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THE PLASTICITY OF FUNCTIONAL TRAITS IN THE DIPTEROCARPS OF
BORNEO

by

Ju Ping Chan

A THESIS

Presented to the Faculty of
The Graduate College at the University of Nebraska
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Under the Supervision of Professor Sabrina E. Russo

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THE PLASTICITY OF FUNCTIONAL TRAITS IN THE DIPTEROCARPS OF BORNEO

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University of Nebraska, 2016

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Plasticity plays an important role in the adaptation of sessile organisms like plants to the environment. Plants have been shown to respond plastically in heterogeneous environments, with plants originating from more resource-diverse environments thought to display greater plasticity. There is also evidence that fast-growing species show greater plasticity, as acquisition of resources from resource flushes is greatly aided by faster adaptations. We tested these theories in a Bornean tropical rain forest among three soil specialization groups (clay specialists, sandy loam specialists, and generalists) using two treatments of soil (clay versus sandy loam) and two treatments of light (high versus low). Here, I address four research questions: (1) Do tree species with different soil specializations exhibit differences in the plasticity of functional traits and growth rates? (2) Does the magnitude of plasticity depend on the type of resource? (3) Do functional traits and growth rates vary in the magnitude of plasticity exhibited? (4) Is plasticity in functional traits correlated with plasticity in growth rates? Overall the results show that clay specialists and generalists are more plastic than their sandy loam counterparts. Second, on average plasticity due to light was greater than plasticity due to soil. Third, growth rates were generally more plastic than functional traits. And finally, the plasticity of functional traits and growth rates were positively correlated. These findings add important insights to the plastic response of long-lived tree species to the environment, where much remains to be explored.

Dedication

To my family, friends, and adviser who never stopped believing in me, even when I stopped believing in myself.

Acknowledgment

Many individuals contributed to this thesis, for which I shall always be grateful. I must first thank my adviser, Sabrina Russo, who gave me the opportunity to obtain a graduate education at one of the best universities in the world; and near limitless patience with me as I struggled to complete my studies. I wish to also thank my committee members Diana Pilson and John DeLong, who gave a helping hand in experimental design and data analysis when it was asked. My further gratitude to my fellow graduate students, especially Melissa Whitman, Nohemi Huanca-Nunez, Jin Yi, Shivani Jadeja, and Benjamin Reed, who all contributed ideas, questions, and input with earnestness. My thanks to Lambir Hills National Park Warden Januarie Kulis and the amiable staff from Sarawak Forestry, whose help was instrumental in conducting this research. Further gratitude to the numerous field and lab assistants who helped out with the labor-intensive work, especially Lela Ali, Amos Lim Zhen Yu, Scholena Leon, Dylan Dingbaum, and Trang Hoang. A special thanks to my neighbors John Grabouski and Kay Graber, who made me feel like part of the community, and helped push me to the finish line. And last but not least, to my family back home in Malaysia, who still made their love known to me despite the increased distance and time of separation. To all others who are not mentioned, I too thank you, although I have not listed you out explicitly, know that your contribution to my work is not forgotten, and that I shall gratefully accept any rebuke you may have for me if I should ever forget.

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1. Introduction

Plants show variable phenotypic responses to heterogeneous environments (Bazzaz 1979). Such phenotypic plasticity is the change in the phenotype due to the effect of the environment upon the genotype (Bradshaw 1965; Schlichting 1986). Since terrestrial plants are sessile, phenotypic plasticity is a particularly important mechanism allowing them to accommodate environmental shifts, and the magnitude of plasticity influences the range of environmental conditions in which a species can persist. While there are instances in which changes in trait values due to phenotypic plasticity result in non-favorable changes from seemingly optimum trait values (Ghalambor et al. 2007) phenotypic plasticity has presumably evolved as a mechanism to maximize fitness in response to a spatially and temporally heterogeneous environment (Sultan 2000). Despite the ecological importance of phenotypic plasticity among plants, the literature is sparse in regards to evaluating plasticity of long-lived tree species in the field.

It is well established that spatially or temporally variable environments select for phenotypic plasticity (Bell and Sultan 1999; Sultan 2000), and so, generalist species that occupy multiple habitat types should have greater capacity for phenotypically plastic response to variation in the environment, as compared to habitat specialists. However, perhaps less well examined is the idea that habitats with plentiful resources in which species with fast-growth strategies are favored, may also select for greater plasticity. This may happen because individuals of fast-growing species should be tuned to respond quickly to take advantage of increased resource availability (Alpert and Simms 2002), and indeed this plasticity likely is a key component of their capacity for fast growth. In

his plant strategy theory (Grime 1977) included greater plasticity as a characteristic of the fast-growing exploitative competitors in contrast to the more conservative stress-tolerant strategy (Grime 2006). This is especially evident for early successional species, for which survival is contingent on fast growth (Kobe et al. 1995), and thus, the need to capture resources in heterogeneous environments as quickly as possible (Bazzaz 1979).

Plant phenotypes are often quantified based on functional traits, which are measurable properties of species that have consequences for the functioning of the plant in its environment. While most studies have focused on the plasticity of singular functional traits, plasticity in individual traits does not necessarily translate into increased growth or survival. Instead, phenotypic plasticity should be analyzed in a multi-trait framework, since phenotypic integration within the individual constrains plasticity and influences whole plant performance (Schlichting 1986; Pigliucci 2003; Valladares et al. 2007). For the purpose of this research, we have introduced a hierarchical framework of functional traits reflecting the effects of phenotypic integration of individual growth rates (Figure 1).

In this study, we assessed whether phenotypic plasticity differs among tree species with different habitat specialization patterns and how this plasticity co-varies with growth rate in a hyper-diverse Bornean rain forest in Lambir Hills National Park. This forest is characterized by high beta diversity caused by dramatic floristic variation among soil types, with most tree species exhibiting specialization on particular soil types along a fertility gradient from the less fertile, well-drained sandy loam soil to the more fertile, moister clay soil (Davies et al. 2005). There is also corresponding variation in

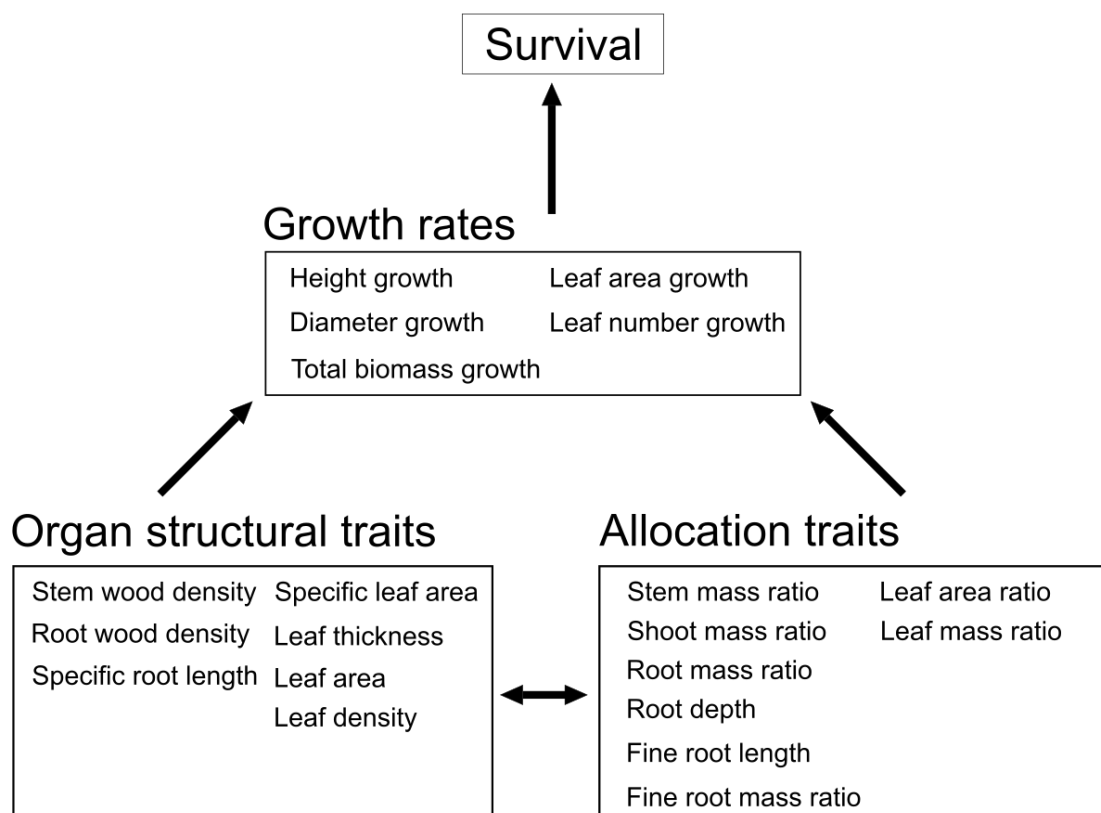


Figure 1: Hierarchy of all functional traits and growth rates. Organ structural traits and allocation traits interact in complex ways that influence growth rates, which ultimately influences survival.

demographic rates of species with contrasting soil specialization, with clay specialists having faster growth rates and higher mortality rates than sandy loam specialists (Russo et al. 2005). To quantify phenotypic plasticity in response to above and below-ground resource availability, we used a reciprocal transplant experiment in which seedlings of 13 dipterocarp tree species (Table 1) were grown directly from seed in experimental plots in high and low light environments and in clay and sandy loam soil in natural forest for approximately three years. The study species are all shade-tolerant canopy trees, and represent five clay specialists, six sandy loam specialists, and two generalists (species with no soil habitat preference), arrayed in congeneric species sets (in which species in

the same genus are represented in each soil specialization group) for all but one genus. We quantified phenotypic plasticity in 17 functional traits and six measures of growth rate (Table 2) on approximately three year old seedlings for each species. Because we focused on seedlings, our study does not address ontogenetic plasticity. Moreover seeds in our experiment were half-siblings from several mothers but with unknown fathers. While they were allocated to seedling plots so that the same genotypes for each species were represented in each treatment combination, the genotype of each seedling was unknown. Phenotypic plasticity was thus assessed with respect to species' soil association, not species or genotype. We addressed four research questions: (1) Do tree species with different soil associations exhibit differences in the plasticity of functional

Table 1: Range of sample sizes of seedlings for each species across the four treatment combinations. Some treatment combinations had no seedlings (2 cases, DIPTPA in sandy-loam + high light, and HOPEBE in sandy-loam + clay).

Species	Code	Soil habitat preference	Sample size
<i>Anisoptera grossivenia</i> Slooten	ANI2GR	Generalist	6-8
<i>Dipterocarpus acutangulus</i> Vesque	DIPTAC	Generalist	3-9
<i>Dipterocarpus globus</i> Vesque	DIPTGL	Sandy loam	6-8
<i>Dipterocarpus palembanicus</i> Slooten	DIPTPA	Clay	0-6
<i>Dryobalanops aromatica</i> C.F.Gaertn.	DRYOAR	Sandy loam	3-8
<i>Dryobalanops lanceolata</i> Burck	DRYOLA	Clay	6-7
<i>Hopea beccariana</i> Burck	HOPEBE	Sandy loam	0-7
<i>Hopea dryobalanoides</i> Miq.	HOPEDR	Clay	1-9
<i>Shorea beccariana</i> Burck	SHORBE	Sandy loam	6-8
<i>Shorea laxa</i> Slooten	SHORLA	Sandy loam	3-8
<i>Shorea macrophylla</i> (de Vriese) P.S.Ashton	SHORML	Clay	6-8
<i>Shorea xantophylla</i> Symington	SHORXA	Clay	2-9
<i>Vatica nitens</i> King	VATINT	Sandy loam	6-8

traits and growth rates with respect to variation in insolation and soil type? (2) Does the magnitude of plasticity depend on the type of resource (soil type or light)? (3) Do functional traits and growth rates vary in the magnitude of plasticity exhibited? (4) Is plasticity in functional traits correlated with plasticity in growth rates?

If plasticity in response to variation in light and soil resource availability is an important mechanism determining differential performance of tree species in preferred

Table 2: Functional traits analyzed, with abbreviation and units of measurement.

Trait	Abbreviation	Unit of measurement
Growth rate traits		
Absolute growth rate of lamina area	agr-LamArea	cm ² /year
Absolute growth rate of number of leaves	agr-NLeaf	No. leaves/year
Absolute growth rate of total biomass	agr-TotalBm	g/year
Relative growth rate of stem diameter	rgr-Diam	mm/mm-year
Relative growth rate of height	rgr-Height	cm/cm-year
Relative growth rate of number of leaves	rgr-NLeaf	No. leaves/No. Leaves-year
Organ structural traits		
Lamina area	LamArea	cm ²
Lamina density	LDen	g/cm ³
Lamina thickness	LamThick	mm
Root wood density	RDden	g/cm ³
Specific leaf area	SLA	cm ² /g
Specific root length	SRL	m/g
Stem wood density	SDden	g/cm ³
Allocation traits		
Fine root length	FRL	cm
Lamina area ratio	LAR	cm ² /g
Lamina mass ratio	LMR	-
Root depth	RDepth	cm
Root mass ratio	RMR	-
Shoot mass ratio	ShMR	-
Stem mass ratio	SMR	-

versus non-preferred soil types, then plasticity should vary significantly between sandy-loam specialists, clay specialists, and generalists. We expected that clay specialists and generalists would show greater trait plasticity compared to sandy-loam specialists. It is well-established that variable environments often select for plasticity (Bell and Sultan 1999), and so it is reasonable that generalists, which have similar abundance across a range of soil habitats, would have greater plasticity. However, we reasoned that fast growth should select for greater plasticity because it would allow individuals to take advantage of resource flushes, making them effective exploitative competitors (Grime 2006). This is especially evident for early successional species, for which survival is contingent on fast growth (Kobe et al. 1995) and thus, the need to capture resources in heterogeneous environments as quickly as possible (Bazzaz 1979). Since clay specialists grow faster than sandy loam specialists (Russo et al. 2005), we accordingly expected them to have greater plasticity. We also predicted the magnitude of plasticity to vary between different functional traits and to respond differently to variation in light versus soil resource availability. We reasoned that not all traits would respond the same way to differing levels of resources (Valladares et al. 2007) specifically, that leaf functional traits should display greater plasticity in response to variation in irradiation compared to soil resources, whereas stem and root traits should show greater plasticity in response to soil resources than irradiance. Furthermore, we also predicted that species showing greater plasticity in functional traits should also have greater plasticity in growth across the experimental treatments.

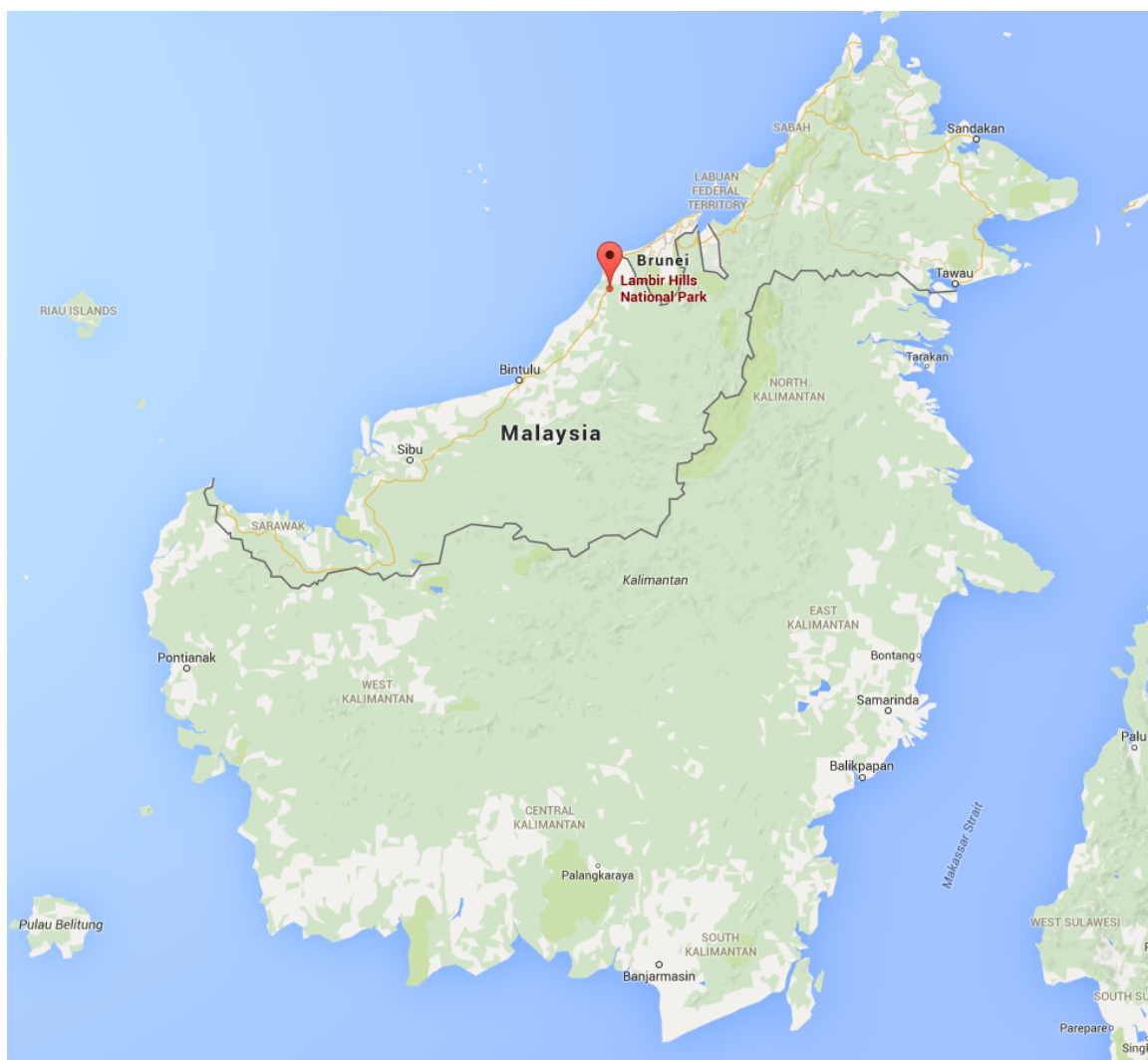


Figure 2: Map of Borneo, indicating Lambir Hills National Park, which is located in the Malaysian state of Sarawak on the northern part of Borneo island.

2. Methods

2.1. Study system

Lambir Hills National Park (Lambir) is located in north-west Borneo, in the Malaysian state of Sarawak (Figure 2, 4°20' N, 113°50' E). Lambir is a hyper-diverse forest with 1152 tree species identified in a 52-ha forest dynamics plot. It experiences ca. 3000 mm of annual rainfall with daily temperatures ranging from 24 to 32 °C (Lee et al. 2002).

Tree species in the Dipterocarpaceae dominate the forest, comprising 42 % of the basal

area and 16 % of all trees ≥ 1 cm in diameter at breast height (DBH) (Lee et al., 2002).

Low fertility sandy loam and comparatively high fertility clay soil are the extremes of the edaphic gradient found within the 52-ha plot in Lambir (Baillie et al. 2006).

2.2. Experimental design

To quantify the differences in plasticity of functional traits and growth rates in response to variation in light and soil resources, we established a reciprocal transplant experiment with 13 species of dipterocarp seedlings representing six genera, 11 of which specialize on clay or sandy loam, plus two generalist species (Table 1). Seeds were collected in and near Lambir in January 2010 during a general fruiting event from 1-5 mother trees of each species, depending on the availability of seeds. Seeds of each species were sown directly into 24 experimental plots established in the forest on clay or sandy loam under high or low light conditions (six plots per soil type by light treatment combination). Plots in the high light treatment had open canopies above them resulting in greater illumination, compared to the low light plots, which were under closed canopy and had no noticeable canopy gaps. Each 5 x 5 m plot was divided into 225 33 x 33 cm subplots. One seed was sown into each subplot, although not all subplots were used, and species were randomly assigned into subplots. Seeds germinated and seedlings grew under natural conditions without irrigation. Because seedlings were grown from seeds that germinated and grew directly in forest plots, and were not transplanted as seedlings, their root systems were allowed to grow naturally, rather than being constrained by potting.

Seedlings were censused in February 2010, February 2011, and June 2012, and harvested over the period of June to September of 2012. At each census and at the final

harvest, stem diameter, height, and leaf number of surviving seedlings were measured to estimate growth rates. A permanent mark was painted on the stem just above ground level as a reference point for diameter and height measurements. Seedling stem diameter was measured in two perpendicular directions using a vernier caliper at the upper edge of the mark, and then averaged to obtain a single diameter. Seedling height was measured as the vertical, straight-line distance from the upper edge of the mark to the base of the apical bud. The total number of living leaves was counted on each seedling at each census. A total of 319 seedlings were eventually harvested after 28 to 38 months, with differences among seedlings in the experimental duration owing to differing phenology of seed production and reseeded due to mortality.

2.3. Quantification of functional traits

Quantification of twelve functional traits (Table 2) was based upon commonly used procedures (Cornelissen et al., 2003). Each leaf lamina was cut from the petiole, and the stem was cut at ground level. Laminas and stems were placed on ice until processing for the quantification of functional traits. We used PVC pipes with a sharpened edge (ranging from 15 cm to 50 cm in diameter, depending on the size of the seedling) as corers to remove the soil core and seedling root system. Root systems and adhering soil were returned to the field station, where they were gently washed with water to separate the roots from the soil.

Fresh laminas were gently cleaned of debris and epiphylls. Lamina thickness was measured with a micrometer at three locations, avoiding secondary veins, on each of three laminas on each seedling, which were averaged as mean lamina thickness for each

seedling. All leaf laminae on a seedling were scanned (Canon LiDE 110), and the images were analyzed with ImageJ (Schneider et al. 2012) to estimate the area of each lamina. The volume of each lamina was calculated by multiplying lamina area by mean lamina thickness. After oven-drying at 60°C for three days, the dry weight of each lamina was recorded. The specific leaf area (SLA) was calculated as fresh area divided by dry weight. Lamina density was calculated by dividing lamina mass by lamina volume. Leaf-level measurements were averaged to obtain seedling-level means of each trait. The total leaf area and total leaf mass per seedling were obtained by summing the areas (or dry masses) of the individual leaves of each seedling.

Rooting depth was estimated by measuring the straight-line length from the stem-root junction at ground level where the stem was cut, to the tip of the longest unstraightened tap root. For each seedling, all fine roots (< 2mm in diameter) were cut from the root system and scanned (Canon LiDE 110 scanner), and images were processed with WinRhizo 2013e (Regent Instruments, Canada) using a customized calibration specific to the images produced by the scanner to estimate the length of fine roots. The scanned fine roots were oven dried at 60°C for 3 days before measuring their dry mass. Specific root length was calculated as total length divided by dry mass of fine roots.

Measurement of wood density was done on fresh seedlings on 5 cm sections towards the base of the main stem and the top of the tap root. The bark was removed with a scalpel, and the remaining secondary xylem was submerged into water for approximately 30 minutes before obtaining the volume of the sections by measuring the weight of water displaced when the section was submerged, according to Archimedes'

Principle. All stem and root components were oven-dried at 60°C for 3 days, and density was calculated as dry mass over fresh volume of each section. A few of the stems had been oven-dried before their volume was obtained. We immersed those samples in water for half-an hour to rehydrate the samples before applying the same fluid displacement measurements. The correlation between the re-hydrated stem and its dried state were significant ($cor = 1.00, p < 0.01$), as was that between the re-hydrated root sections versus their dried state ($cor = 0.89, p < 0.01$). We checked the correlation between the re-hydrated and dried mass for two hour immersions (stem volumes, $cor = 0.96, p < 0.01$; root volumes, $cor = 1.00, p < 0.01$). and 24 hour immersions (stem volumes, $cor = 1.00, p < 0.01$; root volumes, $cor = 1.00, p < 0.01$), and found all the volume measurements to also be significantly correlated. As there was no significant disadvantage for immersing the samples for 30 minutes versus 24 hours, we chose the lesser period of immersion.

The total dry masses of stems and roots were estimated by summing the weights of all of the masses of all components of the stem and root systems, respectively. Total seedling biomass was estimated by summing the dry masses of all components of leaf, stem, and root systems. Lamina area ratio (LAR) was calculated by dividing the total lamina area of a seedling by its total dry biomass; lamina mass ratio (LMR) was calculated as total lamina dry mass of a seedling divided by its total dry biomass. The root mass ratio (RMR) for each seedling was calculated by dividing the dry mass of the roots by the total dry mass of the plant. The fine root mass ratio (FRMR) for each seedling was calculated by dividing the dry mass of the fine roots by the total dry mass of the plant. We also calculated the shoot mass ratio (ShMR) by dividing the aboveground

biomass to the biomass of the entire plant, as well as the stem mass ratio (SMR) through dividing stem biomass to the biomass of the entire plant.

2.4. Growth rate calculations

We calculated relative growth rates (RGR) for each seedling via the formula (Hoffmann and Poorter 2002) $\{\ln(W_i) - \ln(W_f)\} / (t_i - t_f)$, with W_i and W_f being either height, diameter, or leaf number in the initial and final censuses respectively. The denominator is the time interval in years in between the first census in 2010 (t_i) and final census in 2012 (t_f). We calculated the absolute growth rate for each seedling as $W_h / (t_s - t_h)$, where W_h is the leaf area, leaf number, and total biomass (see below) measured at the final harvest, and the difference between t_s and t_h being the period between the sowing and harvesting of the seedling.

2.5. Statistical analyses

Plasticity was estimated for each trait, species and environment combinations using an index calculated with the following formula, $|(x - y) / \sqrt{x * y}|$, where x is the mean trait value for individuals of a species in soil-by-light combination, and y being the same but for the contrasting soil-by-light combination. The benefit of this index is that it scales the magnitude of plasticity according to the geometric mean, so that plasticity can be compared on the same scale across traits with different ranges of values (0, $+\infty$). To account for conditional effects of soil type and light on plasticity, one environmental treatment was held constant, and the other one was varied in the formula above. Thus there were four sets of plasticity indices calculated for each species and trait combination: plasticity due to soil type in high light, plasticity due to soil type in low light, plasticity

due to light on clay, and plasticity due to light on sandy loam. We will refer to these as plasticity response types. For example, to calculate the plasticity of SLA in response to soil type for *D. aromatica* under high light, x was the mean SLA value for individuals grown in clay soil in high light (165.68), and y was the mean SLA value for individuals in sandy-loam soil grown in high light (152.29) to obtain an index of 0.08 for the plasticity due to soil type in high light.

The plasticity indices directly show the magnitude of the plasticity for each trait per species for the four plasticity types, which allowed for direct comparisons of plasticity between contrasting soil specialization groups, functional traits, depending on the type of resource varied, and in relation to growth rate. To analyze variation in trait plasticity in response to light and soil type among contrasting soil specialization groups, we fitted a mixed model with a normal error distribution using R statistical software (R Core Team 2016) as implemented in the lme4 package (Bates et al. 2014). In all models, species was a random effect. To test the effects of soil type and soil specialization group on plasticity due to light, the fixed effects were the soil specialization of the species (clay, sandy loam, generalist) and soil type of the plot where the seedling was growing (clay, sandy loam). To test the effects of light and soil specialization group on plasticity due to soil type, the fixed effects were the soil specialization of the species and canopy status of the plot where the seedling was growing (high light, low light). Interaction terms between the fixed effects were included. The model was thus constructed as $P_t \sim H + Z + H*Z$, where P_t is the plasticity index for trait t , H is soil specialization group, and Z is the environmental factor being varied (either soil type or light), and asterisk represents the

interaction between terms. Similar models were fit for growth rate variables. Post-hoc tests were conducted for models with statistically significant effects with the Welch two-sample t-test. Differences in plasticity among soil specialization groups would be indicated by a significant interaction term or a significant main effect of soil specialization group.

To visualize variation among functional traits in the magnitude of plasticity exhibited, we compared traits using boxplots. All of the plots were constructed with base R and the ggplot2 package (Wickham 2009). A series of four sets of boxplots were constructed for the four different treatment combinations (plasticity due to light in clay soil, plasticity due to light in sandy loam soil, plasticity due to soil in high light, and plasticity due to soil in low light) with a boxplot for each trait, ordered sequentially from lowest to highest median plasticity index. Each trait was assigned a unique color along a color spectrum based on one of the sets, plasticity due to light in clay soil, allowing differences in the rank order to be easily spotted based on colors.

To test whether the magnitude of plasticity in functional traits and growth rates depend on the type of resource varied (i.e., soil type or light), Kendall rank correlation tests were conducted on comparisons of plasticity values for traits and growth under different soil and light treatments. For plastic responses to light, the trait and growth indices in clay were plotted against equivalent indices in sandy loam. For plastic responses to soil type, the trait and growth indices in high light was plotted against equivalent indices in low light.

To test whether trait plasticity correlated with resource-related variation in

growth, Pearson correlation tests was used. Grand plasticity indices for each soil specialization group and plasticity response type were calculated across all functional traits and all growth rates by averaging the plasticity indices by species, soil specialization group, and plasticity response type.

3. Results

3.1. Variation in plasticity among soil specialization groups

A total of two of the 21 functional traits and growth rates examined showed statistically significant variation in plasticity due to light among soil specialization groups (Table 3, Table 4). The plasticity in SLA due to light of generalists was significantly greater than that for both sandy loam and clay specialists (Figure 3A, $p < 0.05$). For LAR, there was a significant interaction between soil specialization and soil type ($F_{2,17} = 3.91$, $p < 0.05$). While there were no significant differences between soil specialization groups when growing on clay soil, there were differences when growing on sandy loam soil. The plasticity in LAR due to light was not significantly different between clay specialists and

Table 3: Summary of statistically significant variation in plasticity due to light and soil. First column shows the type of plastic response tested. The second column is the number of functional traits and growth rates tested. Third column reports the number of traits that showed statistically significant responses in the mixed model test. Fourth column summarizes number of traits and growth rates showing statistically significant differences among soil specialization groups. The last column indicates number of functional traits and growth rates that responded in the predicted direction among soil specialists.

Plastic response due to	No. traits and growth rates	No. of tests that were statistically significant	Tests that showed significance due to specialization	No of significant tests in predicted direction
-light	21	4 (SLA, LAR, rgr-Diam, rgr-NLeaf)	2 (SLA, LAR)	2 (SLA, LAR)
-soil	21	7 (SDen, SLA, SRL, LMR, LAR, RDepth, agr-LamArea)	6 (SDen, SLA, SRL, LMR, LAR, agr-LamArea)	3 (LMR, LAR, agr-LamArea)

Table 4: Summary of mixed models testing variation in plasticity due to light in functional traits and growth rates of seedlings of Bornean tree species in relation to soil specialization groups (Habitat Preference: C, clay specialist; SL, sandy loam specialist, G, generalist), soil type (c, clay; sl, sandy loam), and their interaction. Abbreviations of traits and growth are in Table 2. A dash indicates that this term was not statistically significant or was not interpreted in the presence of an interaction. Post-hoc tests of differences between levels of factors were performed when there was a statistically significant main effect or interaction, and the direction of significant differences is indicated.

	Habitat Preference	Soil	Habitat Preference x Soil Type Interaction
	Significance		
	Organ Structural Traits		
Stem density	-	-	-
Root density	-	-	-
Leaf density	-	-	-
Specific leaf area	G > SL G > C	sl > c	-
Leaf thickness	-	-	-
Lamina area	-	-	-
Specific root length	-	-	-
	Biomass Allocation Traits		
Leaf mass ratio	-	-	-
Root mass ratio	-	-	-
Leaf area ratio	-	-	G > SL in sl
Root depth	-	-	-
Fine root length	-	-	-
Shoot mass ratio	-	-	-
Stem mass ratio	-	-	-
	Growth Rates		
AGR-leaf area	-	-	-
AGR-leaf number	-	-	-
AGR-total biomass	-	-	-
RGR-height	-	-	-
RGR-diameter	-	sl > c	-
RGR-leaf number	-	sl > c	-

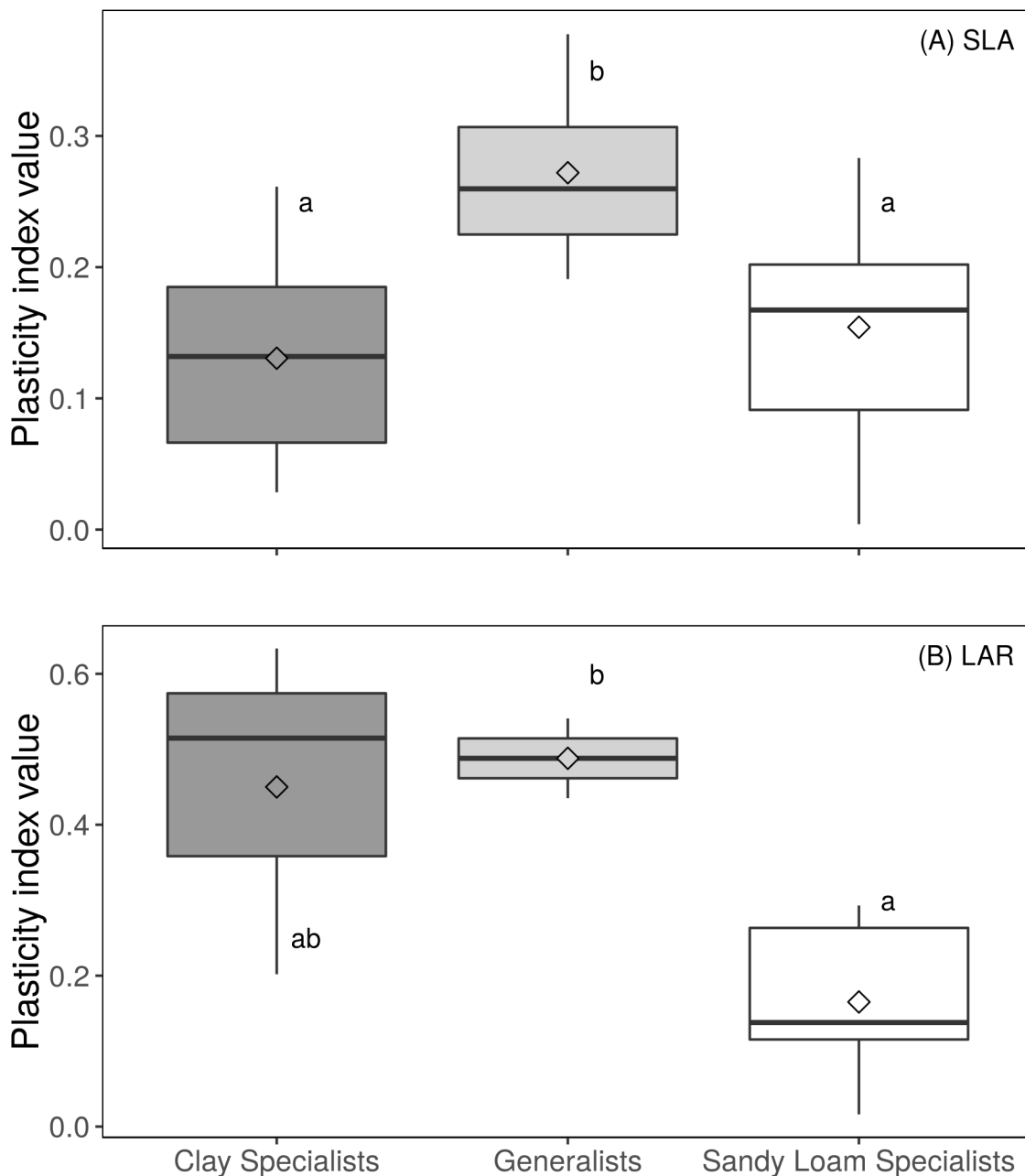


Figure 3: Comparisons of plasticity in functional traits due to light among seedlings of Bornean tree species in three soil specialization groups. (A) specific leaf area (SLA); and (B) lamina area ratio, (LAR) in sandy loam soil. Description of boxplots: middle line, median; diamond, mean, top and bottom hinges of the box, 25th and 75th percentile of data; top and bottom whiskers, extensions to the highest value and lowest within 1.5 times of the inter-quartile (IQR) range, where IQR is the distance between the first and third quartiles of the data. Different letters next to boxplots indicate significant differences among pairs of soil specialization groups.

generalists nor between clay and sandy loam specialists, but generalists showed significantly greater plasticity than sandy loam specialists (Figure 3B).

A total of six of the 20 functional traits and growth rates examined showed statistically significant variation in plasticity due to soil type among soil specialization groups (Table 3, Table 5). Of these, five were functional traits, and one was a growth rate. For plasticity in LMR due to soil type, there was a significant interaction between soil specialization and light ($F_{2,18} = 8.718, p < 0.05$). In high light, clay specialists and generalists had similar plasticity due to soil, and both were significantly higher than that for sandy loam specialists (Figure 4A). In low light, clay specialists showed significantly greater plasticity than the sandy loam specialists, but there were no differences between the generalists and the sandy loam specialists (Figure 4B). For plasticity in LAR due to soil type, there was a significant interaction between soil specialization and light ($F_{2,17} = 10.571, p < 0.05$). In low light there were no significant differences among specialist groups, but in high light, plasticity of LAR due to soil was highest for clay specialists and was significantly greater than that for sandy loam specialists, but generalists were not different from either clay or sandy loam specialists (Figure 4C). For stem wood density, there was a significant interaction between soil specialization and light ($F_{1,7} = 11.037, p < 0.01$). In high light, there were no differences among soil specialization groups, but in low light, sandy loam specialists showed significantly greater plasticity than generalists, but no differences compared to clay specialists, which were also not different from generalists (Figure 5A). The plasticity of growth rate in total lamina area due to soil type was greatest among clay specialists, and was significantly different from sandy loam

Table 5: Summary of mixed models testing variation in plasticity due to soil type in functional traits and growth rates of seedlings of Bornean tree species in relation to soil specialization groups (Habitat Preference: C, clay specialist; SL, sandy loam specialist, G, generalist), insolation (HL, high-light gaps; LL; low-light understory), and their interaction. Abbreviations of traits and growth are in Table 2. A dash indicates that this term was not statistically significant or was not interpreted in the presence of an interaction. Post-hoc tests of differences between levels of factors were performed when there was a statistically significant main effect or interaction, and the direction of significant differences is indicated.

	Habitat Preference	Insolation	Habitat Preference x Insolation Interaction
Trait	Significance		
Organ Structural Traits			
Stem density	-	-	SL > G in LL
Root density	-	-	-
Leaf density	-	-	-
SLA	Significant, but no significant differences in post-hoc tests		-
Leaf thickness	-	-	-
Lamina area	-	-	-
Specific root length	-	-	Significant interaction, but no significant differences in post-hoc tests
Allocation Traits			
LMR	-	-	C > G in LL C > SL in HL G > SL in HL
RMR	-	-	-
LAR	-	-	C > SL in HL
Root depth	-	LL > HL	-
Fine root length	-	-	-
Shoot mass ratio	-	-	-
Stem mass ratio	-	-	-
Growth Rates			
AGR-leaf area	C > SL	Significant effect, but no significant differences in post-hoc tests	-
AGR-leaf number	-	-	-
AGR-total biomass	-	-	-
RGR-height	-	-	-
RGR-diameter	-	-	-
RGR-leaf number	-	-	-

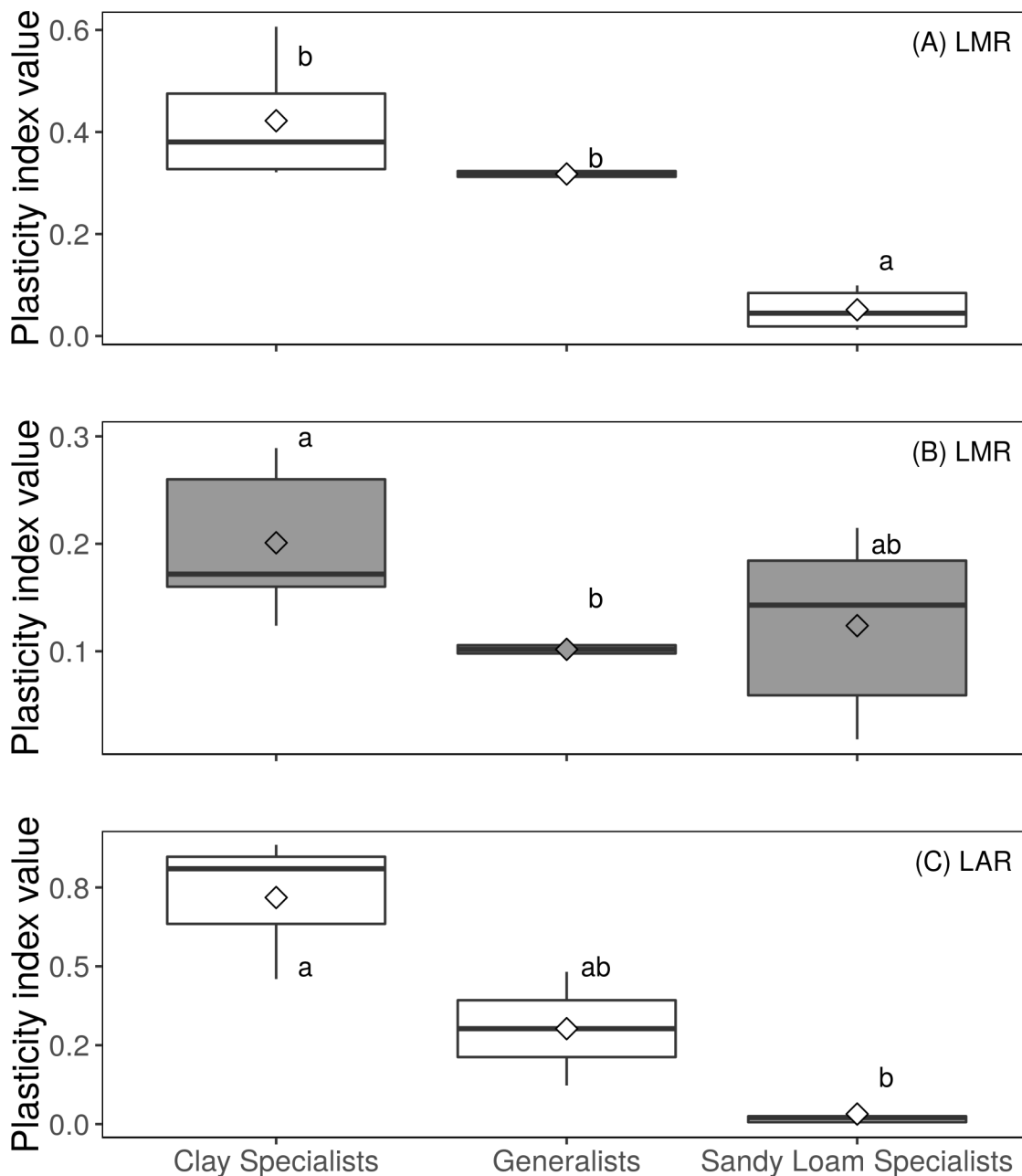


Figure 4: Comparisons of plasticity in functional traits due to soil among seedlings of Bornean tree species in two light treatments. (A) lamina mass ratio (LMR) in high light; (B) LMR in low light; and (C) lamina area ratio (LAR) in high light. Boxplots in A are not shaded to represent high light, and boxplots in B are shaded to represent low light. Description of boxplots: middle line, median; diamond, mean, top and bottom hinges of the box, 25th and 75th percentile of data; top and bottom whiskers, extensions to the highest value and lowest within 1.5 times of the inter-quartile (IQR) range, where IQR is the distance between the first and third quartiles of the data. Different letters next to boxplots indicate significant differences among pairs of soil specialization groups.

specialists, but there were no other statistically significant pairwise differences (Figure 5B). For SLA, there were significant main effects of soil specialization group and light, but none for the interaction of the main effects. While post-hoc tests revealed no significant pairwise differences, the difference in plasticity between high and low light tended to be greater for clay specialists and generalists than for sandy loam specialists (Figure 6A). For plasticity in specific root length due to soil type, there was a significant interaction between soil specialization and light ($F_{2,2} = 53.95$, $p < 0.05$), but post-hoc tests did not reveal any significant pairwise differences (Figure 6B).

3.2. Variation in the magnitude of plasticity depending on resource type

In addition to the response variables showing significant interactions between soil specialization and either soil type or light described in the previous section, several traits and growth rates showed statistically significant variation in plasticity depending on the resource type. Of the four traits and growth rates showing statistically significant main effects of plasticity due to light, two were functional traits and two were growth rates that showed significant variation among soil types (Table 3). For plasticity due to soil, only rooting depth showed significant variation due to light, with greater plasticity in low compared to high light (Figure 6C). The plasticity due to light of SLA was significantly greater on sandy loam than clay soil (Figure 7A; $p < 0.05$). The plasticity indices due to light in relative growth rates of diameter and number of leaves were significantly greater on sandy loam than clay soil (Figure 7B and Figure 7C).

On average, plasticity in response to variation in light (mean = 0.49, range = 0.05-1.66) was greater in magnitude than plasticity due to soil (mean = 0.27, range = 0.04-

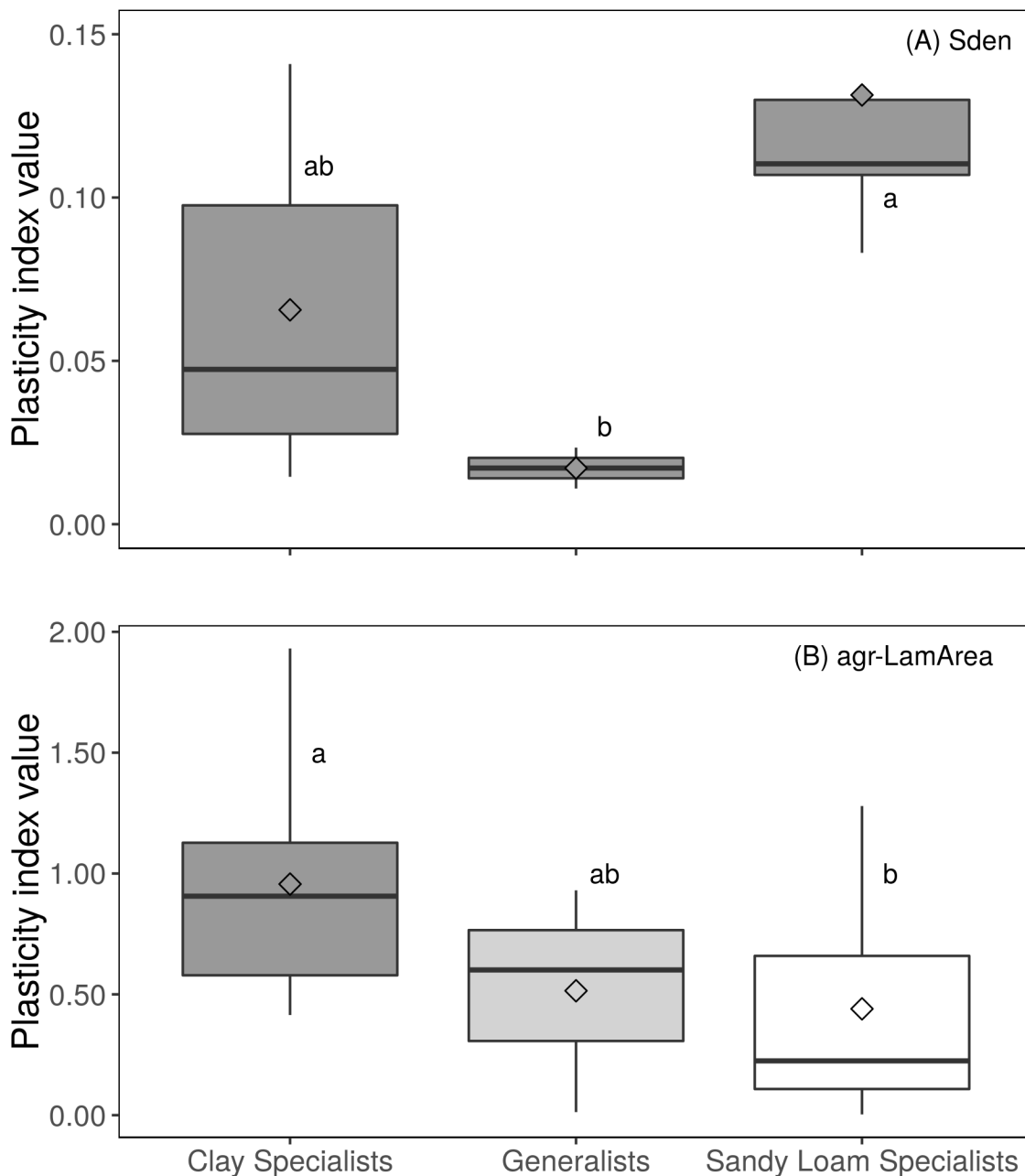


Figure 5: Comparisons of plasticity in functional traits and growth rates due to soil among seedlings of Bornean tree species in two light treatments. (A) stem wood density (SDen) in low light; and (B) absolute growth rate of lamina area (agr-LamArea). Boxplots in A are all shaded to represent low light. Description of boxplots: middle line, median; diamond, mean, top and bottom hinges of the box, 25th and 75th percentile of data; top and bottom whiskers, extensions to the highest value and lowest within 1.5 times of the inter-quartile (IQR) range, where IQR is the distance between the first and third quartiles of the data. Different letters next to boxplots indicate significant differences among pairs of soil specialization groups.

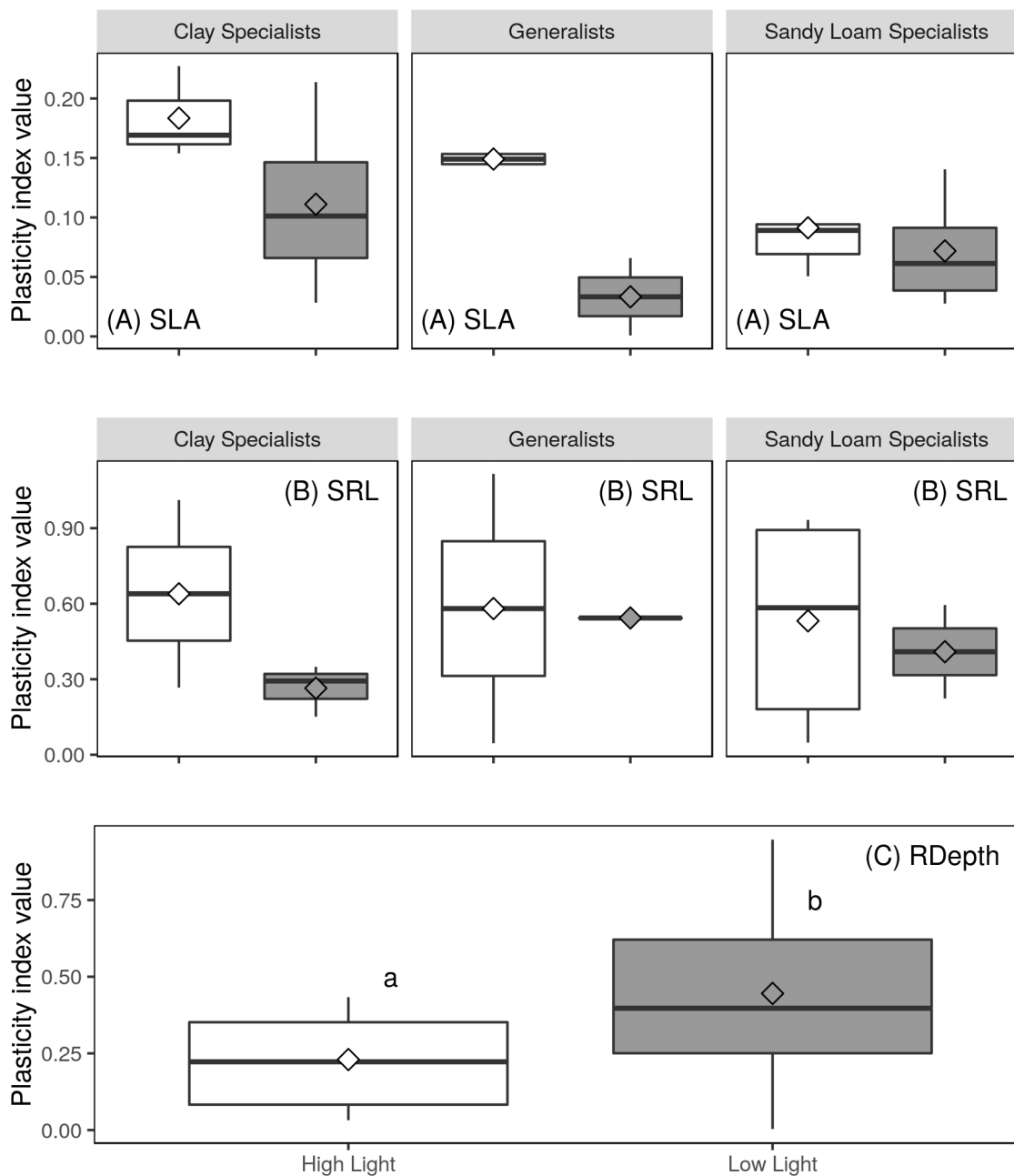


Figure 6: Comparisons of plasticity in functional traits due to soil among seedlings of Bornean tree species in two light treatments. (A) specific leaf area (SLA); and (B) specific root length (SRL); and (C) root depth (RDepth). Boxplots are unshaded to represent high light, and shaded to represent low light. Description of boxplots: middle line, median; diamond, mean, top and bottom hinges of the box, 25th and 75th percentile of data; top and bottom whiskers, extensions to the highest value and lowest within 1.5 times of the interquartile (IQR) range, where IQR is the distance between the first and third quartiles of the data. Different letters next to boxplots indicate significant differences among pairs of soil specialization groups. No letter are present in B and C figures because there are no significant post-hoc differences.

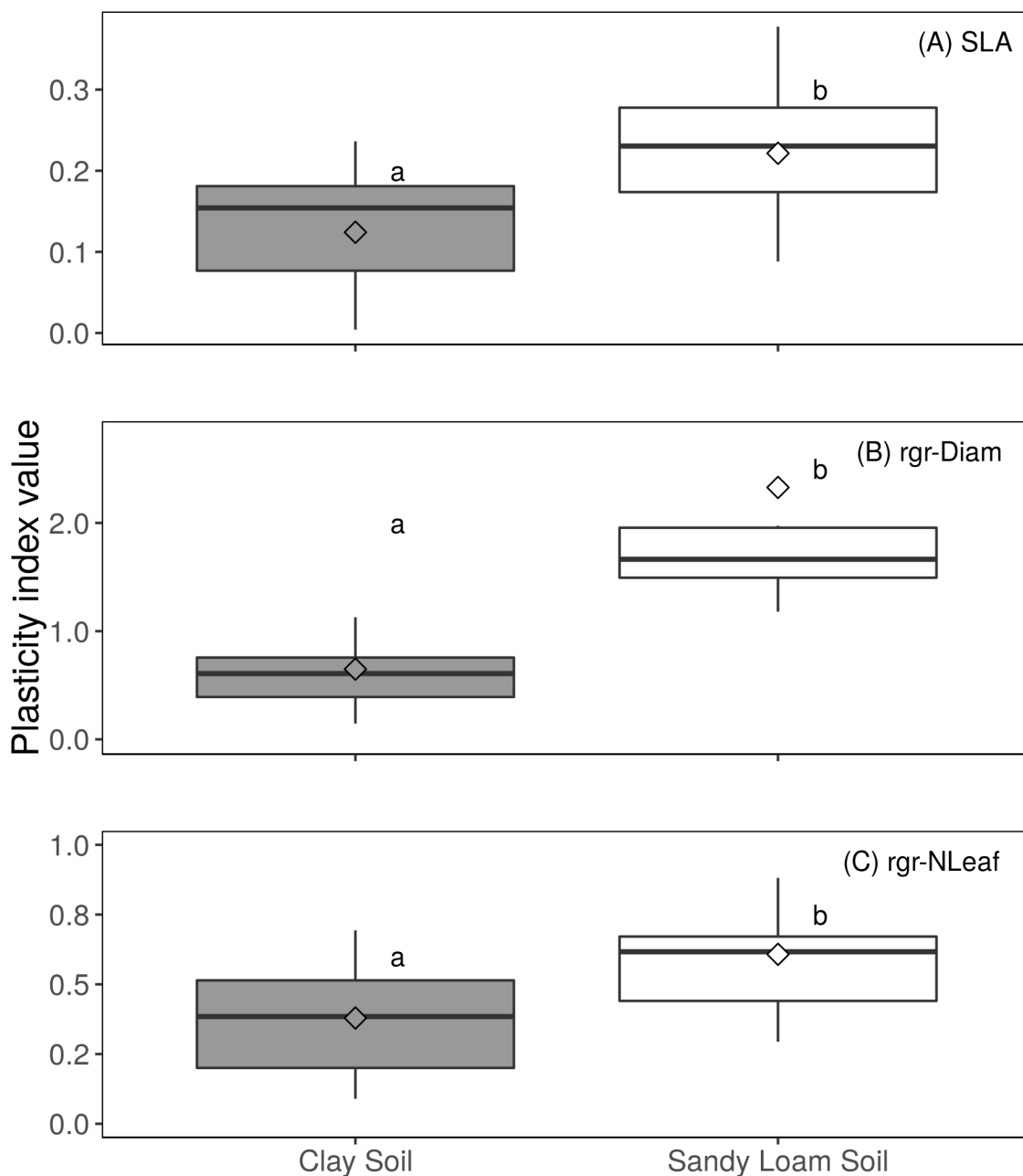


Figure 7: Comparisons of plasticity in functional traits and growth rates due to light among seedlings of Bornean tree species in two soil treatments. (A) specific leaf area, SLA; (B) relative growth rate of diameter, rgr-Diam; and (C) relative growth rate of number of number of leaves, rgr-NLeaf. Description of boxplots: middle line, median; diamond, mean, top and bottom hinges of the box, 25th and 75th percentile of data; top and bottom whiskers, extensions to the highest value and lowest within 1.5 times of the interquartile (IQR) range, where IQR is the distance between the first and third quartiles of the data. Different letters next to boxplots indicate significant differences among pairs of soil specialization groups.

0.84; main effect of plasticity due to soil vs. light: $F_{1,905} = 51.6, p < 0.001$). This was true regardless of the soil type or light environment, respectively (Figure 8: $F_{1,915} = 1.4, p = 0.24$). While plasticity due to light was strongly correlated in sandy loam and clay soil ($\tau = 0.83, p < 0.01$), it was greater in sandy loam soil (Figure 8A; $F_{1,448} = 11.0, p < 0.01$). Similarly, plasticity due to soil type was strongly correlated in high and low light ($\tau = 0.58, p < 0.01$), but variation in plasticity due to soil did not depend on the light environment (Figure 8B; $F_{1,444} = 0.47, p = 0.49$).

3.3. Variation among functional traits and growth rates in the magnitudes of plasticity due to soil and light

As a group and across all soil and light environments, growth rates were generally more plastic than functional traits (Figure 9). When ranked according to their median values across all species, growth rates were also more plastic than functional traits in all four plasticity response types (Wilcoxon rank sum test: plasticity due to light in clay, $W = 7, p < 0.01$; plasticity due to light in sandy loam, $W = 2, p < 0.01$; plasticity due to soil in high light, $W = 14, p = 0.01$; plasticity due to soil in low light, $W = 16, p = 0.02$), but several functional traits related to allocation to roots were also very plastic and frequently changed rank (Figure 9; Table 6). For example, SRL went from having a middle-rank plasticity index for three plasticity response type to being the second most plastic trait in terms of plasticity due to soil in high light. FRMR was the third and fourth most plastic trait in terms of plasticity due to soil in high light and plasticity due to light in clay, versus ranked seventh and eleventh in plasticity due to soil in low light and plasticity due to light in sandy loam, respectively. Relative growth rate in diameter was the most plastic trait in resource-limited environments, namely, for plasticity due to light in sandy loam

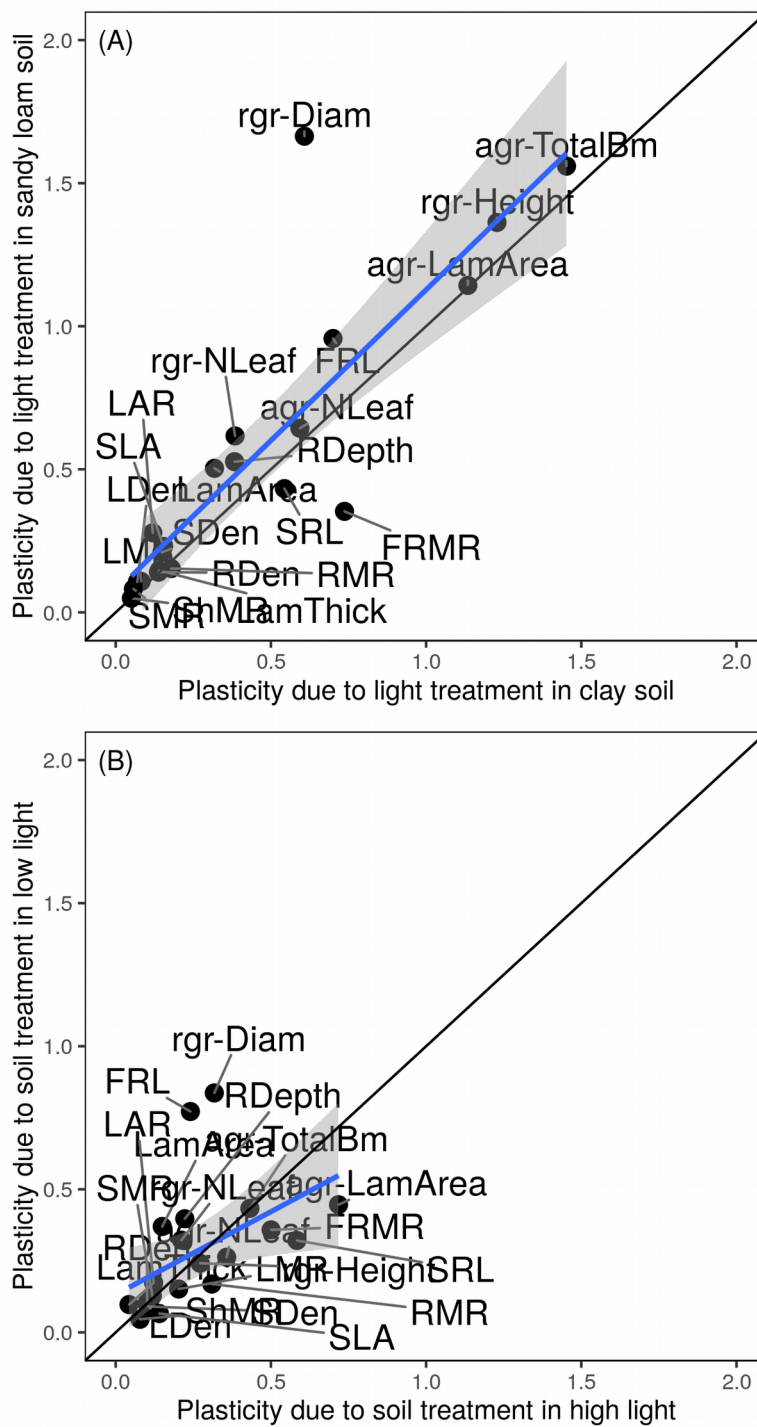


Figure 8: (A) Plasticity due to light for sandy loam versus clay and (B) plasticity due to soil for low light versus high light for all functional trait and growth rate plasticity mean values.

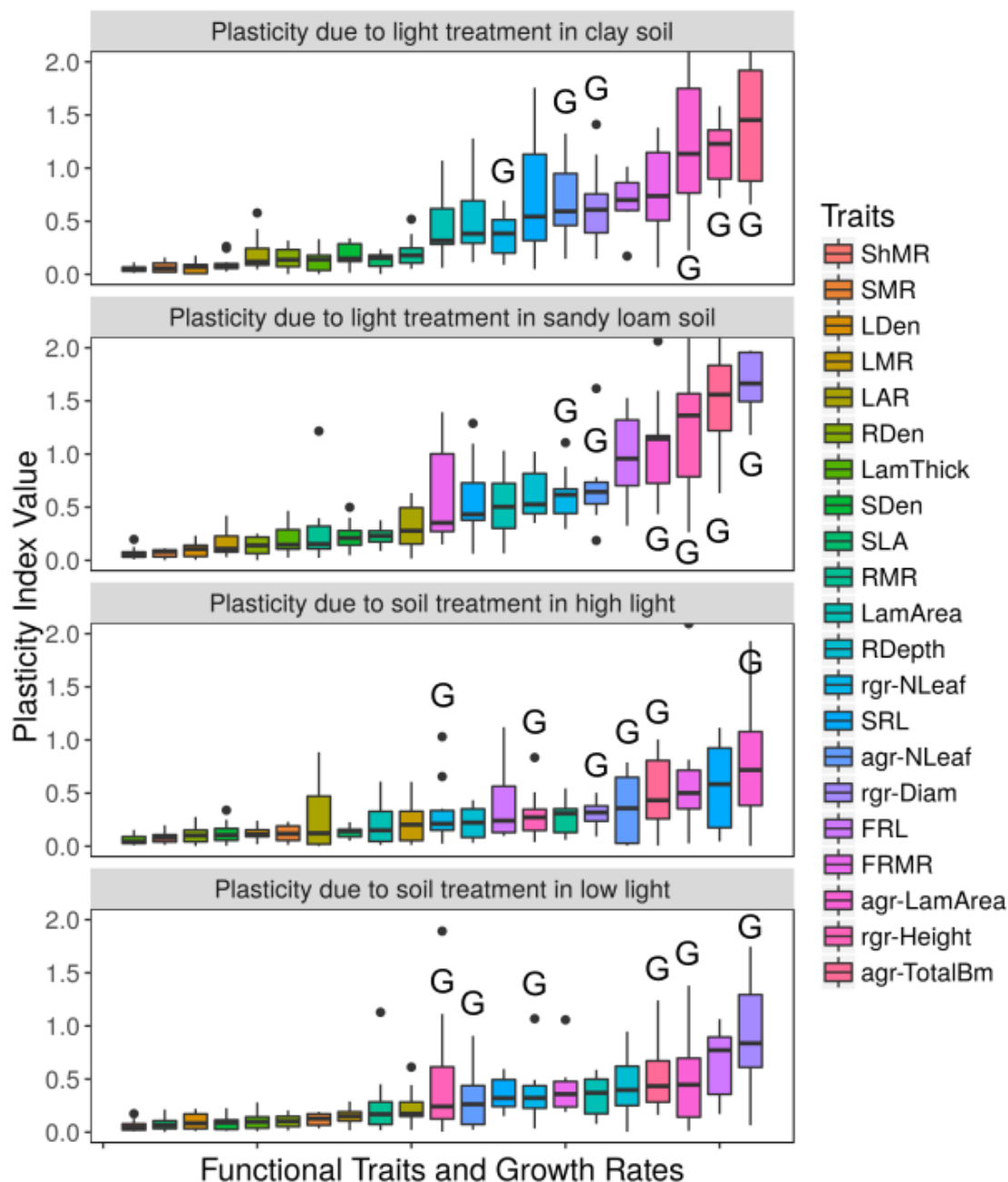


Figure 9: Ranking of median functional trait and growth rate plasticity indices in the four plasticity treatments. The letter “G” in the plot indicates growth rate plasticity. Boxplots in each treatment are arranged in increasing median of plasticity, Plasticity due to light treatment in clay soil was used as a reference point for assigning colors along a rainbow spectrum for each of the functional trait and growth rate boxplots. The color assignment was preserved for the other three treatments. Change in rank can then be observed in reference to the topmost plot.

Table 6: Ranking of plasticity of traits by the four treatment combinations. The lower the number, the higher the relative plasticity of the trait and growth rate in relation to other functional traits and growth rates in each treatment environment.

Functional traits and growth rates	Plasticity due to light treatment in clay soil	Plasticity due to light treatment in sandy loam soil	Plasticity due to soil treatment in high light	Plasticity due to soil treatment in low light
agr-LamArea	3	4	1	3
agr-NLeaf	7	6	5	10
agr-TotalBm	1	2	4	4
FRL	5	5	9	2
FRMR	4	11	3	7
LamArea	11	9	13	6
LamThick	15	16	21	17
LAR	17	12	15	12
LDen	19	19	17	19
LMR	18	18	12	14
RDden	16	17	19	16
RDepth	10	8	10	5
rgr-Diam	6	1	6	1
rgr-Height	2	3	8	11
rgr-NLeaf	9	7	11	8
RMR	12	15	7	13
SDen	14	14	18	18
ShMR	21	21	20	21
SLA	13	13	14	20
SMR	20	20	16	15
SRL	8	10	2	9

and plasticity due to soil in low light. Plasticity in growth rate in the seedling's total lamina area was consistently highly ranked, but was the most plastic trait for plasticity due to soil in high light. Likewise, plasticity in seedling biomass growth was consistently highly ranked and was the most plastic trait for plasticity due to light in clay. Overall, there were more changes in rank when comparing plasticity due to soil in high versus low light (Kendall rank correlation test; $\tau = 0.56$, $p < 0.01$) than when comparing plasticity

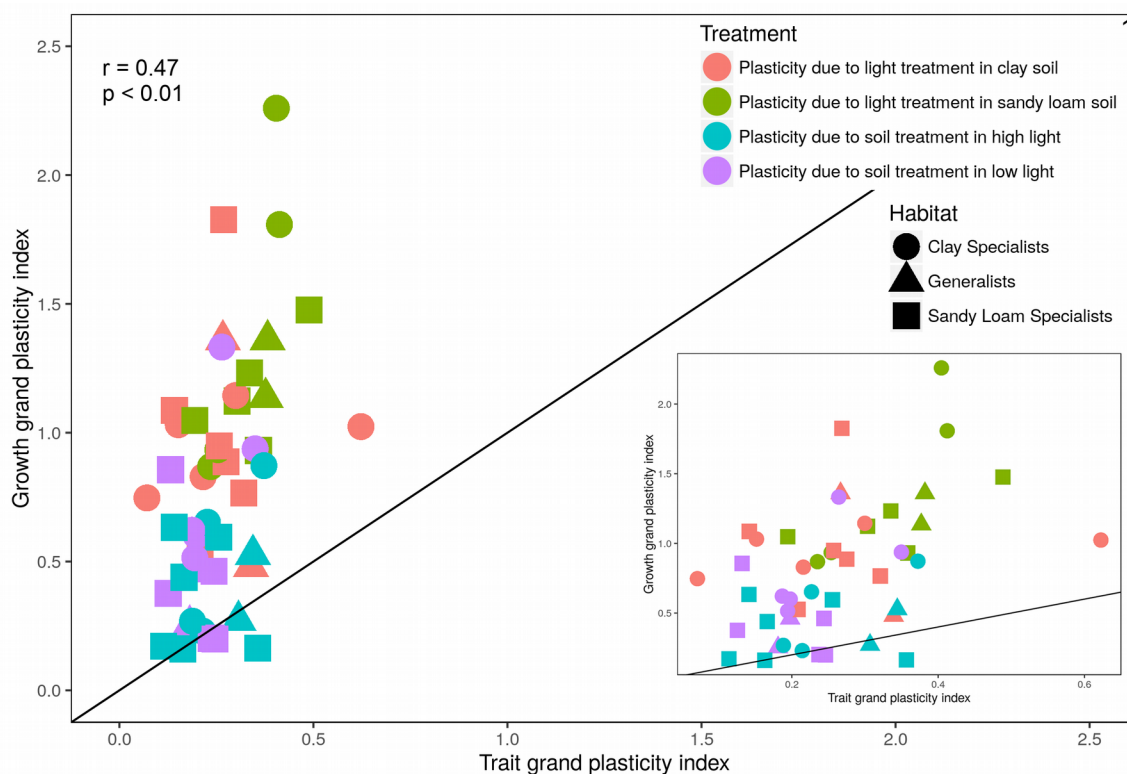


Figure 10: Regression of plasticity indices for growth traits versus functional traits grouped by shape for soil specialization, and by color for treatment. Inset box in the bottom left is a rescaled figure with the x-axis enlarged at a greater ratio than the y-axis to more clearly show the relationship between growth and trait grand plasticity indices.

due to light in clay versus sandy loam (Kendall rank correlation test; $\tau = 0.80$, $p < 0.01$).

3.4. Covariation between plasticity in functional traits and plasticity in growth rates

Plasticity in functional traits and growth rates were positively correlated ($r = 0.47$, $p < 0.01$; Figure 10), but lesser plasticity in functional traits translated into dramatically greater plasticity in growth rates (standardized major axis regression: slope = 4.5, 95% confidence limits of slope = 3.5-5.9, $p < 0.01$, $R^2 = 0.22$). There were no significant differences among soil specialists in the slope or elevation of the relationship between functional trait and growth rate plasticity (standardized major axis regression; likelihood ratio test for common slope, $\chi^2 = 1.13$, $df = 2$, $p = 0.57$; Wald test for common elevation,

Wald statistic = 2.6, $df = 2$, $p = 0.27$), nor was there any significant shifts in the relationship along a common slope among soil specialists groups (standardized major axis regression; Wald statistic = 1.5, $df = 2$, $p = 0.46$). The correlation analysis between growth traits and functional traits showed some significant correlations (Table 7). There was significant positive correlation between the relative growth rate of the stem diameter with lamina thickness ($r = 0.355$, $p < 0.05$), lamina area ($r = 0.316$, $p < 0.05$), and root depth ($r = 0.361$, $p < 0.05$). There was a significantly positive correlation between the relative growth rate of height with lamina area ($r = 0.317$, $p < 0.05$). The absolute growth rate of lamina area was significantly correlated with the wood density of the root ($r = 0.306$, $p < 0.05$), specific leaf area ($r = 0.303$, $p < 0.05$), lamina area ($r = 0.705$, $p < 0.01$), and root depth ($r = 0.316$, $p < 0.05$). The absolute growth rate of number of leaves was positively correlated with woody stem density ($r = 0.294$, $p < 0.05$), woody root density ($r = 0.306$, $p < 0.05$), lamina area ($r = 0.340$, $p < 0.05$), and root mass ratio ($r = 0.392$, $p < 0.01$). The relative growth rate of number of leaves was significantly correlated with specific leaf area ($r = 0.402$, $p < 0.01$), leaf mass ratio ($r = 0.298$, $p < 0.05$), and leaf area ratio ($r = 0.473$, $p < 0.01$). Finally, the absolute growth rate of total biomass was significantly correlated with woody stem density ($r = 0.383$, $p < 0.01$), specific leaf area ($r = 0.421$, $p < 0.01$), lamina thickness ($r = 0.516$, $p < 0.01$), lamina area ($r = 0.759$, $p < 0.01$), and root depth ($r = 0.498$, $p < 0.01$).

Table 7: Correlation (r) between plasticity of growth rates (row header) and plasticity of functional traits (column header). Significant p -values are bolded.

	rgr-Diam		rgr-Height		agr-LamArea		agr-NLeaf		rgr-NLeaf		agr-TotalBm	
	r	p	r	p	r	p	r	p	r	p	r	p
SDen	0.14	0.35	0.20	0.18	0.18	0.23	0.29	0.05	0.20	0.17	0.38	<0.01
RDen	-0.03	0.85	0.21	0.15	0.31	0.04	0.31	0.04	0.10	0.49	0.28	0.06
LDen	-0.16	0.30	-0.06	0.71	0.11	0.47	-0.03	0.83	0.15	0.33	0.04	0.82
SLA	0.28	0.06	0.22	0.15	0.30	0.05	0.21	0.18	0.40	0.01	0.42	<0.01
LamThick	0.36	0.02	0.23	0.13	0.29	0.06	-0.02	0.90	0.24	0.12	0.52	<0.01
LamArea	0.32	0.03	0.32	0.03	0.71	<0.01	0.34	0.02	0.20	0.18	0.76	<0.01
LMR	-0.06	0.71	-0.25	0.08	-0.04	0.79	0.11	0.46	0.30	0.04	-0.09	0.55
FRL	0.21	0.25	0.17	0.35	0.26	0.14	0.24	0.18	0.06	0.75	0.36	0.04
SRL	-0.12	0.51	-0.11	0.53	0.19	0.29	0.14	0.45	-0.03	0.85	0.20	0.28
FRMR	0.07	0.70	0.18	0.31	-0.14	0.45	-0.20	0.28	-0.27	0.13	-0.09	0.62
RMR	-0.02	0.87	-0.14	0.36	0.12	0.45	0.39	0.01	0.08	0.57	0.22	0.15
LAR	-0.03	0.82	-0.07	0.63	-0.09	0.57	-0.04	0.78	0.47	<0.01	-0.05	0.73
RDepth	0.36	0.01	0.26	0.08	0.32	0.04	0.23	0.14	-0.07	0.64	0.50	<0.01
ShMR	-0.16	0.29	-0.18	0.21	0.07	0.64	0.25	0.09	0.18	0.22	0.08	0.62
SMR	-0.22	0.13	-0.25	0.09	0.02	0.90	-0.05	0.74	-0.06	0.66	-0.20	0.19

4. Discussion

The functional trait approach to plant ecology has historically emphasized between-species variation, but there is increasing awareness that within-species variation can have important influences on plant population and community dynamics (Escudero and Valladares 2016). Despite this awareness, comparatively far less information exists about both the relative importance of different sources of within species variation for most functional traits, even commonly measured ones, and the consequences of this variation for plant growth (Russo and Kitajima 2016). Through our experimental analysis of plasticity, we demonstrate that the magnitude of plasticity not only varied among traits,

but also in response to the type of environmental variation, as well as to tree species' ecological strategy (clay specialists, sandy loam specialists, or generalist). Moreover, within species variation in traits across contrasting soil and light environments translated into far greater variation in growth rates, suggesting a non-additive effect of plasticity on phenotypic integration (sensu Marks and Lechowicz 2006). Thus, within species trait variation in response to a heterogeneous environment is not only complex, but has effects on demography that would ultimately have implications for how tree species are distributed along environmental gradients.

4.1. Variation in plasticity among soil specialization groups

Although very few traits and growth rates showed statistically significant evidence of plasticity among soil specialization groups, for the cases that were significant, the direction of variation was generally consistent with our predictions: generalist species and the fast-growing specialists of clay soil were more plastic than the slower-growing specialists of the less fertile sandy loam soil. Ample evolutionary theory predicts that the environmental variation that habitat generalists experience should select for greater capacity for phenotypic plasticity (Scheiner 1993; Sultan et al. 2002), and our findings provide experimental support of this notion for long-lived Bornean tree species.

We also hypothesized that fast-growing tree species should show greater trait plasticity (Grime 1977). Indeed, greater plasticity may be a requirement for achieving a fast-growth strategy, as it would allow trees to take optimal advantage of temporary increases in resources. This advantage would be further amplified by the effects of compound interest on resource acquisition (i.e., the time value of leaf area sensu Westoby

et al. 2000). Traits related to biomass allocation to leaves (LAR and LMR) were among those showing the greatest differences in plasticity due to soil type, between sandy loam and clay specialists, with plasticity due to soil type being far greater among clay, compared to sandy loam, specialists. These results are consistent with previous findings showing the importance of allocation to leaves to habitat-mediated differences in seedling performance across soil gradients (Palmiotto et al. 2004). In addition, we found that plasticity due to soil of absolute growth rate of lamina area was greater for clay compared to sandy loam specialists. As with LAR and LMR, this result indicates that greater leaf-based plastic responses among clay specialists, which supports our idea that increased plasticity is adaptive in environments where faster growth is associated with greater exploitative competition and resource acquisition. Thus, we conclude that plasticity in leaf allocation traits are a key component of plastic responses, not only to variation in light, but also to soil resources, and we hypothesize that they are part of a suite of photosynthetic carbon acquisition strategy traits enabling fast-growing species to maximize carbon acquisition, and hence growth rates, across soil types of varying resource supply.

There was, however, one trait that contrasted with our predictions: for stem wood density, in low light, sandy loam specialists showed greater plasticity to soil type than clay specialists and similar plasticity to generalists. The wood of sandy loam specialists is on average denser than that of clay specialists (Russo, unpublished data). Given the carbon cost of growing dense wood, adjustments in wood density may be one means by which sandy loam specialists increase growth rates in more fertile soil types. The fact that

plasticity due to light for relative growth rate in diameter and number of leaves was greater in sandy loam than clay soil provides some support for this interpretation. In fact, this scenario may be evidence in support of theories for the costs and limits of phenotypic plasticity (Van Tienderen 1997; DeWitt et al. 1998) where sandy loam specialists not only show canalization of depressed levels of plasticity when compared to clay specialists and generalists, but respond plastically only under specific conditions of resource limitation.

4.2. Variation in the magnitude of plasticity depending on resource type

Given their different functional roles within the plant, traits may respond in contrasting ways to variation in different types of resources, and we examined this idea with respect to variation in insolation and soil resource availability. Plasticity of traits and growth rates in response to light was greater in magnitude than plasticity in response to soil type (Figure 8). While this result was not unexpected, we provide an experimental demonstration of this for 21 functional trait and growth variables across 13 Bornean tree species. A result that was unanticipated was that, overall, plasticity in both traits and growth rates due to light was greater on sandy loam than clay soil. Given that growth rates of trees > 1 cm in diameter are faster on clay soil (Russo et al. 2005), that variation in understory insolation is larger on clay soil (Russo et al. 2012), and that infertile soils are thought to limit the capacity to respond to variation in light (Chapin et al. 1993), we anticipated the opposite pattern. A possible explanation is that seedlings exposed to higher average insolation in sandy loam understories (Russo et al. 2012) might have greater capacity for plastic responses to light than do seedlings in the darker clay

understories. In other words, understory suppression due to severe light restriction may limit plastic responses.

In contrast to plasticity due to light, plasticity due to soil type did not vary significantly for seedlings in high versus low light. In other words, seedling responses to belowground resource variation did not depend on aboveground resources. This result contrasts with the prevailing wisdom that light availability constrains responses to soil resource variation and suggests that, despite lower plasticity overall to soil type as compared to light, belowground resources affect tree species functional trait variation in ways that are independent of light availability.

For plasticity due to light, functional traits showing significant effects were at both the organ and allocation levels: specific leaf area, and leaf area ratio Table 4. This result makes sense in that the ability of a plant to vary in response to the availability in light depends upon leaves, the organ responsible for light capture. The significant effects for these three leaf-related traits indicate that variation in how plants build leaves is coordinated with how much biomass is allocated to leaves, and that light availability is a strong determinant of this coordinated plasticity response (Rozendaal et al. 2006).

The plasticity due to light of relative growth rate of stem diameter (Figure 7B) and number of leaves (Figure 7C) was greater in sandy loam compared to clay soil, whereas RGR in seedling height did not show any significant plasticity. Seedlings are considered to prioritize height over diameter growth in order to reach ever-better light environments. However, trade-offs between growth and carbohydrate storage may also play a role in determining the dimensions in which growth occurs in response to

environmental heterogeneity. Given their allometry, stems that are wider for their height may provide more volume of parenchyma for carbohydrate storage, which is important for survival in stressful environments, including lower light and infertile soil (Russo, unpublished data), whereas allocation to growth in terms of photosynthetic capacity may predominate in higher light and more fertile soil.

A greater number of functional traits were affected by the plastic response due to soil, with stem wood density, specific leaf area, specific root length, leaf mass ratio, leaf area ratio, and rooting depth showing some statistical significance (Table 5). Compared to plasticity due to light (Table 3), these results indicate that more traits are involved in responding to variation in the availability of belowground resources. We predicted that leaf traits would respond more to light, and root traits would respond more to soil heterogeneity. This prediction was partially supported. While similar numbers of leaf traits showed variation in plasticity due to soil and light, the only significant plasticity found in root traits was due to soil type.

Overall, we can see a distinct pattern in which leaf traits are the traits that are most consistent with our hypothesis that clay specialists and generalists should be more plastic than sandy loam specialists. We also see that sandy loam specialists can display more plasticity than generalists or clay specialists, but this is largely restricted to the cases in which environmental resources are more limited.

4.3. Variation in plasticity among functional traits and growth rates

There was substantial variation in the magnitude of plasticity among different functional traits and growth rates, with growth rates on average being much more plastic than

functional traits (Figure 9). Changes among traits and growth rates in their rank plasticity were more frequent when comparing plasticity due to soil in high versus low light than when comparing plasticity due to light in clay versus sandy loam. This result suggests that insolation can strongly affect which traits are most important in mediating plastic responses to belowground resource variation. While the converse was also true for plasticity in response to light, the number of changes in the importance of specific traits was fewer. Thus, considering previous research on plant phenotypic integration (Pigliucci and Marlow 2001; Murren et al. 2002; Pigliucci and Kolodynska 2002), the nature of the functional relationship of each trait to the other in terms of whole-plant responses strongly depends on environmental variation, and plasticity in each trait may play a more or less important role in dictating those responses, which ultimately determine performance in a given environment and distributions along environmental gradients.

4.4. Covariation between plasticity in functional traits and plasticity in growth rates

The plasticity of plant functional traits were found to be significantly correlated with the plasticity of growth rates. Moreover, a slight difference in the plasticity of overall functional trait plasticity translates into larger shifts in the plasticity of growth rates (Figure 10). The ease in which small changes in functional trait plasticity leading to larger changes in plasticity of growth rate appears to be an important process for mediating competition, species co-existence, and community composition (Callaway et al. 2003) and that the differences in growth rates can differ significantly for species showing different levels of functional trait plasticity (Pigliucci et al. 1997). These patterns indicate that plastic responses for any single trait or even for functional traits as a

whole are not necessarily a strong indicator of the overall whole-plant plasticity in terms of growth rate, as the theory of phenotypic integration implies.

The correlation of plasticity of functional traits and growth rates (Table 7) appear to mirror plant physiological traits closely, though some trait correlations do present novel interpretations. The plasticity of stem diameter growth is significantly correlated with lamina thickness, lamina area, and root depth. This make structural sense as the a change in the morphology of the leaves would require a corresponding change in the structural traits to support the leaves, hence the plastic response of growth in stem diameter. It is hard to disentangle the role roots would thus play, where a greater or smaller abundance of leaves would lead to a similar change in the rooting depth of the plant, in the acquisition of nutrients to support the maintenance of the leaves (Givnish 1988).

We see a similar pattern for the plasticity of the absolute growth rate of the leaf lamina, with significant correlations with plasticity of specific leaf area, lamina area, rooting depth, and woody root density. Changes in the growth rate of lamina area would be tied to specific leaf area and lamina area plasticity, as the latter two traits would differ depending whether a plant significantly increases its rate of lamina growth. Faster growth of lamina area often means less investment to a plant's leaves, leading to greater specific leaf area as less photosynthates are spent on a greater lamina area. The significant correlation of root depth and woody root density plasticity points towards further structural and physiological changes for acquisition of belowground resources to support varying lamina growth.

When tracking the plasticity of absolute growth rate for number of leaves, we see that woody density for both stem and roots, lamina area, and root mass ratio are significantly correlated; compared to the plasticity of the relative growth rate of leaf numbers, which is significantly correlated with specific leaf area, leaf mass ratio, and leaf area ratio. These two measures of leaf growth imply that over a longer period of time, the balance between structural support and below-ground resource acquisition to leaf number growth is the important long term goals for a plant, while the shorter period in which relative growth rate was measured may indicate that leaf functional traits are more easily adjusted to maximize the acquisition of aboveground resources.

The plasticity of absolute growth rate was significantly correlated with the plasticity of woody stem density, specific leaf area, lamina thickness, lamina area, and root depth. Of these traits, only rooting depth is an allocation trait while the rest are structural traits. This indicates that plants that have greater plasticity in growth require more changes in organ structural traits to compensate for their greater variation in accumulation of biomass. The correlated plasticity in rooting depth would indicate that belowground changes in resource acquisition are necessary to support greater plasticity in biomass allocation.

Thus we can conclude that plasticity of functional traits as well as growth rates is significantly dependent on the plasticity of other traits within a framework of phenotypic integration. Furthermore these traits and growth rates show a greater plastic response due to light within a relatively poorer soil environment (Figure 10). The post-hoc analysis indicates more instances of generalists showing greater plasticity compared to sandy

loam specialists, and greater magnitudes of plasticity in sandy loam soil, potentially illuminating the most important shifts in plasticity generalists employ in establishing themselves in competition with plants on sandy loam soil.

From these results we show that plasticity is potentially a major driver of partitioning of species within the tropical forests of Borneo, where different soil and light combinations lead to unique patterns of change in plasticity values for various growth and functional traits. We speculate that these shifts in plastic values are a major contributor to the evolution of the species, where generalists would give rise to specialists in differing soil environments via the processes of selection. If we consider the generalists as the invaders to the environment equipped to adapt to a certain degree to respond to environmental cues, we can consider the specialists to be the permanent residents that have canalized patterns of functional trait variations that more accurately respond to environmental cues in the local habitat. This is the reason why generalists and clay specialists are not more prevalent in sandy loam environments, for while they may show greater plasticity than the sandy loam specialists, they however may not be as consistently adaptive to the relatively poorer environment (Ghalambor et al. 2007). Increased plasticity in a resource poor environment may lead to responses to erroneous environmental cues, which are more fatal as a whole to a more plastic population.

Further research can be conducted to analyze how these traits may respond in a maladaptive manner to the environment for the generalists, and more plastic clay specialists, as well as the specific patterns of functional trait plasticity that allows sandy loam specialists to outlast their more plastic cousins in their home environment.

Additional research can also be performed on intra-specific plasticity, which could explain why certain species show more generalists tendencies although they may belong to either one of the putative soil specialization groups. Finally, a more indepth analysis of the actual trait values with plasticity values should shed further light on the role of plasticity in determining the evolution of trees in Borneo, and which species are more prone to increased or decreased specialization.

Overall, we hope we have shed more light upon the intricate relationships between the plasticity of functional traits, and the role they play in influencing growth and survival in a hyper-diverse ecological environment.

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