Article title: Partitioning of soil phosphorus among arbuscular and ectomycorrhizal trees in tropical and subtropical forests

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Partitioning of soil phosphorus among arbuscular and ectomycorrhizal trees in tropical and subtropical forests

Abstract

Partitioning of soil phosphorus (P) pools has been proposed as a key mechanism maintaining plant diversity, but experimental support is lacking. Here, we provided different chemical forms of P to 15 tree species with contrasting root symbiotic relationships to investigate plant P acquisition in both tropical and subtropical forests. Both ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) trees responded positively to addition of inorganic P, but strikingly, ECM trees acquired more P from a complex organic form (phytic acid). Most ECM tree species and all AM tree species also showed some capacity to take up simple organic P (monophosphate). Mycorrhizal colonization was negatively correlated with soil extractable P concentration, suggesting that mycorrhizal fungi may regulate organic P acquisition among tree species. Our results support the hypothesis that ECM and AM plants partition soil P sources, which may play an ecologically important role in promoting species coexistence in tropical and subtropical forests.

INTRODUCTION

High plant diversity is a striking feature of almost all tropical and subtropical forests, and a long-standing goal in ecology is to explain how these numerous plant species are able to coexist despite competing for the same limited set of resources (Tilman 1982; Silvertown 2004). Classical niche theory hypothesizes that species diversity is promoted by trade-offs that result in species partitioning limiting resources, which requires that different species exhibit unique acquisition strategies for a resource in limited supply (Tilman 2004). In addition to specializing on different elemental resources, or specific resource supply ratios, species may also specialize in terms of their capacity to acquire different chemical forms of the same elemental resource (McKane *et al.* 2002).

Unlike temperate and arctic ecosystems, where nitrogen is generally considered the key limiting nutrient (Vitousek & Howarth 1991), phosphorus (P) is the nutrient thought to most strongly limit plant growth in lowland tropical and subtropical forests (Vitousek 1984; Condit *et al.* 2013). P limitation or co-limitation occurs in many other terrestrial ecosystems worldwide (Elser *et al.* 2007), and P has been suggested as the strongest predictor of plant species persistence (Wassen *et al.* 2005), diversity (Ceulemans *et al.* 2014) and net primary productivity (Cleveland *et al.* 2011). Soils in lowland tropical rainforests and subtropical evergreen forests are old and generally strongly weathered (Sánchez 1976), which leads to P depletion from the soil profile (Walker & Syers 1976). With considerable variation in P forms and amounts across and within sites, tropical and subtropical forest soils generally contain a high proportion of the total P in organic forms (typically 30-80%; Harrison 1987). It has been suggested that species distributions of lowland tropical plants are driven to a large extent by "plant-available" inorganic soil P (Turner & Engelbrecht 2011). Organic forms of soil P are also highly diverse, but dominated by a mixture of phosphate monoesters and phosphate diesters, with smaller amounts of phosphonates and organic polyphosphates (Turner &

Engelbrecht 2011). These increasingly complex organic P forms are thought to represent a gradient of decreasing availability to plants (Turner 2008).

Symbiotic associations with mycorrhizal fungi are an important strategy to enhance P acquisition by plants (Smith & Read 2008). Two of the main types of mycorrhizal association are formed by ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) fungi. In pure culture, many ECM fungi grow well on a range of inorganic and organic P forms and express extra-cellular phosphatase enzymes that break-down many P monoesters and diesters (Joner & Jakobson 1995; Plassard & Dell 2010). Expression of phosphatases is related to uptake of P from inositol phosphates in ECM birch plants (Joner & Jakobson 1994). Previous work has also provided strong evidence that ECM fungi have key roles in hydrolysing P from patches of organic matter, leading to significant improvements in plant nutrition (Perez-Moreno & Read 2001). A similar situation is seen in AM plants (Munkvold *et al*. 2004), although here the consensus is that AM fungi have greater affinity for uptake of inorganic forms of P (Moyersoen *et al.* 1998), which is determined by their possession of inorganic phosphate transporters and the absence of the genetic machinery for organic P uptake (e.g. Harrison *et al.* 2002). Within these two broad groups of mycorrhizal fungi, it is known that different fungal species have different affinities for P (Newbery *et al*. 1988; Alexander & Lee 2005), suggesting a key role of mycorrhizal fungal diversity, acting via P uptake, in regulating tropical and subtropical plant community composition.

It has been suggested that competing plants possess differential capacities to access this diversity of inorganic and organic P forms in soils, and that this contributes to soil P partitioning in P limited ecosystems (Turner 2008). P resource partitioning has been recently investigated among plant species in temperate peatlands (Ahmad-Ramli *et al*. 2013) and grasslands (Ceulemans *et al*. 2017), and these studies have demonstrated differences in plant growth on various P forms. In a lowland tropical system, seedling roots of ECM tree species expressed

twice the phosphatase activity as co-existing AM tree species, but had similar growth responses when provided with organic P in any form (Steidinger *et al.* 2015). Hence, how seedling performance responds to different P forms remains unclear in hyper-diverse tropical and subtropical forests. In this study, we experimentally investigated the capacity of tropical and subtropical tree species with different mycorrhizal associations to exploit P from different chemical forms of soil P. We hypothesized that plant species specialize on exploiting different soil organic P compounds, and that mycorrhizal fungi play a central role in partitioning organic P among plants. We predicted that ECM plants would have greater affinity for experimental additions of more complex organic P forms than AM plant species.

MATERIALS AND METHODS

Study sites and focal species

We conducted shade-house experiments around both Kabili-Sepilok Forest Reserve, Malaysia and Heishiding Nature Reserve, China, to determine the extent to which our findings can be generalized across different forest biomes. Both locations are characterized by an over-storey dominated by ECM tree species with limited phylogenetic diversity, and a diverse understorey dominated by AM tree species. Kabili-Sepilok Forest Reserve (5°49'N, 117°57'E) is a remnant of lowland tropical rainforest on the east coast of Sabah, Malaysia. The reserve is a 5543 ha patch of lowland dipterocarp, heath and mangrove forests ranging between 0 m and 170 m a.s.l. Mean annual rainfall is 2975 mm, with no month receiving less than 100 mm. Mean annual temperature ranges between 26.7 and 27.7 °C. April is generally the driest month and December or January the wettest; 45% of the annual precipitation falls from early November to mid-February. The Heishiding Nature Reserve (111°53'E, 23°27'N, 150-927 m a.s.l.) located in Guangdong Province of south China, consists of approximately 4200 ha of subtropical evergreen broad-leaved forest located on the Tropic of Cancer. The region has a

subtropical moist monsoon climate. Mean annual temperature is 19.6 °C and mean monthly temperatures range from 10.6 °C in January to 28.4 °C in July. Annual precipitation is about 1744 mm, occurring mainly between April and September (79% of annual rainfall), and a pronounced dry season lasts from October to March.

At each field site, eight common tree species with sufficient seeds or fruits available at the time of collection were selected for shade-house experiments (Table 1), and the mycorrhizal status of each species was determined by Brundrett (2009). We used experimentally germinated seedlings to evaluate their preference for soil P, using the following treatments: (1) two mycorrhizal types (ECM vs AM), and (2) five P forms (inorganic, simple organic, complex organic, mixture of the three or control with water alone).

Shade-house experiments

The shade-house experiment at Sepilok was conducted between November 2015 and May 2016, and the Heishiding experiment was conducted from September 2015 to April 2016. We collected fruits and seeds throughout the study sites between October and December 2014 at Heishiding and August 2015 at Sepilok. Seeds were surface-sterilized (1 min 70% ethanol, 3 min 2.63% NaOCl, 1 min 70% ethanol, 1 min distilled water) and kept in a refrigerator at 4 °C until late March 2015 (Heishiding) or germinated directly on the day of collection (Sepilok). Seeds were left to germinate in plastic boxes filled with autoclaved sterilized sand.

Three months after germination, we transplanted the seedlings into plastic pots (8 cm diameter × 10 cm height) containing sterilized field soil and sand, where the field soil was collected from a common forest understory location at the study sites and thoroughly mixed with sand (v 1:1). For each species, we randomly selected and transplanted seedlings into the pots (one seedling per pot), and then added 20 g live soil per pot which had been collected at a depth of 0-30 cm and at a distance of 0-2 m beneath adult trees of the focal species. The field

soil and sand mixture guaranteed homogeneous soil nutrients among all of the pots, and the live soil introduced soil microbes that were associated with adult trees of each species. One week after the transfer of seedlings into pots, we removed the seedlings that were dead or poorly growing due to injuries during the transfer, and replaced them with new seedlings.

To investigate different preferences for inorganic and organic soil P among the focal species with different mycorrhizal associations, we treated the seedlings of each focal species with five chemical forms of P, representing inorganic P (Na_3PO_4), simple organic P ($C_{10}H_{14}N_5O_7P$, adenosine monophosphate, AMP), complex organic P ($C_6H_{18}O_{24}P_6$, myo-inositol hexakisphosphate, phytic acid), and a mixture (1/3 Na_3PO_4 + 1/3 AMP + 1/3 phytic acid). A control treatment received an equal volume of water. Based on the background soil P concentration at each site, we added either 0.24 mg P per 1 g soil (Heishiding) or 0.27 mg P per 1 g soil (Sepilok) with 10 mL solution added to each pot, and the chemical treatments were repeated once every month for 6 months. The experimental units consisted of 12 blocks (replicates) for both sites, each block containing an entire treatment unit (i.e. 40 pots = 8 focal species × 5 P treatments; n = 480 pots per site). We randomly arranged the treatments within each block and separated all blocks by a distance of 0.5 m. We regularly watered the seedlings and monitored seedling heights every month. All seedlings were allowed to grow for 6 months and then harvested to determine their biomass. Seedlings of *Canarium album* at Heishiding were removed from subsequent sampling and analysis due to low overall survival.

At the end of the experiments, we thoroughly watered each pot and then carefully removed the seedlings. Each seedling was washed to remove any attached soil and separated into shoot and root for laboratory analysis. At the harvest, we collected fresh root and soil samples from each pot of the first 6 blocks for subsequent analysis. One 50-g soil sample was collected from each pot, air-dried and passed through a 2-mm mesh screen for nutrients analysis. We randomly collected 10 fine root fragments of 1 cm length from each seedling, and washed

them repeatedly with distilled water to remove any soil. Fresh root fragments were stored in centrifuge tubes with a piece of wet filter paper in the bottom, kept at 4 °C and transferred to a laboratory within two days for analysis of mycorrhizal colonization.

Laboratory analysis

We measured the shoot and root dry weights separately for each seedling after oven-drying at 60 °C for 72 hours. For each seedling of the 6 blocks from which root and soil samples had been collected, we sampled the oven-dried leaves for analysis of leaf N, P and K concentrations. Leaf or soil material was ground into a fine powder after removing any petiole or rachis. Total N is the total amount of N per unit of dry soil or leaf mass (mg g^{-1}) and was measured using the Kjeldahl method by a Foss Kjeltec^{TM} 2300 Analyzer Unit (Foss Tecator AB, Hoganas, Sweden). The analyses of total P and K were performed by inductively coupled optical emission spectrometry (Optima 2100DV; Perkin-Elmer, Waltham, MA, USA) after the samples were wet digested at 180 °C with conc. HNO_3 and HCl (1:3 v/v). The soil available P was analysed using the Olsen method (Carter & Gregorich 2008).

Mycorrhizal colonization of roots among focal species was quantified using the grid-line intersection method (Giovannetti & Mosse 1980). For AM species, the cleaned roots were stained with trypan blue, and then each root segment was examined under a stereomicroscope (SteREO Lumar.V12, Carl Zeiss, Germany) at 150× magnification to determine percent colonization by AM fungi (including hyphae, vesicles and arbuscules, McGonigle *et al.* 1990). We counted 200 intersections for each seedling and the colonization was calculated as the number of intersections where we observed mycorrhizas divided by total intersections. For ECM species, the cleaned fine roots were placed in a Petri dish filled with water, and assessed by counting all ECM root tips with the stereomicroscope at 10-60× magnification. Live roots (identified as swollen, without root hairs and covered by fungal mantles) were considered

ECM-colonized and were counted for 30-50 root tips per individual seedling. The colonization percentages were expressed as the number of ECM-colonized tips divided by total counted tips for each seedling.

Statistical analysis

We performed one-way analyses of variance (ANOVA) for each response variable, to determine differences among individual mean values of the five different P treatments for each focal species. To reveal the overall response of ECM and AM species to the various P treatments, we also combined all ECM and all AM species in one analysis, respectively. Seedling biomass of each focal species was scaled into 0 to 1 by dividing them with the maximum value of their own species, and then least significant differences multiple comparison post hoc tests (LSD) were performed again to detect significant differences in seedling biomass among the P treatments for both ECM and AM species. We calculated the relative growth responses of seedlings when treated with the three P forms (Na_3PO_4, AMP, and phytic acid) to compare them with the water treatment for each focal species. The mean total biomass in a specific P treatment was subtracted from, and then divided by, the mean total biomass in the water treatment. We then standardized the growth responses by dividing them by the sum of the three P treatments for each species, and the P preferences among different species were then visualized using the R package *bipartite* (Dormann *et al.* 2009).

We also constructed linear mixed-effects models to detect differences in seedling biomass between mycorrhizal types using the lme4 package (Bates *et al.* 2015) in R, where data from the two sites were combined together and study sites, focal species, their family names and blocks were treated as random effects and mycorrhizal type, P treatments, and their interaction were fixed effects in the models. We selected the best fitting model through sequential forward addition of the candidate variables that most improved Akaike information criterion (AIC),

starting with the main effects and then all potential two-way interactions. All statistical analyses were performed using R (version 3.2.0; R Development Core Team, Vienna, Austria).

RESULTS

Seedlings had the greatest total biomass when treated with inorganic P for five out of the nine ECM species (Fig. 1a) and for all of the six AM species (Fig. 1b), and these values were significantly greater than the total biomass of seedlings that were treated with water for all 15 study species. Seedlings in the mixture treatment also grew faster than those in the control treatment (Fig. 1). The positive response to added P in all species indicates that soil P is a limiting resource for plant growth at both sites. For the ECM species, the total seedling biomass of five focal species treated with phytic acid did not differ significantly from the inorganic P treatment, while the other four species had greater biomass in the phytic acid treatment than in the inorganic P treatment (Fig. 1a). Compared with the phytic acid treatment, ECM tree species had lower biomass when treated with AMP, except for *S. argentifolia*, but five species still produced significantly more biomass in the AMP treatment than in the control treatment (Fig. 1a). These results indicate that ECM tree species can effectively acquire P from complex forms (phytic acid) and have some capability to respond to simple organic P (AMP).

For the six AM species, total biomass did not differ between the phytic acid and control treatments, and was greater in response to the addition of inorganic P, alone in or mixture, than in either of these treatments. Half of the species had greater biomass in the AMP treatment compared with the phytic acid treatment (Fig. 1b), indicating preferences for inorganic and simple organic P for AM species. Although all AM species had greater biomass in the AMP treatment compared with the treatment with water, only *Cinnamomum porrectum* had a significant difference (Fig. 1b). The overall figures showed similar trends when we combined all ECM and all AM species together (Fig. 2). Comparing the overall responses to P treatments

for these two types of tree species with different mycorrhizal associations, the ECM species had the highest biomass with the phytic acid treatment (Fig. 2a) and the AM species had the lowest (Fig. 2b), while they had similar responses to the other three treatments (Fig. 2). We obtained similar results when we analysed root biomass alone rather than total biomass (Fig. S1), while height data were inconclusive because of high variance.

Although root colonization varied considerably among different species, the shade-house experiment yielded relatively high colonization when seedlings were treated with AMP, phytic acid, and water, while seedlings in the Na_3PO_4 treatment had the lowest root colonization in all cases (Fig. 3). The percentage colonization by mycorrhizal fungi was negatively correlated with soil extractable P in each pot. The estimated coefficient (± SE) of the linear mixed-effects model was -0.104 ± 0.016 ($P < 0.001$), with site, species, and block as random effects (Fig. S2). Among the linear mixed-effects models with total biomass as the dependent variable, the one including mycorrhizal types, P chemical treatments, and their interaction term as the fixed effects had the lowest AIC (Table 2), indicating that tree species with different mycorrhizal associations had different preferences for soil P forms, which could significantly influence seedling performance.

DISCUSSION

Our study comprised two independent, but closely linked, experiments on species derived from tropical and subtropical forests, and demonstrated striking preferences and partitioning of soil P forms between ECM and AM tree seedlings (Fig. 4), thus supporting the hypothesis put forward by Turner (2008). Previous studies found that fertilization with inorganic P often generates an increase in plant growth in both pot and field experiments (Burslem *et al.* 1994; Juliana *et al.* 2009), and stand-level productivity of Bornean forests correlates with extractable soil P concentrations (Paoli & Curran 2007). The overall patterns in plant biomass contrasted

markedly between AM and ECM tree species when supplied with different P forms, which is particularly apparent when expressed relative to performance in pots amended with water only (Fig. 4). Our study demonstrated that seedling growth of both AM and ECM host species could benefit from adding inorganic P to the pots. However, ECM species can also exploit organic P compounds, while AM species had only limited ability to acquire P from the simplest organic P compounds added (Fig. 4). This reflects the contrasting ability of ECM and AM fungi to enhance P acquisition, although the roles of mycorrhizal fungi were not investigated directly by controlling presence versus absence of mycorrhizal hyphae in our study. The primary mechanism by which AM fungi acquire soil P is to extend the volume of soil explored by short lived hyphae, with a diameter about one order of magnitude smaller than that of fine roots (Staddon *et al.* 2003). The hyphae of ECM fungi also greatly increase the P-absorbing surface (Rousseau *et al.* 1994), and additionally can mobilize some sorbed P through the release of organic anions and hydrolyse organic P using extracellular phosphatases (Plassard & Dell 2010). Hence, ECM trees have been broadly characterized as more capable of exploiting nutrients in organic forms than AM trees (Phillips *et al.* 2013). We also detected a slight promotion in seedling growth for all AM species when adding AMP compared with the water only treatment (Fig. 1b), which indicates that AM fungi may be able to exploit simple organic P.

Most tree species form symbiotic associations with AM fungi in tropical lowland forests and subtropical evergreen forests (Alexander 1989). By contrast, ECM fungi are restricted to fewer forest taxa such as the Dipterocarpaceae, Fagaceae, Myrtaceae and Caesalpinioideae (Alexander & Lee 2005). However, the dominant tree species in the canopy of forests in east and south-east Asia are usually ECM species, e.g. Dipterocarpaceae at Sepilok and Fagaceae at Heishiding. As ECM species have the capacity to exploit organic P, which is the dominant form of soil P at Sepilok and Heishiding, seedling survival and growth may be greatly enhanced

because of the presence of established host-specific ECM networks. Ectomycorrhizal fungi have also been found to have the enzymatic capability to access organic N directly from soil organic matter, which generates a competitive advantage over AM plants (Lindahl & Tunlid 2015; Shah *et al.* 2016). In our study, we used thoroughly mixed substrate in all pots at each site to ensure that soil N and K remained constant while only soil P changed among pots (Figs. S3-6).

Another mechanism for the ECM facilitation of local dominance is that ECM fungi could weaken the strength of negative plant-soil feedbacks driven by host-specific pathogens, and increase the survivorship rates of ECM seedlings around conspecific adult trees (Bennett *et al.* 2017). Although AM fungi were also been found to offer effective protection to tree hosts against soil pathogens (Liang *et al*. 2015), the amount of protection provided by ECM fungi is greater than that provided by AM fungi (Bennett *et al.* 2017). Herein, we used three-month seedlings to lessen the impact of soil pathogens on seedling performance, as pathogen-related mortality is believed to dominate in the first few weeks after germination (e.g. Maycock *et al.* 2005). This design ensured that we suppressed interference by other factors, to reveal the effect of different P forms on seedling performance.

Although P resource partitioning has been detected among plant species in temperate peatlands (Ahmad-Ramli *et al.* 2013), grasslands (Ceulemans *et al.* 2017), and lowland tropical forests (Nasto *et al.* 2017), these studies focused on limited numbers of species growing for a relatively short period (Ahmad-Ramli *et al.* 2013; Nasto *et al.* 2017) or added only two P forms (Ceulemans *et al.* 2017). Roots of ECM species have been found to have greater phosphatase enzyme activity than AM roots (Phillips & Fahey 2006; Steidinger *et al*. 2015), which could provide an explanation for the greater ability of ECM species to exploit organic P and their higher biomass compared to AM species in our study. A previous study of tropical montane tree seedling responses to inorganic and organic P sources failed to detect enhanced growth

rate of an ECM species compared to an AM species when limited to organic P, and a non-mycorrhizal tree species was the only species capable of exploiting phytate (Steidinger *et al.* 2015). This may due to the relatively short growth period of 3.5 months for the tree seedlings in the Steidinger *et al.* (2015) study, which may have been an insufficient time for the greater phosphomonoesterase activity of ECM species to translate into growth or nutritional benefits. Another possible reason is that only one species of each mycorrhizal type was tested by Steidinger *et al.* (2015), which may be insufficient to capture the typical pattern of response. For example, in our study although most species exhibited consistent results for the ECM and the AM types, in a few cases they did not: the ECM species *Shorea argentifolia* displayed greatest biomass in the simple organic P treatment (Fig. 1a), and the AM species *Ormosia glaberrima* and *Mangifera sp.* did not respond to organic P in any form. A final possibility is that patterns of nutrient limitation and soil resource partitioning are fundamentally different between the lowland tropical and subtropical study systems we examined and the tropical montane study system examined by Steidinger *et al.* (2015), as predicted by other data (Vitousek 1984). Nonetheless, combining the experimental evidence that non-mycorrhizal and mycorrhizal tree species exploit different fractions of the soil P pool (Steidinger *et al.* 2015), and that ECM and AM species have different preferences for inorganic and organic P forms (Fig. 2), reveals the important role of mycorrhizal fungi in governing patterns of P acquisition. This supports the hypothesis that partitioning of the varied array of possible chemical forms of P in soil potentially enhances the dimensions of the niche (Turner 2008), and facilitates plant species coexistence in tropical and subtropical forests.

While our results indicated that AM fungi specialized on inorganic P (Figs. 1b & 4), and ECM fungi can take-up both inorganic and organic forms of P (Figs. 1a & 4), the plant-mycorrhizal interactions could facilitate species coexistence by creating trade-offs in resource competition according to the contemporary niche theory (Chase & Leibold 2003; Peay 2016;

356 Jiang *et al.* 2017). One important possible trade-off is that acquisition of organic P through
357 ECM symbioses will cost increased carbon and nutrient investment from host plants (Jiang *et*
358 *al.* 2017). This trade-off could restrict ECM plants from competitively dominant and allow the
359 coexistence between ECM and AM trees. Another possible trade-off for mycorrhizal fungi to
360 promote coexistence is that ECM and AM trees specialize on different forms of soil organic P.
361 In this study, we only used two different types of organic P, and found that ECM trees
362 performed better with phytic acid compared to AMP, while AM trees preferred AMP (Figs 2 &
363 4). The soils at our study sites contain a high proportion of total P in organic forms that are
364 likely to be chemically highly heterogeneous, and this heterogeneity could increase the
365 diversity of soil resource axes and therefore the potential for coexistence (Peay 2016; Jiang *et*
366 *al.* 2017). However, detailed analysis on the fine-scale distribution of soil P fractions will be
367 needed to reveal their associations with mycorrhizal communities and tree distributions.
368 Mycorrhizal fungi have traditionally been considered to have relatively low specificity
369 between host plant and fungus (Hart *et al.* 2003; Peay *et al.* 2015). We did not investigate the
370 host specificity of ECM and AM fungi, but other studies have found evidence of host-
371 specificity of mycorrhizas (Kiers *et al.* 2000; Bidartondo *et al.* 2002; Liang *et al.* 2015), and
372 we detected interspecific variation in responses to P forms among ECM host species (Fig. 1a)
373 as well as among AM host species (Fig. 1b). These results suggest that there is potential
374 variation in the capacity to acquire organic P within as well as between ECM and AM species.
375 Other functional traits may be also important in regulating P acquisition strategies, even among
376 tree species belonging to a single mycorrhizal functional group. For example, tropical
377 dinitrogen (N_2)-fixing and non-N_2-fixing trees were found to exploit different chemical P
378 compounds, and the P partitioning among these species was related to trade-offs in their
379 investment in root phosphatases versus AM fungi (Nasto *et al.* 2017). The assembly of
380 mycorrhizal communities on plant roots is not random (Davidson *et al.* 2011), and Reinhart *et*

381 *al.* (2012) even detected a phylogenetic signal for AM colonization of roots and plant growth
382 responses to arbuscular mycorrhizal fungi. As plant species richness may increase phosphatase
383 activity in soil (Hacker *et al.* 2015), further experimental investigations are required to
384 determine the role of fungal diversity in shaping P uptake, as well as competitive interactions
385 within and among mycorrhizal types when supplied with different P forms. Indeed, species-
386 specific responses within our experiment may have been driven by differences in the diversity
387 and abundance of particular mycorrhizal taxa. Previous work in African tropical forests
388 suggests that identity of the dominant mycorrhizal fungi is related to soil P form and availability
389 (Newbery *et al.* 1988), and in a Southeast Asian forest, the distribution of mycorrhizal fungi is
390 also related to underlying soil properties and spatially autocorrelated up to 5 m (Peay *et al.*
391 2010). Given the heterogeneity of forest understory soils and spatial clustering of soil nutrients
392 in both tropical and subtropical forests, there is a need for future work to consider plant
393 diversity and soil P partitioning in a spatial context.

394 Although mycorrhizal fungi have been broadly found to exploit nutrients in organic
395 forms, especially for ECM fungi (Phillips *et al*. 2013; Lindahl & Tunlid 2015; Shah *et al.* 2016),
396 a recent paper has provided evidence that not all evolutionary lineages of ECM have retained
397 the potential to degrade soil organic matter (Pellitier & Zak 2018). Apart from symbiotic
398 association with mycorrhizal fungi, higher plants could also acquire P from organic
399 compounds through other mechanisms, including the synthesis of phosphatase enzymes by
400 plant roots, secretion of organic anions, and formation of proteoid roots (Richardson *et al.*
401 2005). For example, agroforestry tree species have been demonstrated to produce phosphatase
402 directly and enhance phosphatase activity in their rhizosphere (George *et al.* 2002), which
403 catalyze the release of inorganic phosphate from organic forms. A variety of free-living fungi
404 (Tarafdar *et al.* 1988) and bacteria (Satyaprakash *et al*. 2017) in the soil also have the capacity
405 to solubilize P which then becomes available for plants to scavenge. All these mechanisms

represent opportunities for plants to acquire limited soil P, and provide the scope to enhance niche dimensionality for coexisting species.

In summary, our study demonstrated that coexisting plants partition soil P through symbiotic associations with different mycorrhizal fungi (Fig. 4), which may reduce competition between tree species with different mycorrhizal associations and provide an additional mechanism to explain the coexistence and distribution of plant species in tropical and subtropical forests. Importantly, P is a key nutrient controlling ecosystem productivity (Elser *et al.* 2007), plant species diversity (Ceulemans *et al.* 2014), and occurrence of endangered plant species (Wassen *et al.* 2005; Fujita *et al.* 2014), especially in the ecosystems where productivity is highly limited by the availability of soil P including tropical and subtropical forests.

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602 **Table 1** The list of focal tree species for the shade-house experiments.

Site	Focal species	Family	Mycorrhizal type	Species code
Sepilok, Malaysia	*Shorea multiflora*	Dipterocarpaceae	ECM	SMUL
	Shorea argentifolia	Dipterocarpaceae	ECM	SARG
	Shorea parvifolia	Dipterocarpaceae	ECM	SPAR
	Dryobalanops lanceolata	Dipterocarpaceae	ECM	DLAN
	Parashorea tomentella	Dipterocarpaceae	ECM	PTOM
	Vatica sp.	Dipterocarpaceae	ECM	VASP
	Mangifera sp.	Anacardiaceae	AM	MASP
	Adenantera pavonina	Fabacaeae	AM	APAV
Heishiding, China	*Castanopsis fissa*	Fagaceae	ECM	CFIS
	Castanopsis faberi	Fagaceae	ECM	CFAB
	Engelhardtia fenzelii	Juglandaceae	ECM	EFEN
	Schima superba	Theaceae	AM	SSUP
	Cryptocarya concinna	Lauraceae	AM	CCON
	Cinnamomum porrectum	Lauraceae	AM	CPAU
	Ormosia glaberrima	Fabaceae	AM	OGLA
	Canarium album	Burseraceae	AM	CALB

603

Table 2 Results of the best linear mixed-effects model with the lowest Akaike information criterion testing for the effect of added chemical forms of soil phosphorus on seedling total biomass in the shade-house experiments.

Fixed effects	Estimate	SE	*t*	*P*
Intercept	0.968	0.401	2.414	**0.029**
Mycorrhizal type (ECM)	-0.587	0.511	-1.148	0.282
Na_3PO_4	0.389	0.033	11.880	< **0.001**
AMP	0.154	0.033	4.713	< **0.001**
Phytic acid	-0.007	0.033	-0.225	0.822
Mixture	0.203	0.033	6.225	< **0.001**
Mycorrhizal type : Na_3PO_4	-0.058	0.042	-1.382	0.167
Mycorrhizal type : AMP	0.076	0.042	1.788	0.074
Mycorrhizal type : Phytic acid	0.440	0.042	10.395	< **0.001**
Mycorrhizal type : Mixture	0.129	0.042	3.053	**0.002**

608 **Figure Legends**

609 **Figure 1** The effects of added chemical forms of soil phosphorus on seedling growth of tree
610 species with (a) ectomycorrhizal (ECM) and (b) arbuscular mycorrhizal (AM) associations in
611 a tropical rain forest and a subtropical evergreen broad-leaved forest. Bars show mean total dry
612 biomass ± SE of each focal species in the shade-house experiments, when seedlings were
613 treated with an inorganic phosphorus form (Na_3PO_4), a simple organic P form ($C_{10}H_{14}N_5O_7P$,
614 adenosine monophosphate, AMP), a complex organic P form ($C_6H_{18}O_{24}P_6$, myo-inositol
615 hexakisphosphate, phytic acid), a combination of these three forms (1/3 Na_3PO_4 + 1/3 AMP +
616 1/3 phytic acid, mixture), and a control treatment (Water). Different lowercase letters represent
617 significant differences among treatments ($P < 0.05$) based on one-way ANOVA.

618 **Figure 2** The overall effects of added chemical forms of soil phosphorus on seedling growth
619 of ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) tree species. Bars show mean
620 total dry biomass ± SE of each type of focal species in the shade-house experiments (n = 108
621 and 72 with each P treatment for the ECM species and the AM species, respectively).

622 **Figure 3** Fine root colonization among different phosphorus treatments for tropical and
623 subtropical tree species with (a) ectomycorrhizal (ECM) and (b) arbuscular mycorrhizal (AM)
624 associations in shade house experiments. Experimental treatments and abbreviations are as in
625 Fig. 1.

626 **Figure 4** Different phosphorus (P) preferences among ectomycorrhizal (ECM) and arbuscular
627 mycorrhizal (AM) plants promote the coexistence of tree species in tropical and subtropical
628 forests. Lines depict observed responses in tree sapling biomass to the three P forms used in
629 the shade-house experiments, with line thickness proportional to growth response relative to
630 that observed when plants were supplied with water only. Widths of grey boxes represent the
631 overall preferences to different P forms for all ECM plants (upper panel) and all AM plants
632 (lower panel). The corresponding species name of the 4-letter codes are shown in Table 1. Note

633 that four out of the six AM tree species (SSUP, CCON, CPOR and APAV) had slightly lower
634 total biomass when grown with phytic acid compared to water, hence the absence of lines in
635 these combinations.

Figure 1 (a)

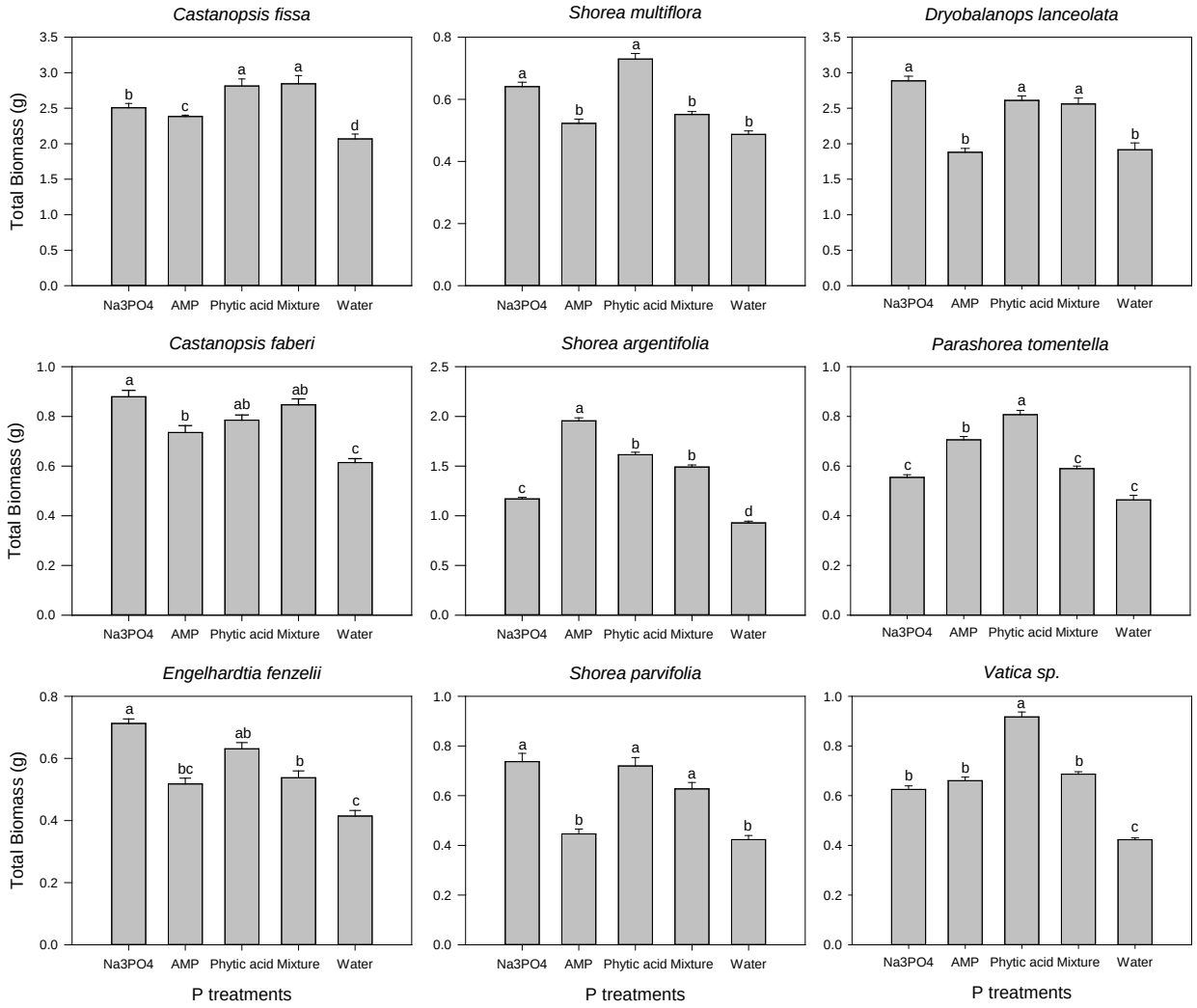
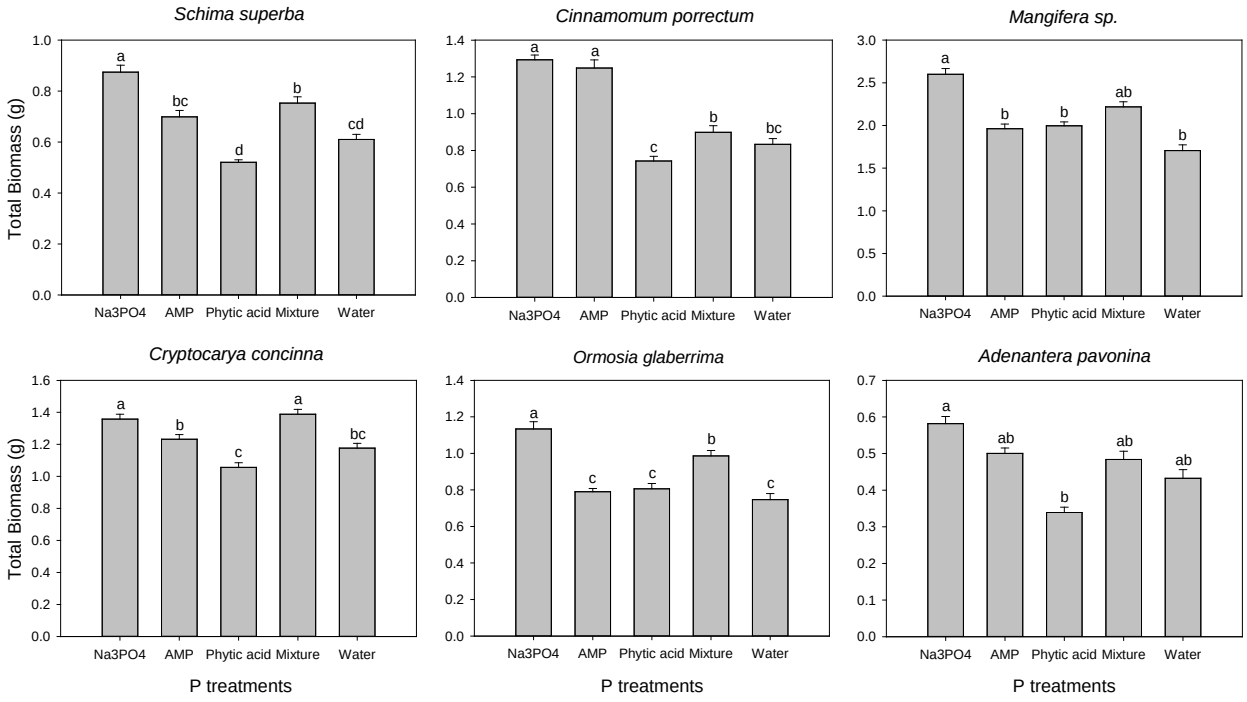


Figure 1 (b)



640 **Figure 2**

641

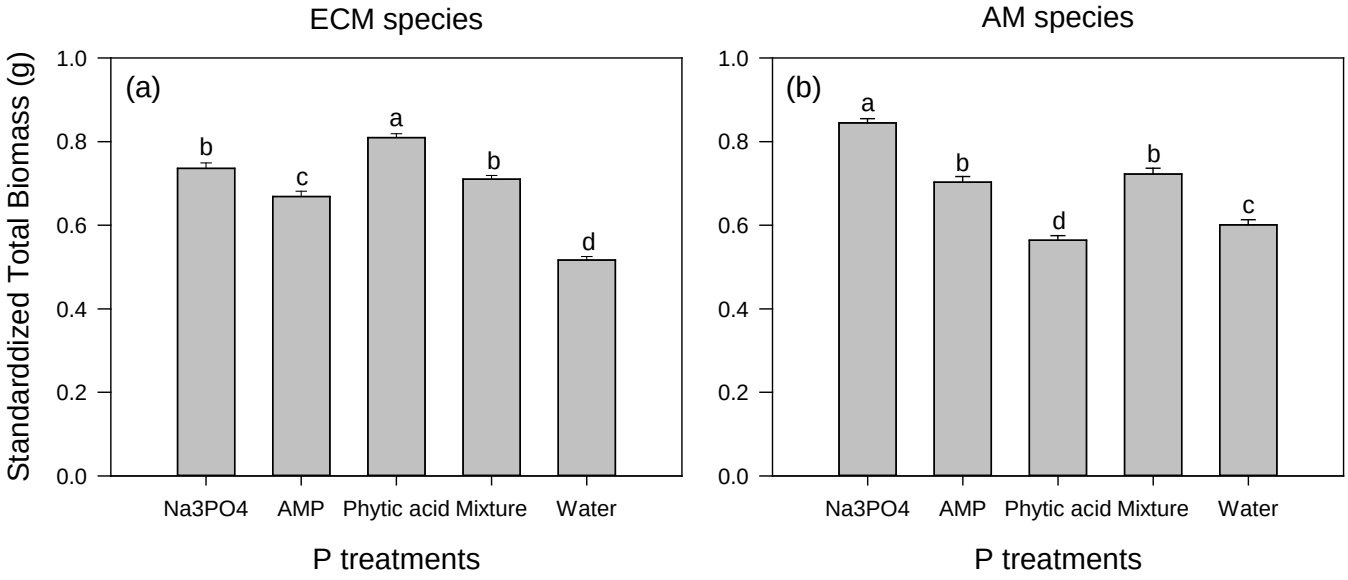
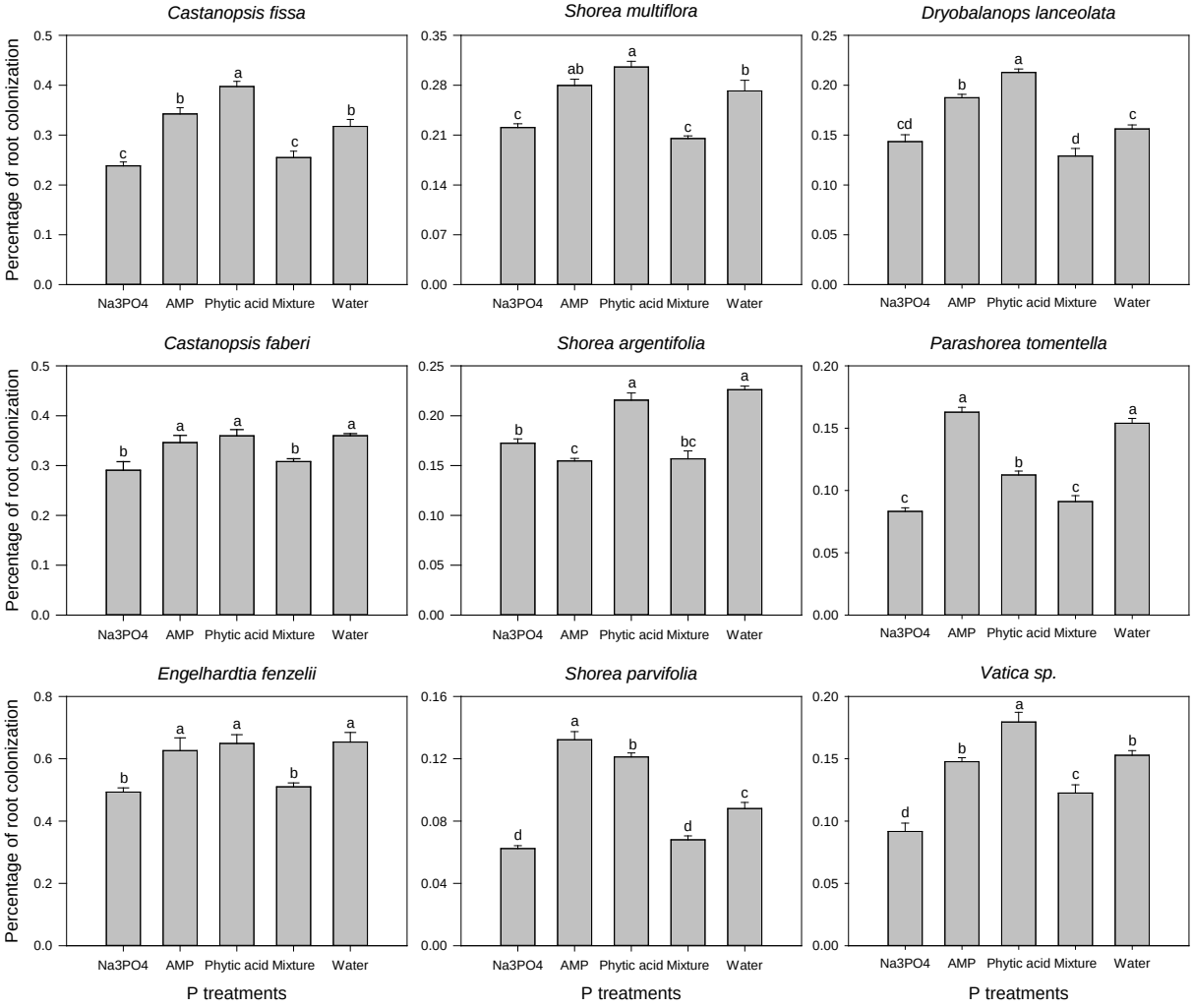


Figure 3 (a)



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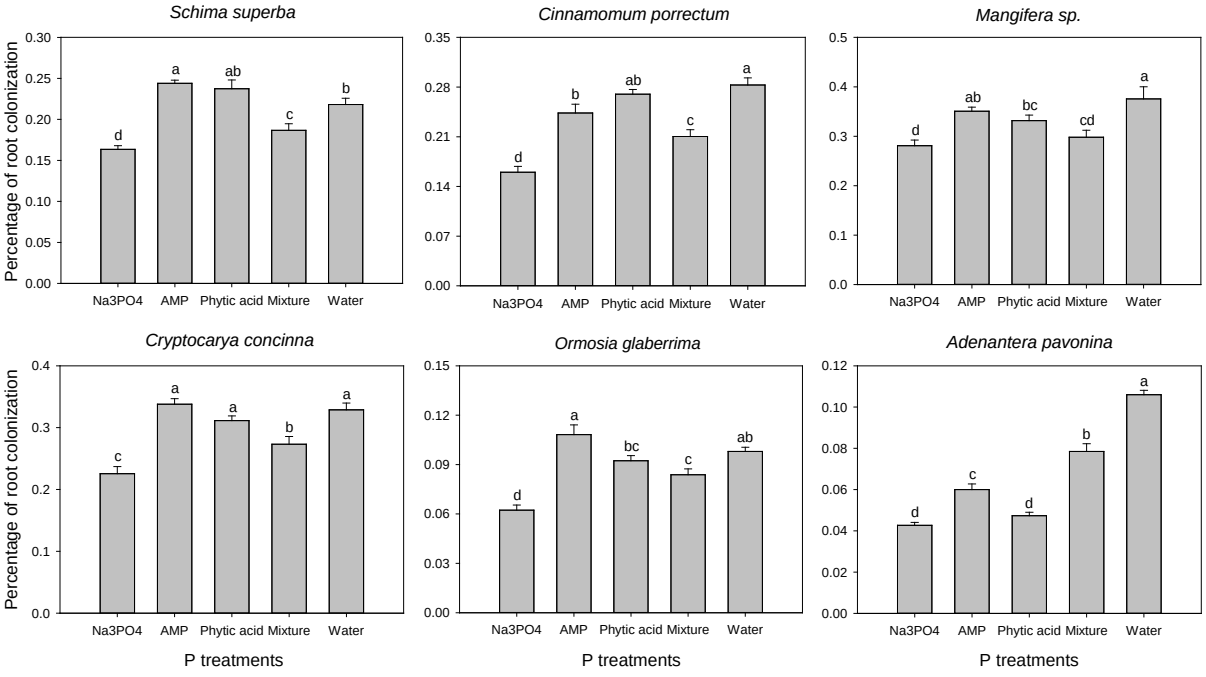

646 **Figure 4**
647