

# Lithological constraints on resource economies shape the mycorrhizal composition of a Bornean rain forest

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## Summary

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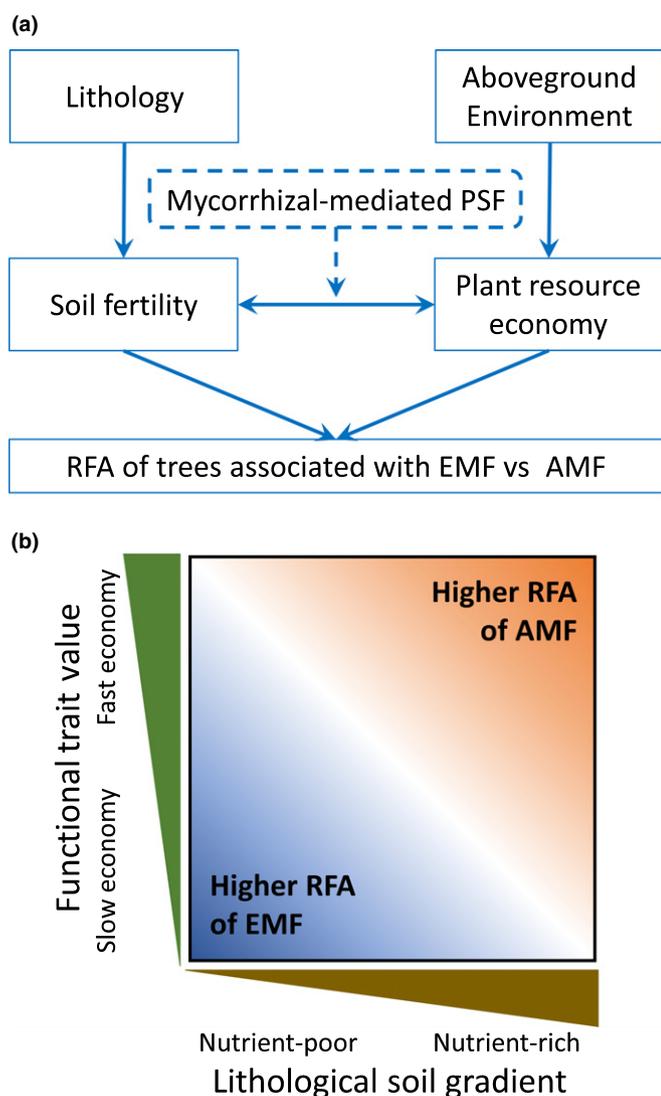
**Key words:** arbuscular mycorrhiza, ectomycorrhiza, functional traits, nutrient cycling, plant–soil feedback, soil fertility, tropical forests.

- Arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF) produce contrasting plant–soil feedbacks, but how these feedbacks are constrained by lithology is poorly understood.
- We investigated the hypothesis that lithological drivers of soil fertility filter plant resource economic strategies in ways that influence the relative fitness of trees with AMF or EMF symbioses in a Bornean rain forest containing species with both mycorrhizal strategies.
- Using forest inventory data on 1245 tree species, we found that although AMF-hosting trees had greater relative dominance on all soil types, with declining lithological soil fertility EMF-hosting trees became more dominant. Data on 13 leaf traits and wood density for a total of 150 species showed that variation was almost always associated with soil type, whereas for six leaf traits (structural properties; carbon, nitrogen, phosphorus ratios, nitrogen isotopes), variation was also associated with mycorrhizal strategy. EMF-hosting species had slower leaf economics than AMF-hosts, demonstrating the central role of mycorrhizal symbiosis in plant resource economies.
- At the global scale, climate has been shown to shape forest mycorrhizal composition, but here we show that in communities it depends on soil lithology, suggesting scale-dependent abiotic factors influence feedbacks underlying the relative fitness of different mycorrhizal strategies.

## Introduction

About 92% of land plants form some kind of mycorrhizal association (Brundrett, 2009; Brundrett & Tedersoo, 2018), and these associations differ in ecologically important ways (Smith & Read, 2008) that can have dramatic effects on the structure and functioning of plant communities (Rillig, 2004; Bever *et al.*, 2010; Corrales *et al.*, 2016; Bennett *et al.*, 2017; Wurzbürger *et al.*, 2017). Many of these effects are mediated by plant–soil feedbacks, the processes whereby plants and their associated symbionts alter the properties of the soil where they are growing, causing feedbacks that affect plant growth and survival in the future (Bever *et al.*, 1997). The two most common types of mycorrhizal fungi, ectomycorrhizal fungi (EMF) and arbuscular mycorrhizal fungi (AMF), differ in several traits that cause mycorrhizal mediated plant–soil feedbacks to vary between plant species hosting different mycorrhizal types, particularly among trees (Bennett *et al.*, 2017; Teste *et al.*, 2017; Segnitz *et al.*,

2020). Ectomycorrhizal fungi are considered more effective competitors for organic forms of nutrients because they have more recently diverged from free-living saprotrophic fungi and so have retained key enzymatic capabilities associated with the degradation of lignocellulose, such as the production of peroxidases and other oxidative enzymes (Rineau *et al.*, 2012; Lindahl & Tunlid, 2015). By contrast, AMF lack or have only limited enzymatic capacities to degrade organic compounds (Hodge, 2001; Read & Perez-Moreno, 2003), and depend primarily on saprotrophic microbiota to mineralize nutrients or liberate simple organic and inorganic compounds before uptake (Smith & Smith, 2011). However, the carbon costs of ectomycorrhizal symbiosis to plants may be higher than those of arbuscular mycorrhizal symbiosis (Leake *et al.*, 2004; Hobbie, 2006; Brzostek *et al.*, 2014; Lu & Hedin, 2019), in part because EMF produce greater amounts of biomass, as thick mantles covering the root tip and prolific extramatrical hyphae and rhizomorphs that allow more extensive soil resource exploitation and long-distance transport to the host



**Fig. 1** Conceptual framework integrating two drivers of mycorrhizal mediated plant–soil feedbacks: the resource economic spectrum of trait variation and lithological determinants of soil fertility, which affect the relative fitness advantage of trees hosting ectomycorrhizal fungi (EMF) vs arbuscular mycorrhizal fungi (AMF) in a single climatic regime. As a model, our framework is not comprehensive, but it emphasizes the interactions and processes that are the focus of our study. (a) A conceptual model showing the processes and mechanisms influencing the relative fitness advantage of trees hosting AMF vs EMF. Soil fertility is jointly determined by the direct effects of lithology and by its coupling with plant resource economies as modified by mycorrhizal mediated plant–soil feedbacks. Plant traits may also be influenced by aboveground environmental factors other than soil fertility. For example, while leaf functional trait variation of plant species often correlates with soil fertility gradients (Ordoñez *et al.*, 2010; Katabuchi *et al.*, 2012; Russo & Kitajima, 2016), not all species on nutrient-depleted soil, for instance, have trait values at the slow end of the spectrum. This is because leaf trait values also vary with respect to shade tolerance (Walters & Reich, 1996; Poorter, 2009), and light-demanding species with trait values at the fast end of the spectrum are also found on nutrient-depleted soils (Davies *et al.*, 1998). (b) Variation in the relative fitness advantage of trees hosting AMF vs EMF, with respect to plant species' functional traits defined by the resource economics spectrum and a lithological soil gradient of fertility. While plant trait variation and lithology do not directly determine the relative fitness advantage (see panel (a)), due to their indirect effects, the relative fitness advantage, and hence relative dominance of trees hosting AMF vs EMF, should vary with trait variation and lithological soil gradients. In addition to the effects of the environment, traits may also vary given the plant species pool, and lithology varies among natural systems, so the axes conceptually represent a range of possible relative states that natural systems may possess. Regions of the same color represent combinations of trait values and lithological soil fertility that yield an equal relative fitness advantage to an EMF- or AMF-hosting tree; darker orange colors indicate an increasing relative fitness advantage for AMF-hosting species, whereas darker blue colors indicate an increase in the relative fitness advantage for EMF host species. Functional trait variation is represented with respect to the resource-economy spectrum, from slow (e.g. thicker, tougher, longer lived leaves with high carbon : nutrient ratios) to fast (e.g., thinner, weaker, shorter-lived leaves with low carbon : nutrient ratios) positions along the spectrum (Reich, 2014). Lithological soil gradient refers to variation in soil fertility arising due to the lithology of the parent materials of the soils, from soils with lithologically low (nutrient-poor) to high (nutrient-rich) nutrient supply. This conceptual model does not quantify the global relative fitness advantage corresponding to a given mycorrhizal association, lithological soil fertility, or leaf functional traits: it is agnostic to the ecological set-point of the system, and only conveys relative differences in a conceptual way. The actual relative fitness advantage of hosting EMF or AMF in a particular system depends strongly on the properties and dominant ecological processes in that system. Here, we have emphasized nutrient fertility, but lithological soil fertility also encompasses other factors affecting plant productivity, such as soil moisture, which could alter the shapes of these relationships, and this conceptual model could be modified to account for such effects. In the model shown, regions of equal relative fitness advantage are linear and have a slope of one, implying that functional trait variation and soil nutrient supply operate as independent, additive factors of equal importance to determining the relative fitness advantage of a given mycorrhizal association. However, trait variation and lithology might differ in the strength of their effects. For example, if lithology were less influential than trait variation in determining the relative fitness advantage of a given mycorrhizal strategy, then the slope would be more shallow, whereas if trait variation were less influential, then the slope would be steeper. In addition, trait variation and lithology may have interactive effects and not be strictly additive, in which case the regions of equal relative fitness advantage would be curved rather than linear. A curvilinear relationship may also arise if the gradient of lithological soil fertility included variation in nutrient availability, as well as other factors, such as water availability, affecting plant productivity. PSF, plant–soil feedbacks; RFA, relative fitness advantage.

plant (Smith & Read, 2008; Phillips *et al.*, 2013). Because of the varying costs and benefits to trees of hosting EMF vs AMF, mycorrhizal mediated plant–soil feedbacks shape forest structure and dynamics (Corrales *et al.*, 2016; Bennett *et al.*, 2017; Corrales *et al.*, 2018; Steidinger *et al.*, 2019).

At least three inter-related hypotheses make predictions about the consequences of mycorrhizal mediated plant–soil feedbacks in forests sharing similar climate. The Gadgil hypothesis states that EMF outcompete saprotrophs for nutrients bound in organic matter. Whereas saprotrophs depend on the decomposition of organic matter for carbon (C) uptake, EMF obtain C directly from the host plant and are thus less C-limited than saprotrophs. Consequently, the greater uptake of nutrients, and particularly nitrogen (N), by EMF limits the growth of saprotrophs, leading to suppressed leaf litter decomposition (Gadgil & Gadgil, 1971; Fernandez & Kennedy, 2016). The short-circuit hypothesis states that the superior ability of EMF to access nutrients bound in organic matter enables them to competitively preempt AMF for nutrients, making it more adaptive for EMF-hosting trees to produce leaf litter made recalcitrant to

decomposition by, for example, high concentrations of secondary compounds or C polymers (e.g. lignin) (Northup *et al.*, 1995; Torti *et al.*, 2001). The mycorrhizal associated nutrient economy (MANE; Phillips *et al.*, 2013) hypothesizes that, due to these effects, trait-mediated biogeochemical syndromes exist in communities dominated by tree species associating with AMF vs EMF, which promote more open, inorganic vs more closed, organic nitrogen economies, respectively (Lin *et al.*, 2018). These hypotheses make predictions about the differences in C and nutrient cycling between communities that are dominated by trees associated with AMF vs EMF, but they are less explicit about how variation in the relative dominance of these mycorrhizal types is established in the first place. They focus on the traits of the trees and fungi as principal determinants of soil fertility, but underlying lithological drivers of soil fertility also have strong direct effects on plants and the soil microbiota, known as edaphic effects. In soils where rock-derived nutrients, such as phosphorus (P), are more limiting than N, as is often the case in tropical systems (Walker & Syers, 1976; Vitousek, 2004), accounting for lithology is essential for a more complete understanding of mycorrhizal mediated plant–soil feedbacks (Augusto *et al.*, 2017). Here, we develop and empirically evaluate an integrated framework for how trait-based and lithological drivers of soil fertility can jointly shape mycorrhizal mediated plant–soil feedbacks and thereby govern the relative fitness advantage of AMF- vs EMF-hosting tree species in forests growing on different soil types (Fig. 1).

Plant–soil feedbacks during pedogenesis affect many properties of soils that together define fertility, defined as the capacity of a soil to promote plant growth, including any resource, such as water and nutrients, and condition, such as acidity, affecting plant function (Jenny, 1980; Augusto *et al.*, 2017). However, plant–soil feedbacks and other biotic processes operating in and on soils do so within envelopes that are fundamentally limited by the lithology of the parent materials, which ultimately constrain processes determining soil fertility (Jenny, 1980; Augusto *et al.*, 2017). This is particularly true for rock-derived nutrients and minerals that are limited in highly weathered soils (Chadwick *et al.*, 1999; Yang & Post, 2011; Vitousek & Chadwick, 2013). Even in areas sharing the same regional species pool and climate, the community structure, population dynamics, functional trait variation, and ecosystem processes in forests have been shown to vary greatly among soil types originating from different parent materials of similar age but contrasting lithology (Baillie *et al.*, 1987; Ashton & Hall, 1992; Baltzer *et al.*, 2005; Russo *et al.*, 2005; Dent *et al.*, 2006; Coomes *et al.*, 2009; Fine & Kembel, 2011; Katabuchi *et al.*, 2012).

A common thread among the above hypotheses is that, due to mycorrhizal mediated plant–soil feedbacks, it is adaptive for trees hosting EMF to make tougher, longer-lived, and better-defended organs that are lower in nutrient concentrations (Cornelissen *et al.*, 2001; Averill *et al.*, 2019) and that thus produce less decomposable leaf litter, compared to AMF-hosting trees, a pattern observed in several studies (Read, 1991; Phillips *et al.*, 2013; Averill *et al.*, 2019; Keller & Phillips, 2019; See *et al.*, 2019). However, plant functional trait variation not only shapes, but also

responds to, the environment. Plant communities on soils that are nutrient-depleted due to the properties of the parent material (which we will refer to as *lithologically* less fertile soils) typically occupy the slower end of the resource economics spectrum (Reich, 2014) and have more conservative resource-use strategies (Chapin *et al.*, 1993; Wright & Westoby, 1999; Aerts & Chapin, 2000; Liu *et al.*, 2012; Russo & Kitajima, 2016). Plant species making tough, thick, dense, long-lived, and well-defended leaves with low nutrient concentrations and high resorption efficiency generally produce leaf litter recalcitrant to decomposition (Horner *et al.*, 1988; Grime *et al.*, 1996; Cornelissen *et al.*, 2004; Kurokawa & Nakashizuka, 2008), which can slow nutrient cycles (Hobbie, 1992, 2015) and contribute to the accumulation of organic matter (Aerts & Chapin, 2000; Baillie *et al.*, 2006). For example, functional trait combinations enabling a resource conservative strategy for trees growing on lithologically less fertile soils would also presumably favor nutrient access by EMF, compared to AMF, as nutrients would remain in complex organic forms for longer periods of time, giving EMF, and their host trees, preferential access to them (Northup *et al.*, 1995, 1998). An additional benefit for EMF-hosting trees could be greater ability to weather soil minerals, such as apatite, which may release cations (Landeweert *et al.*, 2001; Blum *et al.*, 2002; Quirk *et al.*, 2014), although evidence has not always been found for differences between AMF- and EMF-hosting trees in mineral weathering capacity (Koele *et al.*, 2014). Given the higher C costs of EMF symbiosis, then on lithologically more fertile soils, trees associating with AMF should be more favored, as leaf litter is more decomposable, and soil-derived mineral resources are more available. Therefore, lithological effects on soil fertility may filter plant resource economic strategies in a way that influences the potential for MANE or mycorrhizal short-circuits to develop, and thus the relative fitness of trees with EMF or AMF symbioses. This conceptual framework for the relative fitness of mycorrhizal symbioses (Fig. 1) allows for codominance of AMF- and EMF-hosting species on a given soil type, assuming that the biogeographic species pool available for colonization includes both AMF- and EMF-hosting species.

Here, we evaluate this conceptual framework by quantifying patterns of variation in mycorrhizal composition and functional trait variation in tropical forest tree assemblages along a fertility gradient of lithologically distinct soil types in Borneo. Much of the original literature on mycorrhizal mediated plant–soil feedbacks is focused on temperate forests (Gadgil & Gadgil, 1971; Read, 1991; Northup *et al.*, 1995; Phillips *et al.*, 2013; Rosling *et al.*, 2016; Cheeke *et al.*, 2017). However, there are reasons to think that mycorrhizal mediated plant–soil feedbacks may operate differently in tropical systems (Waring *et al.*, 2016; Corrales *et al.*, 2018; Lin *et al.*, 2018; Liu *et al.*, 2018; Keller & Phillips, 2019). Tropical and temperate forests have different regional species pools of trees and fungi, due to their distinctive evolutionary histories and biogeography, as well as climatically driven differences in the duration and speed of pedogenesis. Our study site, a long-term forest dynamics plot in Lambir Hills National Park (Lee *et al.*, 2002b), is an ideal setting in which to examine how trait-based and lithological drivers of soil fertility can jointly

shape mycorrhizal mediated plant–soil feedbacks at the forest community scale. The plot contains a diversity of AMF- and EMF-hosting tree species, which provides sufficient power to test for mycorrhizal differences in forest composition and trait variation. This is important because many tropical forests are strongly dominated by AMF-hosting tree species, except in unusual cases of monodominance by tree species associated with EMF (Peay, 2016). In addition, the plot encompasses four lithologically distinct soil types experiencing the same climate. The soil types are derived from parent materials differing in texture and mineral composition, comprising a gradient varying in concentrations of total organic C, N and P, cation exchange capacity, soil moisture holding capacity, and other soil properties influencing fertility (Baillie *et al.*, 2006; Tan *et al.*, 2009; Russo *et al.*, 2010) (Supporting Information Methods S1, Table S1, Fig. S1). The long history of research on the fertility gradient shows that these soil types shape forest diversity and function at Lambir. The forest composition varies dramatically (Kochsiek *et al.*, 2013) due to strong soil-type associations of tree species (Davies *et al.*, 2005). Tree functional traits (Katabuchi *et al.*, 2012; Kochsiek *et al.*, 2013; Russo & Kitajima, 2016), leaf litter decomposition (Baillie *et al.*, 2006), and soil bacterial and ectomycorrhizal fungal communities (Peay *et al.*, 2009; Russo *et al.*, 2012) also differ across the soil types. Moreover, all of the soil types at Lambir are nutrient-depleted, but they differ most strongly in rock-derived nutrients, particularly P (Table S1), in contrast to many temperate forest and tropical forests on younger soils (Walker & Syers, 1976; Vitousek, 2004), indicating the importance of accounting for lithology.

To evaluate predictions from our conceptual framework, we used data on the distributions of 1245 tree species and on variation in 14 functional traits (13 leaf traits and wood density) of between 94 and 150 tree species (depending on the trait; Table 1) across mycorrhizal associations and lithologically defined soil types in Lambir. First, we expected that, all else being equal, the relative fitness advantage, and hence the relative dominance of EMF-hosting species, should increase with declining lithological soil fertility (transition from orange to blue along the *x*-axis of

Fig. 1b). Second, the relative fitness advantage of a species with a given mycorrhizal type on a given soil type should also depend on where the species lies on the resource economics spectrum in terms of functional trait variation. Trait values at the faster end of the spectrum should be advantageous for AMF-hosting species and become more advantageous to EMF-hosting species towards the slower end (transition from orange to blue along the *y*-axis of Fig. 1b). We therefore evaluated the following: whether EMF-hosting species had trait values at the slower end of the resource economics spectrum (i.e. towards more conservative values associated with slower decomposition rates); whether the trait values of EMF and AMF host species shift across the soil types in accordance with the resource economics spectrum (i.e. towards more conservative values on lithologically less fertile soil); and whether interactions between mycorrhizal type and soil type affected trait variation, in other words, whether the effect of soil type on trait values differed between EMF- and AMF-hosting tree species.

## Methods and Materials

### Study site and species

Lambir Hills National Park, Sarawak, Malaysia (4°11'N, 114°01'E) encompasses 6800 ha of lowland mixed dipterocarp forest, and has very high tree species diversity (Ashton, 2005). It receives *c.* 3000 mm of rainfall annually, with all months averaging > 100 mm, and monthly mean temperatures range from 26 to 28°C (Watson, 1985). Within the Park, a 52-ha long-term research plot (hereafter, Lambir) was established, encompassing an elevation range of 139 m (Lee *et al.*, 2002a). In the plot, all trees ≥ 1 cm in diameter at breast height (DBH) have been identified to species, mapped, and are censused every 5 yr using standardized methods of the Smithsonian ForestGEO plot network (Condit, 1998). See Methods S1 for more details about plot establishment. As of the 2008 census, the plot hosts approx. 1245 tree species from 95 families, with 808 species in 59 families that are known to contain at least some species with AMF associations and 111 species in three families that are known to contain at

**Table 1** Plant functional traits included in this study.

Trait (no. of species analyzed)	Abbreviation (unit)	Total no. of trees (N within species)	Means (range)	
			Saplings	Adults
Wood density (94)	- (g cm <sup>-3</sup> )	337 (1–20)	0.55 (0.36–0.72)	0.60 (0.20–1.01)
Leaf area (151)	LA (cm <sup>2</sup> )	705 (1–28)	149.51 (7.79–2025.39)	90.73 (8.42–1064.22)
Leaf thickness (148)	- (mm)	512 (1–22)	0.19 (0.11–0.37)	0.24 (0.11–0.55)
Specific leaf area (150)	SLA (cm <sup>2</sup> g <sup>-1</sup> )	698 (1–28)	154.2 (60.4–502.9)	110.2 (38.9–305.8)
Leaf dry matter content (140)	LDMC (g g <sup>-1</sup> )	670 (1–28)	0.39 (0.19–0.58)	0.43 (0.16–0.59)
Leaf tissue density (145)	LTD (g cm <sup>-3</sup> )	488 (1–21)	0.38 (0.16–0.61)	0.43 (0.13–0.68)
Leaf C concentration (137)	C (%)	622 (1–25)	48.9 (30.55–58.62)	47.29 (31.19–56.23)
Leaf N concentration (137)	N (%)	623 (1–21)	1.52 (0.58–4.12)	1.67 (0.78–3.22)
Leaf P concentration (135)	P (%)	621 (1–19)	0.06 (0.02–0.25)	0.06 (0.02–0.15)
Leaf C : N (137)	C : N	622 (1–25)	34.96 (11.42–88.69)	30.25 (14.99–64.84)
Leaf C : P (135)	C : P	619 (1–25)	914 (186–2707)	914 (321–2754)
Leaf N : P (135)	N : P	620 (1–25)	26.38 (40.43–85.00)	30.01 (10.25–71.87)
Leaf δ <sup>13</sup> C (135)	- (per mil)	620 (1–25)	–34.76 (–38.35––27.73)	–32.90 (–37.48––27.33)
Leaf δ <sup>15</sup> N (135)	- (per mil)	613 (1–25)	–0.60 (–7.84–4.58)	–0.97 (–5.03–5.40)

least some species with EMF associations (Wang & Qiu, 2006; Brundrett, 2009; Tedersoo & Brundrett, 2017).

The soils and geomorphology of Lambir are described in detail elsewhere (Lee *et al.*, 2002b; Tan *et al.*, 2009). To summarize from previous studies (Davies *et al.*, 2005; Baillie *et al.*, 2006), the soils are derived from interbedded sandstone and shale, which are the lithologically distinct parent materials giving rise to the ends of the fertility gradient represented in Lambir. The sandstone-derived soils are well-drained humult ultisols, with a surface horizon of loosely-matted and densely-rooted raw humus, and have low nutrient status. The shale-derived soils are relatively more fertile, clay-rich udult ultisols with greater water holding capacity and a shallow leaf-litter layer. These two soils represent the extremes in the range of soil types in Lambir. Four soil types (sandy loam, loam, fine loam, clay, ranked in ascending order of nutrient concentrations and moisture) have been defined at Lambir based on multivariate analyses of variation in total soil C and soil nutrient concentrations (N, P, and exchangeable potassium (K), calcium (Ca) and magnesium (Mg)) and elevation (Davies *et al.*, 2005; Baillie *et al.*, 2006) (Fig. S1; Table S1). These soil types comprise a gradient in lithological fertility, as they are derived from different relative amounts of the two lithologically distinct parent materials. Each 20 × 20 m quadrat within the Lambir plot was categorized as one of these soil types, which share the same climate due to their close proximity (Davies *et al.*, 2005).

### Soil and mycorrhizal-specific tree distributions

Tree species in the plot were assigned to a mycorrhizal type based on the genus and family-level data in Brundrett (2009) and Wang & Qiu (2006). While many families of trees are known to predominantly or exclusively host AMF (e.g. Myristicaceae) or EMF (e.g. Dipterocarpaceae; Fagaceae) (Brearley, 2012), there can be variation within families (e.g. Rosaceae) (Tedersoo & Brundrett, 2017), and mycorrhizal status has not been investigated for every tree species in Lambir. We therefore were conservative in assigning mycorrhizal types to tree species, and coded species as unknown when the genus or family had multiple records of both mycorrhizal associations.

As in previous studies at Lambir (Methods S1), each individual tree was assigned to one of the four soil types based on the location where it was growing in the plot and the soil type map (Fig. S1). The basal area of each tree was calculated in m<sup>2</sup> using diameters of trees alive in the 2008 census of Lambir. Using each tree's location, the basal area of trees was summed within 20 × 20 m quadrats in the plot for all trees and for mycorrhizal associations separately. The same calculations were done using stem abundances in two size classes, 1–20 and ≥ 20 cm in DBH. Basal area was expressed per unit area (m<sup>2</sup> ha<sup>-1</sup>) and both basal area and stem abundance were expressed as proportions of the total that were trees of either AMF or EMF-hosting species.

### Functional trait variation

Between May and August 2009, we quantified variation in wood density and 13 leaf functional traits for up to 150 tree species

(depending on the trait; Table 1), 25 of which occur on both the more fertile clay, and less fertile sandy loam soils for saplings (1–5 cm DBH, 452 individuals in total) and adult trees (≥ 5 cm DBH, 245 individuals in total) separately, resulting in the following sampling distributions for adult trees (56 AMF-hosting and 14 EMF-hosting species on fertile soil, 55 AMF-hosting and 23 EMF-hosting species on infertile soil) and for saplings (15 AMF-hosting and 5 EMF-hosting species on more fertile soil, 14 AMF-hosting and 6 EMF-hosting species on less fertile soil). The number of trees sampled differed between traits (Table 1) and across species × size class (sapling vs adult), ranging from 1 to 25 saplings, and 1 to 8 adult trees per species (mean = 12.9 saplings, 1.8 adults per species; overall mean = 4.7 trees per species). Leaf functional traits reflected leaf chemical and structural properties that are associated with species' resource economics (Wright *et al.*, 2004; Reich, 2014) and leaf litter decomposition rates (Cornwell *et al.*, 2008; Kurokawa & Nakashizuka, 2008; Freschet *et al.*, 2012). Three to five mature, sunlit, minimally damaged leaves were harvested per tree, and their functional trait values were determined following standardized protocols (Pérez-Harguindeguy *et al.*, 2013) explained in greater detail in Methods S1. All EMF-hosting species in our functional trait data are in the Dipterocarpaceae. Each tree was assigned a crown exposure index varying from 1–5 (1 = no direct light, 5 = crown completely exposed; Clark & Clark, 1992) to account for variation in insolation.

### Statistical analyses

All analyses were conducted using R statistical software (R Core Development Team, 2017). To test the hypothesis that the relative dominance of AMF- vs EMF-hosting tree species varies among soil types, we fit linear models of four response variables as a function of soil type separately for each mycorrhizal type: the tree basal area in each quadrat expressed per unit area that hosted either AMF or EMF, the proportion of total tree basal area in each quadrat that hosted either AMF or EMF, the proportion of total number of stems 1–20 cm in DBH in each quadrat that hosted either AMF or EMF, and the proportion of total number of stems ≥ 20 cm in DBH in each quadrat that hosted either AMF or EMF. We used *post-hoc* pairwise comparisons after a significant omnibus test to quantify which soil types differed significantly from each other.

We used linear mixed effects models as implemented in the 'lmer' function (Bates *et al.*, 2015) to test differences in leaf traits between trees with different mycorrhizal associations (AMF and EMF) and growing on soil types of lithologically different fertility. For trait analyses, the four soil types were grouped as more fertile (fine loam and clay) and less fertile (sandy loam and loam) soils. Models were fit for each trait separately, but included trees of all diameters. Mycorrhizal association, soil fertility, and their interaction were included as fixed factors. To account for trait variation with insolation, crown exposure was included as a fixed covariate. Tree species identity was included as a random intercept to account for the fact that different numbers of individuals were sampled for each species and because we were interested in

community-level, not species-specific, patterns. We accounted for the unequal variance in several leaf traits and wood density between AMF- and EMF-hosting species. We controlled the false discovery rate resulting from multiple testing using the Benjamini–Hochberg method (Benjamini & Hochberg, 1995).

Leaf trait differences between trees of different mycorrhizal association and on different soil types in relation to the resource economics spectrum were visualized using principal component analysis (PCA). Wood density was not included in these analyses because this was measured for fewer species than the leaf traits were (Table 1), and  $\delta^{15}\text{N}$  was not included because it does not clearly relate to the resource economy spectrum. Species were grouped into four treatment categories combining their mycorrhizal association and soil type (AMF–clay, AMF–sandy loam, EMF–clay, EMF–sandy loam). As some species occurred on both soil types, we omitted individual trees from the soil type on which they were sampled least in order to avoid double representation of one species in our PCA; species for which not all leaf data were available were omitted as well, so that our PCA included 140 tree species  $\times$  soil type records (adult trees: 47 AMF-hosting and 11 EMF-hosting species on more fertile clay soil, 35 AMF-hosting and 13 EMF-hosting species on less fertile sandy loam soil; saplings: 12 AMF-hosting and 3 EMF-hosting species on fertile soil, 13 AMF-hosting and 6 EMF-hosting species on infertile soil). The PCA was performed using species' trait means calculated separately for juvenile and adult trees, all of which were ordinated together on common axes. However, we visualize them separately to identify whether patterns in trait variation differed between trees in different size classes. We used permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; Zapala & Schork, 2006), as implemented in the VEGAN package ('adonis' function to compare centroids, 'betadisper' function to compare variances between treatment groups; Oksanen *et al.*, 2019) to identify differences among groups in multivariate trait variation. PERMANOVA was performed for adults and saplings separately since trait variation can change with ontogeny.

### Data availability

The Lambir plot stem and trait data are available at <http://ctfs.si.edu/datarequest/>.

### Results

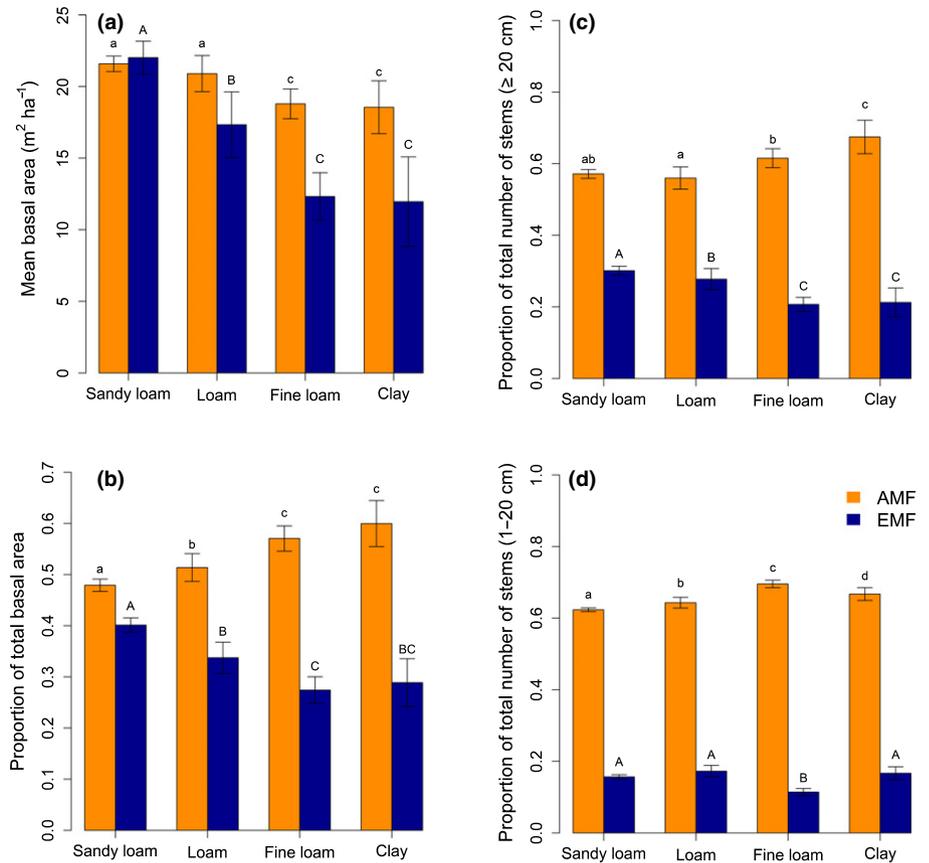
On all four soil types, AMF-hosting trees were equal or greater in basal area and stem abundance than EMF-hosting tree species (Fig. 2). The basal area per hectare of both mycorrhizal types increased significantly with declining lithological soil fertility (from clay to sandy loam), but the increase was substantially larger for EMF- than AMF-hosting trees (Fig. 2a). Expressed as a proportion of the total basal area, the mycorrhizal types comprised similar proportions on the lithologically less fertile sandy loam, but EMF-hosting trees declined significantly to nearly half of the proportion of basal area represented by AMF-hosting trees on clay (Fig. 2b). In terms of the

proportion of the total stem abundance, AMF-hosting trees dominated the assemblages on all four soil types (Fig. 2c,d). For larger stems, the patterns were more similar to those in basal area, in that with increasing lithological soil fertility, from sandy loam to clay, the proportion of AMF-hosting trees significantly increased, whereas that of EMF-hosting trees significantly decreased (Fig. 2c). Patterns for smaller stems were more idiosyncratic (Fig. 2d). Lower proportions of AMF-hosting trees were found on the lithologically less fertile soil types (sandy loam and loam), compared with the more fertile soil types (fine loam and clay), with the greatest proportion found on fine loam (Fig. 2d). By contrast, EMF-hosting trees represented overall far lower proportions that were lowest on the fine loam, and greater on the less fertile sandy loam and loam, which were not different from the more fertile clay (Fig. 2d).

The functional traits we analyzed were correlated with each other to varying degrees, as expected (Fig. S2). Six out of thirteen leaf traits differed significantly between AMF- and EMF-hosting trees after accounting for multiple comparisons (Tables 2, S2, Figs 3, S3). Leaves of EMF-hosting species had denser tissue, higher dry matter content, lower specific leaf area (SLA), higher %C, lower N : P, and higher  $\delta^{15}\text{N}$  than leaves of AMF-hosting species, and trait values of both AMF- and EMF-hosting tree species became more conservative on the lithologically less fertile sandy loam, relative to clay. Wood density and all leaf traits, except %C, differed significantly between trees growing on less vs more fertile soils after accounting for multiple comparisons (Tables 2, S2, Figs 3, S3). Trees on the more fertile clay soil had lower wood density, larger and thinner leaves of higher SLA, lower leaf dry matter content (LDMC) and tissue density, and lower  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  than trees on less fertile sandy loam soils. Also, their leaves were higher in %N and %P, and lower in C : N, C : P and N : P ratios than the leaves on trees on sandy loam soils. For wood density and leaf C : P ratio, there was a significant interaction between mycorrhizal association and soil type, but these interactions did not remain statistically significant after accounting for multiple comparisons (Tables 2, S2; Figs 3, S3). For wood density, the difference between clay and sandy loam tended to be larger for EMF- than for AMF-hosting species (Fig. S3a), whereas for leaf C : P, the difference tended to be larger for AMF- than EMF-hosting species (Fig. 3i). Crown exposure affected all traits except %P, C : P, and wood density (Tables 2, S2), demonstrating that light availability affects trait variation.

The first two axes of the PCA explained 42% (PC1) and 13% (PC2) of the total variation in leaf traits of all species, but neither PC1 nor PC2 aligned cleanly with the resource economics spectrum of trait variation (Fig. 4). The first axis correlated positively with leaf %P, SLA, and leaf %N and negatively with leaf dry matter content, leaf C : P and C : N (Table S3). The second axis correlated most strongly with leaf %N (negatively) and with leaf C : N (positively). Multivariate variation in leaf traits segregated among the four mycorrhizal  $\times$  soil type groups for adults and saplings (Fig. 4), but was structured more by soil type than mycorrhizal association in that it varied significantly with soil type, but not mycorrhizal type (Table 3).

**Fig. 2** Variation in the relative dominance of trees with different mycorrhizal associations (AMF, arbuscular mycorrhizal fungi; EMF, ectomycorrhizal fungi) on four soil types on a lithological fertility gradient in a Bornean mixed dipterocarp forest: (a) basal area ( $\text{m}^2$ ) per hectare (ha), (b) and proportion of total basal area, (c) stems 1–20 cm in diameter at breast height (DBH), (d) stems ( $\geq 20$  cm in DBH). Soil types are ordered from less to more fertile (left to right). Bars show means across  $20 \times 20$  m quadrats in the Lambir plot, with error bars showing 95% confidence limits. Lower- and upper-case letters indicate statistical significance of pairwise differences between soil types for AMF and EMF-hosting tree species, respectively. Within each soil type, the basal area per hectare, the proportion of total basal area, and the proportions of smaller and larger stems differed significantly between mycorrhizal types, except for basal area per hectare on sandy loam. Mean proportions do not sum to one because there was insufficient information for some tree species to classify them according to mycorrhizal association.



## Discussion

The lithology of soils constrains their inherent fertility, which influences the composition and function of the plant communities that grow on them (Jenny, 1980; Augusto *et al.*, 2017). Likewise, mycorrhizal mediated plant–soil feedbacks affect soil fertility within these constraint envelopes and further shape plant communities (Gadgil & Gadgil, 1971; Northup *et al.*, 1995; Phillips *et al.*, 2013; Averill *et al.*, 2019). Here, we integrated these frameworks (Fig. 1) and found that tree species composition and functional trait variation was related to both soil lithology and mycorrhizal association in this Bornean rain forest, supporting the hypothesis that soil fertility inherited from the parent material shapes plant resource economics and the relative fitness advantage of trees with different mycorrhizal associations. Although AMF-hosting tree species almost always comprised more of the total basal area and abundance than EMF-hosting species in this tropical rain forest, the relative dominance of these mycorrhizal types changed across soil types along a lithological fertility gradient. The relative dominance of AMF- over EMF-hosting trees decreased with declining lithological fertility, especially for basal area and the abundance of larger stems. Variation in the relative abundance of smaller stems was broadly consistent with these patterns, but more variable, which is to be expected if it takes time for differences in the relative fitness advantage of these long-lived AMF- vs EMF-hosting trees (i.e. via growth and survival rate differences) to

play out. Thus, in this Bornean rain forest, forest community structure varied not only among soil types on a lithological fertility gradient, as has been previously shown (Davies *et al.*, 2005), but also in relation to the mycorrhizal associations of trees, suggesting strong edaphic effects on the relative fitness advantage of EMF- vs AMF-hosting trees.

At least some of the soil type-related variation in the relative dominance of tree species with different mycorrhizal associations can be traced to coordinated variation in tree functional traits in this forest. Confirming previous studies (Katabuchi *et al.*, 2012; Russo *et al.*, 2013; Russo & Kitajima, 2016), we not only found significant variation in nearly all leaf and wood traits across soil types that was consistent with the resource economics spectrum, but also found variation in many, but not all, leaf traits, to differ between AMF- and EMF-hosting tree species. All plant traits, including those we analyzed, are not independent of each other, as they are part of coordinated phenotypic variation (Pigliucci, 2003). EMF-hosting tree species generally had more conservative leaf trait values than AMF-hosting species, particularly for SLA, LDMC, tissue density, and %C. These leaf traits are correlated with leaf litter traits, such as lignin concentration (Cornwell *et al.*, 2008), that are associated with reduced leaf litter decomposability (Kurokawa & Nakashizuka, 2008; Freschet *et al.*, 2012). Other traits, like foliar N and C : N, that are thought to be associated with mycorrhizal mediated plant–soil feedbacks (Read, 1991; Phillips *et al.*, 2013), did not differ between mycorrhizal types in our study. This contradictory result may be a

**Table 2** Effects of mycorrhizal type (ecto- or arbuscular mycorrhizal symbiosis), lithological soil type (more or less fertile), and crown exposure and their interactions on ten fresh leaf traits in a mixed dipterocarp forest in Malaysian Borneo.

	df <sub>num</sub>	df <sub>den</sub>	F	P
<b>Specific leaf area (150)</b>				
Mycorrhizal type	1	148	16.54	<0.001*
Soil type	1	542	27.64	<0.001*
Crown exposure	1	542	219.65	<0.001*
Mycorrhizal type × soil type	1	542	0.95	0.329
Mycorrhizal type × crown exposure	1	542	0.25	0.619
Soil type × crown exposure	1	542	1.44	0.231
Mycorrhizal type × soil type × crown exposure	1	542	2.84	0.093
<b>Leaf dry matter content (140)</b>				
Mycorrhizal type	1	138	12.43	0.001*
Soil type	1	524	22.51	<0.001*
Crown exposure	1	524	167.26	<0.001*
Mycorrhizal type × soil type	1	524	0.69	0.407
Mycorrhizal type × crown exposure	1	524	0.15	0.702
Soil type × crown exposure	1	524	1.06	0.305
Mycorrhizal type × soil type × crown exposure	1	524	2.80	0.095
<b>Leaf tissue density (145)</b>				
Mycorrhizal type	1	143	19.96	<0.001*
Soil type	1	337	9.68	0.002*
Crown exposure	1	337	107.52	<0.001*
Mycorrhizal type × soil type	1	337	0.00	0.985
Mycorrhizal type × crown exposure	1	337	0.90	0.343
Soil type × crown exposure	1	337	13.45	<0.001*
Mycorrhizal type × soil type × crown exposure	1	337	0.31	0.581
<b>Leaf %C (137)</b>				
Mycorrhizal type	1	135	8.52	0.004*
Soil type	1	479	4.28	0.039
Crown exposure	1	479	25.47	<0.001*
Mycorrhizal type × soil type	1	479	1.04	0.309
Mycorrhizal type × crown exposure	1	479	3.08	0.080
Soil type × crown exposure	1	479	1.34	0.248
Mycorrhizal type × soil type × crown exposure	1	479	0.00	0.957
<b>Leaf %N (137)</b>				
Mycorrhizal type	1	135	0.44	0.509
Soil type	1	480	6.79	0.009*
Crown exposure	1	480	11.86	0.001*
Mycorrhizal type × soil type	1	480	0.95	0.330
Mycorrhizal type × crown exposure	1	480	0.61	0.435
Soil type × crown exposure	1	480	6.98	0.009*
Mycorrhizal type × soil type × crown exposure	1	480	0.91	0.341
<b>Leaf %P (135)</b>				
Mycorrhizal type	1	133	1.92	0.168
Soil type	1	480	60.24	<0.001*
Crown exposure	1	480	0.03	0.863
Mycorrhizal type × soil type	1	480	3.70	0.055
Mycorrhizal type × crown exposure	1	480	0.26	0.610
Soil type × crown exposure	1	480	1.63	0.203
Mycorrhizal type × soil type × crown exposure	1	480	1.60	0.207
<b>Leaf C : N (137)</b>				
Mycorrhizal type	1	135	0.45	0.505
Soil type	1	479	9.37	0.002*
Crown exposure	1	479	30.64	<0.001*
Mycorrhizal type × soil type	1	479	1.86	0.173

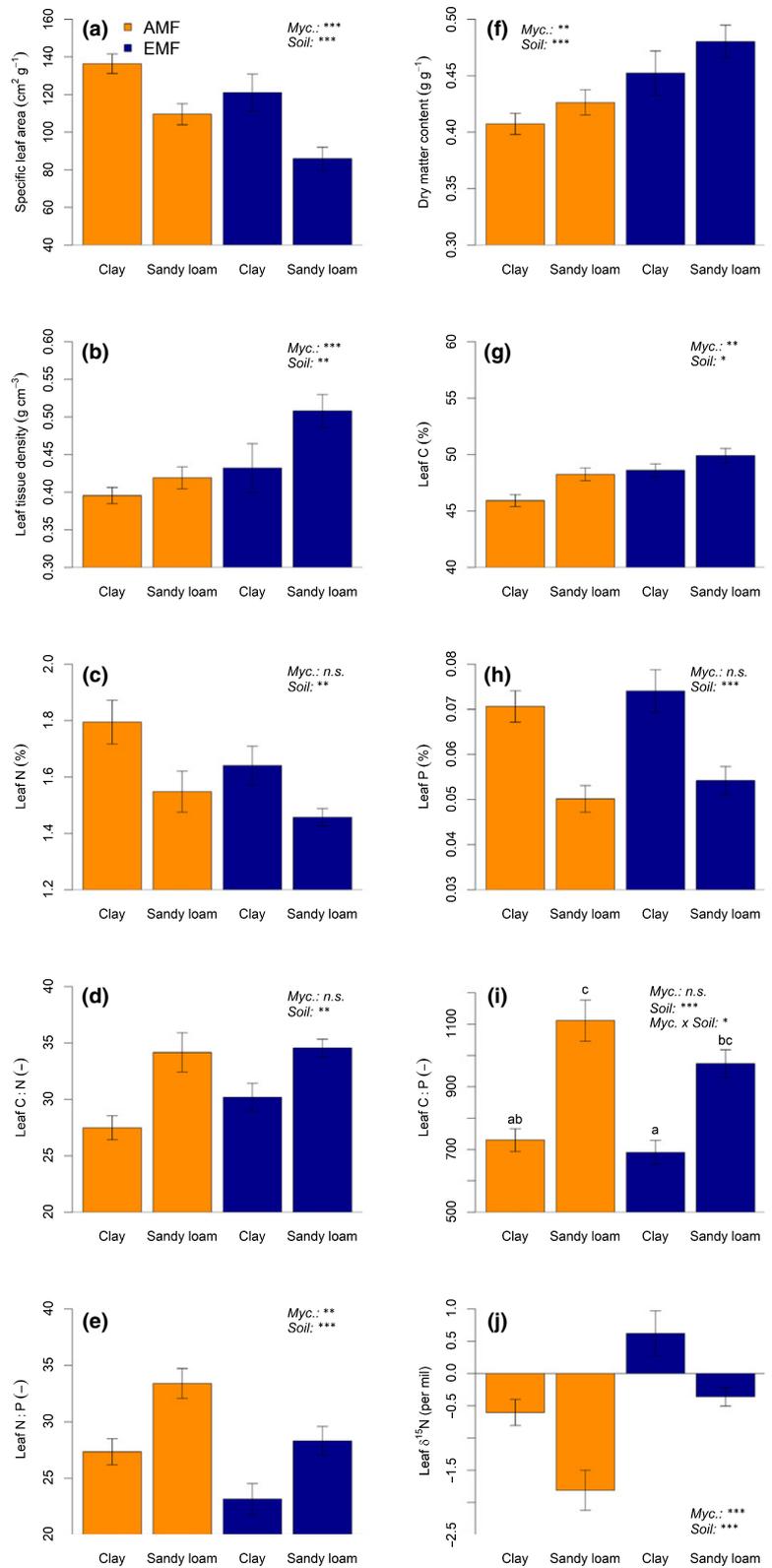
**Table 2** (Continued)

	df <sub>num</sub>	df <sub>den</sub>	F	P
Mycorrhizal type × crown exposure	1	479	1.08	0.299
Soil type × crown exposure	1	479	4.12	0.043
Mycorrhizal type × soil type × crown exposure	1	479	0.22	0.643
<b>Leaf C : P (135)</b>				
Mycorrhizal type	1	133	0.41	0.523
Soil type	1	478	66.04	<0.001*
Crown exposure	1	478	0.54	0.462
Mycorrhizal type × soil type	1	478	4.72	0.030
Mycorrhizal type × crown exposure	1	478	0.60	0.437
Soil type × crown exposure	1	478	2.20	0.139
Mycorrhizal type × soil type × crown exposure	1	478	1.63	0.202
<b>Leaf N : P (135)</b>				
Mycorrhizal type	1	133	7.32	0.008*
Soil type	1	479	40.56	<0.001*
Crown exposure	1	479	4.40	0.037
Mycorrhizal type × soil type	1	479	3.50	0.062
Mycorrhizal type × crown exposure	1	479	0.27	0.602
Soil type × crown exposure	1	479	0.24	0.625
Mycorrhizal type × soil type × crown exposure	1	479	1.10	0.294
<b>Leaf δ<sup>15</sup>N (135)</b>				
Mycorrhizal type	1	133	24.01	<0.001*
Soil type	1	478	111.07	<0.001*
Crown exposure	1	478	10.34	0.001*
Mycorrhizal type × soil type	1	478	0.01	0.922
Mycorrhizal type × crown exposure	1	478	0.63	0.429
Soil type × crown exposure	1	478	1.60	0.206
Mycorrhizal type × soil type × crown exposure	1	478	0.08	0.784

Numbers in parentheses indicate the number of species measured per trait. Summary statistics from linear mixed effects models are given: bold probability (*P*) values indicate significant effects; df<sub>num</sub>, df<sub>den</sub> indicate numerator and denominator degrees of freedom; and *F* indicates the test statistic for each factor. See Supporting Information Table S2 for test statistics for other traits. For each factor, an asterisk indicates whether the probability remained statistically significant after accounting for the false discovery rate.

function of the fact that hypotheses about the drivers of mycorrhizal associated nutrient economies were originally developed and tested in forests of the temperate zone, in which N is often more limiting than in tropical forests (Walker & Syers, 1976; Vitousek, 2004). Our trait analyses instead point to P as important in the mycorrhizal mediated plant–soil feedbacks in this forest, since foliar C : P and N : P were higher for AMF- than EMF-hosting trees. To the extent that foliar chemistry correlates with access to soil nutrients, our results suggest that EMF-hosting trees have access to more P per unit C or N than do AMF-hosting trees, especially on the less fertile sandy loam. Thus, which nutrients are important for understanding mycorrhizal mediated nutrient economies may vary across systems.

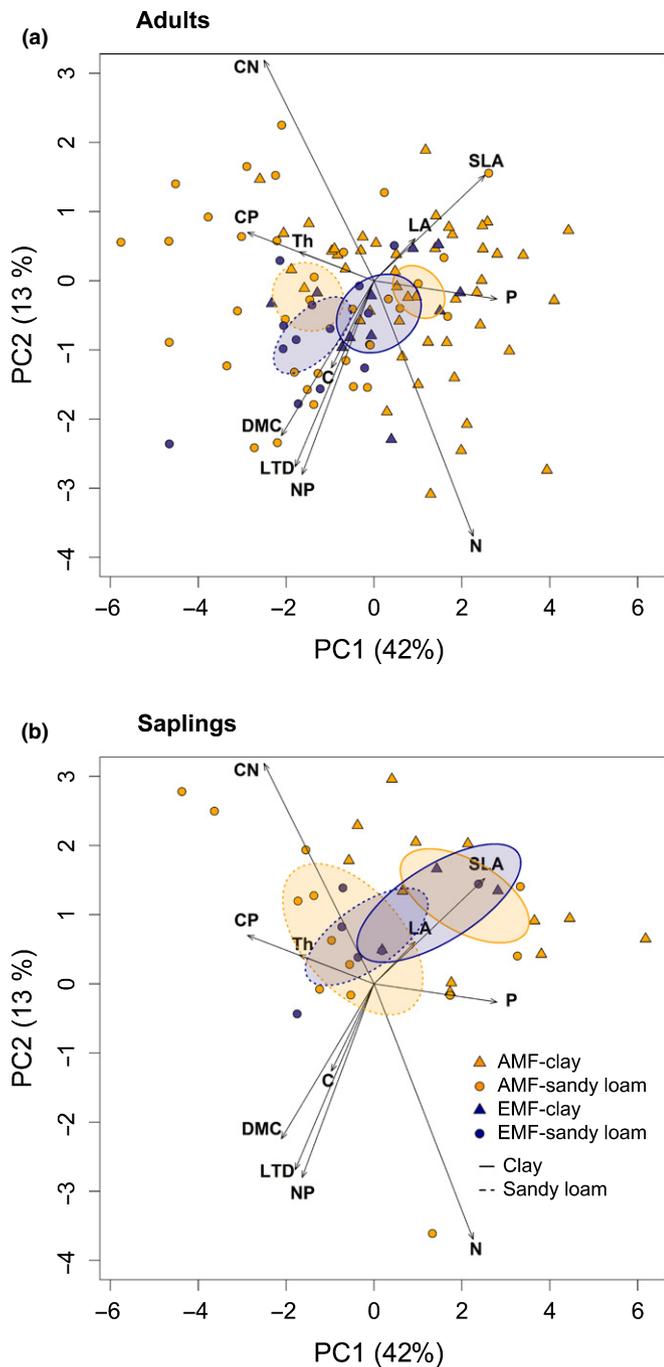
While we do not have data on leaf litter decomposition for species of different mycorrhizal types across the gradient, our results suggest that on soils of lower fertility, associating with EMF, some of which may have more direct access to nutrients in organic matter (Rineau *et al.*, 2012; Talbot *et al.*, 2013; Bödeker



**Fig. 3** Mean leaf traits ( $\pm 1$  SEM) of arbuscular mycorrhizal fungus (AMF; orange bars) and ectomycorrhizal fungus (EMF; blue bars) hosting trees growing on two lithologically distinct soil types (more fertile clay and less fertile sandy loam) in a Bornean mixed dipterocarp forest. To attribute equal weight to each species, traits were first averaged per species and then averaged per mycorrhizal type and soil type for display. Letters above bars indicate significant differences between groups for traits that showed a significant interaction effect of soil and mycorrhizal type (Table 2). Asterisks indicate significance levels for mycorrhizal type (Myc.) and soil type (Soil) effects on traits tested with linear mixed models: ns, not statistically significant; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ . The interaction of mycorrhizal and soil type (Myc.  $\times$  Soil) was only statistically significant for C : P. All factors except Myc.  $\times$  Soil for C : P remained statistically significant after controlling the false discovery rate (Table 2). See Supporting Information Table S2 and Fig. S2 for results for the other three leaf traits and wood density.

*et al.*, 2014; Lindahl & Tunlid, 2015; Shah *et al.*, 2016; but see Pellitier & Zak, 2018), could provide a competitive advantage (Brearley *et al.*, 2003). Consistent with this, the fungal genus *Cortinari*, which is known for enzymatic oxidation of humus (Bödeker *et al.*, 2014), was found exclusively on the lower fertility

sandy loam at Lambir, whereas genera thought to be associated primarily with mineral nutrient uptake, such as *Russula*, were more common on clay soils (Peay *et al.*, 2009; Hobbie & Agerer, 2010). Associating with AMF, which do not have as strong decomposer capacities, but that evidence suggests are also less



**Fig. 4** Plots of the first two axes of a principal component analysis illustrating variation in leaf traits between (a) adults and (b) saplings of tree species hosting arbuscular mycorrhizal fungi (AMF) or ectomycorrhizal fungi (EMF) and growing on two lithologically distinct soil types (more fertile clay and less fertile sandy loam) in a Bornean mixed dipterocarp forest. Triangles represent means of species growing on more fertile soils, circles refer to means of species on less fertile soils; orange data points indicate AMF-hosting tree species, and blue data points refer to EMF-hosting species. Ellipses with solid lines represent the 95% confidence interval around the overall mean of species on fertile soils; ellipses with dashed lines mark confidence intervals of species on infertile soils. Trait data for juveniles and adults were included in the same ordination to facilitate identification of the resource economics spectrum, and so percentages of variance explained by each principal component are the same.

**Table 3** Effects of mycorrhizal type (ecto- or arbuscular mycorrhizal symbiosis), lithological soil type (more or less fertile), their interaction, and crown exposure on species' mean multivariate leaf traits for adult trees and saplings

	df	SS	MSS	F	P
<b>Adults</b>					
Mycorrhizal association	1	0.033	0.033	1.434	0.223
Soil type	1	0.862	0.862	37.001	<b>0.001</b>
Crown exposure	1	0.021	0.021	0.899	0.384
Mycorrhizal association × soil type	1	0.021	0.021	0.915	0.383
<b>Saplings</b>					
Mycorrhizal association	1	0.023	0.023	0.746	0.499
Soil type	1	0.303	0.303	9.801	<b>0.001</b>
Crown exposure	1	0.011	0.011	0.359	0.702
Mycorrhizal association × soil type	1	0.005	0.005	0.148	0.898

df, degrees of freedom; SS, sum of squares; MSS, mean sum of squares; F, F statistic; P, probability from permutational multivariate analysis of variance. Bold probability values indicate statistically significant effects.

costly to the plant in terms of carbon allocation (Leake *et al.*, 2004; Hobbie, 2006), may suffice to acquire the soil nutrients needed by the host tree on more fertile soils, where more easily accessible, inorganic forms of nutrients are thought to comprise a greater proportion of the total nutrient pool. An additional advantage of hosting EMF could be enhanced weathering of primary minerals (i.e. minerals directly from the parent material) to release nutrients (Landeweert *et al.*, 2001; Blum *et al.*, 2002; Quirk *et al.*, 2014). However, this potential advantage is unlikely to be realized at Lambir because the soils there are already sufficiently old and weathered that virtually none of the primary minerals remains, and only nutrient-poor secondary minerals, like kaolinite and iron oxides, are present (I. C. Baillie, pers. comm.). Thus, our results indicate that complex interactive effects of lithology, plant-resource economy, and mycorrhizal mediated plant–soil feedbacks could lead to the variation in relative dominance of EMF- vs AMF-hosting trees that we observed across lithological soil types in the Lambir forest.

#### Foliar traits as indicators of the drivers of mycorrhizal mediated plant–soil feedbacks

Most hypotheses addressing mycorrhizal mediated plant–soil feedbacks make predictions about trait variation of the leaf litter of AMF- vs EMF-hosting trees (see the Introduction section). There are no species-specific data on leaf litter at Lambir to test whether litter traits or decay rates vary by mycorrhizal type and whether there are interactive effects of soil type, but aggregated leaf litter from trees on clay decays significantly faster than litter from sandy loam at Lambir (Baillie *et al.*, 2006). Given that leaf traits often correlate with leaf litter traits associated with decomposability (Kurokawa & Nakashizuka, 2008; Freschet *et al.*, 2012) and that nutrient resorption often correlates with plant resource economies (Wright & Westoby, 2003; Kobe *et al.*, 2005), especially for evergreens (Zhang *et al.*, 2018), then the

same predictions concerning leaf litter should hold for leaf traits. Although the expected differences have not always been found (Koele *et al.*, 2012), some studies have shown that EMF-hosting tree species from both temperate and tropical lineages produced leaves with lower N and P concentrations than AMF-hosting species (Cornelissen *et al.*, 2001; Averill *et al.*, 2019). By contrast, using a data set including more leaf traits (13), we did not find %N and %P to differ between mycorrhizal types, but did find traits related to leaf structural properties and C concentration (SLA, LDMC, leaf tissue density (LTD), %C), nutrient ratios (C:P, N:P), and foliar  $\delta^{15}\text{N}$  to differ significantly. While not all traits varied significantly between mycorrhizal types, all but one did vary significantly between soil types in our study, indicating that in some systems foliar trait variation and plant resource economies can be more strongly constrained by lithological soil fertility than by mycorrhizal associations at the community scale.

To the extent that leaf traits respond to lithological drivers of soil fertility and indicate plant resource economies, they may be indicators of which are the important resources driving mycorrhizal mediated plant–soil feedbacks in a system. Mycorrhizal infection may directly affect access to and use of water (Auge *et al.*, 1992; Lehto & Zwiazek, 2011). However, the lack of significant variation among mycorrhizal types in foliar  $\delta^{13}\text{C}$ , a measure of plant water use efficiency (Ehleringer *et al.*, 1993), suggests that variation in access to soil moisture mediated by mycorrhizas is not a principle driver of the patterns that we observed. Along wider or other types of lithological gradients, other controls on fertility, along with nutrients, may affect the relative fitness advantage of contrasting mycorrhizal types. For example, the white sand heath forests of Borneo have lower forest basal area and are on soil types that are even more nutrient-depleted, acidic, and well-drained, compared to the sandy loam at Lambir (Davies & Becker, 1996; Proctor, 1999; Jucker *et al.*, 2018). We speculate that the relative fitness advantage of mycorrhizal types may not always vary monotonically with lithological fertility, as suggested in our study, but likely depends on the balance between multiple factors limiting tree growth in relation to mycorrhizal function.

In the forests of Northwest Borneo, soil P is hypothesized to be a key determinant of soil type-related floristic variation (Baillie *et al.*, 1987; Potts *et al.*, 2002). At Lambir total P, most of which is likely in organic forms given the low concentrations of orthophosphate, is particularly low in sandy loam (Baillie *et al.*, 2006; Kochsiek *et al.*, 2013). The foliar N:P > 30 for AMF-hosting trees on sandy loam suggests that AMF-hosting trees are strongly P-limited there (Güsewell, 2004). Moreover, foliar N:P was higher among AMF- vs EM-hosting trees on both soil types. These findings may be explained by the fact that, unlike EMF, AMF depend on free-living decomposers to release nutrients bound in organic matter, and AMF-hosting trees have been shown experimentally to benefit from a more inorganic P-economy (DeForest & Snell, 2020). By the time organic matter is mineralized, much of the P in it may have already been acquired by EMF (Liu *et al.*, 2018). If so, then one hypothesis is that enhanced access by EMF-hosting trees to organic P in the more recalcitrant leaf litter may increase their relative fitness advantage on this

lithologically infertile soil type, which could contribute to added niche space (Peay, 2016). Our results suggest this might be the case at Lambir. The total basal area increases with declining fertility across the four soil types, and 68% of the total per ha increase in basal area on sandy loam compared to clay can be attributed to EMF-hosting trees, whereas only 21% of that increase is due to AMF-hosting trees. Viewed through the lens of plant competition theory (Tilman, 1982), our findings suggest that the difference between AMF and EMF in the ability to access a key nutrient limiting the growth of their plant hosts effectively changes the nutrient supply rate for tree species of different mycorrhizal strategies. This would lead to different competitive outcomes, even in the same environment, than if these tree species were associated with the same mycorrhizal types. Evidence for this has been found in forests where depletion of mineralizable N from soil organic matter by EMF (Corrales *et al.*, 2016) and low soil N availability (Zhu *et al.*, 2018) were associated with dominance of EMF-hosting tree species. While trait-based and environmental feedbacks promoting a relative fitness advantage for EMF-hosting trees with conservative nutrient syndromes have been hypothesized by global scale studies (Averill *et al.*, 2019; Steidinger *et al.*, 2019), here we show edaphic effects on such fitness advantages that contribute significantly to local habitat specialization and distributional patterns of tree species at the community scale.

Based on leaf nutrient concentrations and ratios, we found stronger evidence for the importance of P than N in mycorrhizal associated plant–soil feedbacks in our system. However, the dramatically higher foliar  $\delta^{15}\text{N}$  of EMF- vs AMF-hosting species suggests that N may also be involved, but perhaps in ways that are not reflected in foliar C:N or %N. Uptake of N by plants and translocation within the plant are considered to cause minimal isotopic fractionation (Hogberg, 1997; Dawson *et al.*, 2002). To the extent that foliar  $\delta^{15}\text{N}$  indicates the  $\delta^{15}\text{N}$  of the N source used by plants (Houlton *et al.*, 2007) and ecosystem N-cycling processes (Robinson, 2001), the additive effects between soil and mycorrhizal type on foliar  $\delta^{15}\text{N}$  that we found may be explained by AMF- and EMF-hosting trees accessing pools of soil N with different isotopic signatures, regardless of the soil type on which they are growing. Interpretation of foliar  $\delta^{15}\text{N}$  alone is, however, complicated, partly because many microbial processes can fractionate N (Hobbie & Hobbie, 2008), and we have no information on the isotopic signatures of inorganic or organic soil N across soil types at Lambir. In contrast to our results in this tropical forest, previous work, mostly in temperate and boreal systems, has found that EMF-hosting plants have more depleted (lower) foliar  $\delta^{15}\text{N}$  than plants with AMF associations (Hogberg, 1997; Michelsen *et al.*, 1998; Hobbie & Colpaert, 2003; Craine *et al.*, 2009). One previous study on EMF-hosting species in lower latitude forests found, as we did, that EMF-hosting plants did not exhibit  $^{15}\text{N}$  depletion (Mayor *et al.*, 2015), but they did not account for soil type, which we show here and others have shown (Martinelli *et al.*, 1999) also strongly affects foliar  $\delta^{15}\text{N}$ . We suggest that foliar  $\delta^{15}\text{N}$ , in combination with data on the isotopic signatures of inorganic and organic soil N and  $\delta^{15}\text{N}$  of mycorrhizal tissues, may reveal key mechanisms involved in N-related mycorrhizal mediated plant–soil feedbacks. Moreover, together,

our results and those of Mayor *et al.* (2015), imply the intriguing possibility that differences in foliar  $\delta^{15}\text{N}$  among mycorrhizal types may vary latitudinally, which may be evidence of differences in mycorrhizal functioning, limiting nutrients, or relative dependence of N derived from N-fixing trees in tropical vs temperate systems.

### Biogeographical constraints on investigating the mycorrhizal composition of tropical forests

Since congeneric AMF- and EMF-hosting species were sampled on both sandy loam and clay, the patterns of trait variation that we observed are not only a result of phylogenetic signal, although we do not have enough statistical power to discern the relative influence of species turnover vs plasticity. While, in our study, the distribution of trait values between mycorrhizal types changed consistently with predictions from the Gadgil, 'short-circuit', and MANE hypotheses, it is important to note that all of the EMF-hosting species we sampled for traits belonged to the Dipterocarpaceae family. As a result, some of the observed leaf trait differences between EMF- and AMF-hosting trees may partly represent a 'Dipterocarpaceae effect'. There are fagaceous EMF-hosting genera in the Lambir plot (*Castanopsis*, *Lithocarpus*), but they account for only a small fraction of individuals and biomass, making the variance in EMF dominance at Lambir, and Borneo in general, inextricably linked to the Dipterocarpaceae. While cause and effect are hard to discern, it seems likely that the widespread success of the Dipterocarpaceae arises in part from their EMF associations, combined with their wide range of trait values allowing them to be competitive on soil types ranging from infertile to fertile. In order to evaluate the generality of our findings, future tests in tropical systems should prioritize forests where additional EMF host lineages are present. Such cases, are, however, limited, since outside of Southeast Asia, EMF host lineages are less diverse, and EMF-hosting species are abundant mainly in monodominant stands (McGuire, 2007; Peay, 2016; Fukami *et al.*, 2017).

### Conclusions

The composition of any forest community depends upon the relative fitness advantage of the alternative ecological strategies of the species available to colonize from a biogeographic species pool. Fundamental to those strategies are the coevolved associations that trees have with mycorrhizal fungi and the interplay of these associations with plant resource economics (Averill *et al.*, 2019). The relative fitness advantage of alternative mycorrhizal strategies is defined by their costs and benefits, which depend on the environment, but the key environmental factors, and at what scales they are most influential, are still poorly understood. At the global scale, the mycorrhizal composition of forests varies with climate, suggesting that temperature and precipitation shape the relative fitness advantage of alternative mycorrhizal symbioses (Steidinger *et al.*, 2019). Here, at the community scale, we show that the mycorrhizal composition of this southeast Asian rain forest depends on soil lithology, suggesting that soil fertility inherited from the parent material shapes the relative fitness

advantage of trees with different mycorrhizal associations. Our finding that functional trait variation of tree species is to some degree coordinated with mycorrhizal type reinforces the central role of mycorrhizal symbiosis in plant resource economics strategies. A comprehensive understanding of the mechanisms causing variation in these relative fitness advantages is critical to explaining the extensive local and global variation in mycorrhizal composition of forests and to accurately representing mycorrhizal–vegetation interactions in Earth system models predicting carbon and nutrient cycling.

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### Author Contributions

SER and KGP conceived the study; SER, MM, SJD, AI and ST collected the data; MW and SER analyzed the data; all authors contributed to the interpretation of the results and the writing of the manuscript.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Distribution of four lithological soil types in the 52-ha forest dynamics plot in Lambir Hills National Park, Malaysian Borneo.

**Fig. S2** Matrices showing correlations between species mean trait values for all pairs of functional traits for tree species in a mixed dipterocarp forest, Borneo.

**Fig. S3** Variation in tree species' functional traits associated with mycorrhizal symbiosis and lithological soil type in a mixed dipterocarp forest in Borneo.

**Methods S1** Supplemental methods section.

**Table S1** Variation in soil properties and elevation among the four lithological soil types at Lambir forest dynamics plot, Borneo.

**Table S2** Statistics for tests of variation in tree species' functional traits associated with mycorrhizal symbiosis and lithological soil type in a mixed dipterocarp forest in Borneo.

**Table S3** Factor loadings for the first two components of a principle components analysis of leaf traits of tree species in a mixed dipterocarp forest, Borneo.

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