitment outside of monodominant stands can be particularly poor, because of low ECM fungal inoculum (McGuire, 2007a), thus restricting the expansion of these stands (McGuire, 2014). It would be worth investigating whether ECM plants face a trade-off, whereby they are better protected against soil-borne pathogens (at least in the presence of sufficient ECM fungal inoculum) than nonmycorrhizal or AM plant species, but are less effective than nonmycorrhizal plants at acquiring P.

## 4. How are soil-borne pathogens spatially distributed?

We know relatively little about the fine-scale spatial distribution and dispersal of soil-borne pathogens (Ristaino & Gumpertz, 2000), especially within hyperdiverse plant communities. However, in plant–soil feedback experiments, in which seedlings are grown in soils ‘conditioned’ by conspecific or heterospecific mature plants, the composition and/or abundance of soil-borne pathogens found within the root zones of mature plants differs among neighbouring plant species. For example, in lowland tropical rainforests in Panamá, tree seedlings performed worse in soils collected under conspecific than in those collected below heterospecific mature trees (Mangan *et al.*, 2010), suggesting clear spatial patterns consistent with the local build-up of host-specific pathogens.

The use of next-generation sequencing approaches to study community composition and diversity of soil-borne pathogens is becoming increasingly common, although very few studies so far have focused on oomycetes (e.g. Vannini *et al.*, 2013). A promising recent advance has been the development of *Phytophthora*-specific primer sets (Scibetta *et al.*, 2012). We are currently using these primers to explore the distribution, dispersal and diversity of *Phytophthora* species in species-rich kwongan (T. I. Burgess, unpublished). Such studies are needed because the spatial distribution of soil-borne pathogens and their dispersal are important to understand Janzen–Connell dynamics and their influence on local plant species diversity (Gilbert, 2002; Adler & Muller-Landau, 2005).

## 5. A role for K limitation?

Although our review has focused on P availability, we note that a possible trade-off between the efficient acquisition of growth-limiting nutrients and fine root lifespan might also occur for K, which has been shown to co-limit some components of plant productivity in a lowland tropical rainforest (Wright *et al.*, 2011). Like P, K is required in large amounts by plants and is a rock-derived nutrient whose supply becomes limited in old, strongly weathered soils, such as those found in lowland tropical rainforests (Vitousek & Sanford, 1986). Moreover, like P, K also forms depletion zones around roots and moves towards roots to a large extent by diffusion (Barber, 1962). K availability is also very low in the strongly weathered sandy soils supporting species-rich kwongan, although it does not appear to be a growth-limiting nutrient in these soils (Laliberté *et al.*, 2012; Hayes *et al.*, 2014). Interestingly, contrary to P, there is little evidence for the direct involvement of AM fungi in plant K acquisition (Smith & Read, 2008), presumably because it is more mobile than P. Consequently, the many AM tree species in lowland tropical rainforests would rely to a much greater extent on their fine roots (as opposed to AM fungi) for the acquisition of K. Therefore, the trade-off that we propose between efficient P acquisition and fine root lifespan should also be relevant for K. We note that, although ECM fungi contribute directly to plant K uptake (Smith & Read, 2008), plant K deficiency, contrary to P deficiency, leads to reduced allocation of photosynthates to ECM fungi (Ekblad *et al.*, 1995), so that ECM fungi might not play a major role in enhancing K acquisition under

K limitation (Smith & Read, 2008). A possible relationship between efficient K acquisition, fine root lifespan and susceptibility to soil-borne pathogens in K-limited lowland tropical rainforests deserves further attention.

## VII. Conclusions

In this review, we have proposed a hypothesis whereby P limitation of plant productivity in hyperdiverse lowland tropical rainforests and seasonally dry shrublands favours plant species possessing fine root traits that enhance P acquisition, yet also increase susceptibility to soil-borne pathogens. This trade-off equalizes the differences in competitive ability among co-occurring species, thereby contributing to species coexistence. This hypothesis is based on the observations that many plant species from these P-limited ecosystems, despite having well-defended long-lived leaves, tend to have short-lived fine roots, and on the increased recognition of soil-borne pathogens as important drivers of plant species coexistence in hyperdiverse lowland tropical rainforests. We have also proposed that enhanced seedling protection against soil-borne pathogens by ECM fungi is the main mechanism explaining the formation of ECM monodominant stands in lowland tropical rainforests and, possibly, in kwongan. Although our hypothesis remains untested, major gaps in our basic understanding of plant–soil interactions in these hyperdiverse plant communities currently limit our ability to test it. Aiming to stimulate further research, we have presented some of the key research questions that we believe need to be addressed. Exploring the links between P limitation, fine root traits, mycorrhizas and susceptibility to soil-borne pathogens should advance our mechanistic understanding of NDD in hyperdiverse forests and shrublands and its role in the maintenance of local plant diversity, and help to explain the occurrence of monodominant stands among otherwise species-rich vegetation.

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