Bark traits and life-history strategies of tropical dry- and moist forest trees

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Summary

1. Bark is crucial to trees because it protects their stems against fire and other hazards and because of its importance for assimilate transport, water relationships and repair. We evaluate size-dependent changes in bark thickness for 50 woody species from a moist forest and 50 species from a dry forest in Bolivia and relate bark thickness to their other bark characteristics, species life-history strategies and wood properties.

2. For 71% of the evaluated species, the allometric coefficient describing the relationship between bark thickness and stem diameter was significantly < 1 (average 0·74; range 0·38–1·20), indicating that species attain an absolute increase in bark thickness with increasing stem diameter but invest relatively less in bark thickness at larger diameters.

3. We hypothesized that in response to more frequent fires, dry-forest species should have thicker barked trees. Contrary to this prediction, dry- and moist-forest tree species were similar in allometric bark coefficients and bark thickness.

4. In both forest types, about 50% of the species never developed bark thick enough to avoid fire damage to their vascular cambia. Recent increases in fire frequency and extent may therefore have potentially large effects on the composition of these forests.

5. Within each forest, coexisting species displayed a diversity of bark investment strategies, and bark thickness of trees 40 cm stem diameter varied up to 15-fold across species (ranging from 1·7 to 25·7 mm).

6. In both forests, sapling bark thickness was positively related to adult stature (maximum height) of the species, possibly because trees of long-lived species are more likely to experience fire during their life span, whereas for species that are characteristically small or short-lived, it may not pay off to invest heavily in bark and they may follow a resprouter strategy instead. Sapling bark thickness was not related to species' shade tolerance.

7. Bark and wood traits were closely associated, showing a trade-off between species with tough tissues (high densities of bark and wood) on the one hand vs. species with watery tissues (high water contents of bark and wood) and thick bark on the other hand.

8. Species with different bark investment strategies coexist in both the moist and the dry tropical forest studied. Bark and wood fulfil many functions, and the observed trade-offs may reflect different plant strategies to deal with fire, avoidance and repair of stem damage, avoidance and resistance of drought stress, and mechanical stability.

Key-words: adult stature, allocation, bark thickness, defence, fire, shade tolerance, tropical forest, water storage, wood density

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Introduction

Fire exerts a major control over many ecosystems in the world, affecting vegetation structure and composition, species distributions and ecosystem processes (Bond, Woodward & Midgley 2005; Keeley *et al.* 2011). In the wet tropics, large-scale forest fires occur only rarely during extreme droughts (Van Nieuwstadt & Sheil 2005), but the frequency of tropical forest fires has increased dramatically over the past decades, due to increased slash-and-burn agriculture, and the synergistic effects of logging and major droughts (Siegert *et al.* 2001; Aragao & Shimabukuro 2010).

STRATEGIES TO DEAL WITH FIRE: RESEEDERS, RESPROUTERS AND BARK DEFENCE

Plant species display a variety of fire adaptations and life-history strategies. For example, woody species from short-statured Mediterranean woodlands have been classified into reseeders and resprouters (Pate *et al.* 1990; Pausas *et al.* 2004). Reseeders are small and reach reproductive maturity between fires, whereas resprouters mainly regenerate by resprouting from large root systems with storage reserves. In ecosystems with long-lived and tall trees, other strategies become apparent; many species protect their vascular cambia from lethal fire damage with thick insulating bark.

BARK AND FIRE INSULATION

Bark refers to all tissues outside the vascular cambium. It consists of inner bark that contains secondary phloem that transports and stores photosynthates and outer bark produced by the cork cambium that next to the inner bark provides additional stem protection (Romero 2013). Bark has excellent fire insulating properties, which is mostly determined by bark thickness (Vines 1968) and to a lesser extent by high bark density and bark moisture content (Reifsnyder, Herrington & Spalt 1967; but see Pinard & Huffman 1997; Brando *et al.* 2012). Bark insulation increases with the square of bark thickness, and bark thickness is therefore the best predictor of tree stem survival after fire (e.g. Ryan, Peterson & Reinhardt 1988). In most tree species, bark thickness increases with stem diameter, and the allometric shape of this relationship could reflect the fire regime under which a species evolved. Where fire return intervals are short, plants should invest in thick bark when being young and small, whereas if fire return intervals are long, species should invest in bark defence when being old and large (Jackson, Adams & Jackson 1999).

GRADIENTS IN FIRE REGIMES AND BARK THICKNESS FROM DRY TO WET FORESTS

Fire intensity and frequency decrease along the gradient (Hawthorne 1996) from savannas (every 1–3 years) to dry forest (every 4 years when it borders savanna, Cochrane *et al.* 1999) and less than once a century in wet forests. Bark thickness decreases along this fire gradient from savanna trees to (gallery) forest trees to wet forest trees (Hoffmann *et al.* 2009; Lawes, Midgley & Clarke 2013). Fire-induced tree mortality also increases along the rainfall gradient, from 8 to 23% of the trees in dry forests to 34% in wetter tropical forests (Hoffmann *et al.* 2009), but it is unclear whether low tree mortality in dry forests can be attributed to the trees being thicker barked and having more root reserves or because dry forests experience a lower fire intensity because of less combustible material on the forest floor (Dickinson & Kirkpatrick 1985). The aim of this study is to evaluate how bark thickness relates to bark traits, wood traits and life-history strategies of tropical dry- and moist forest species.

LIFE-HISTORY STRATEGIES AND INVESTMENTS IN BARK DEFENCE

Apart from fire insulation and assimilate transport, bark fulfils many other functions including defence against herbivores and pathogens, avoidance of mechanic injury by large mammals, reduction in water loss from stems, provision of structural support and repair after injury (Paine *et al.* 2010; Romero 2013). Bark traits are therefore likely to form part of a general stem defence syndrome (Romero & Bolker 2008; Baraloto *et al.* 2010).

Little is known how bark investment is related to the life-history strategies of tree species. In closed-canopy forests, light is one of the most limiting factors for tree growth and survival. Adult stature (i.e. the maximum average tree size a species attains) and light requirements for regeneration present therefore the main strategy axes of tropical forest trees because they allow species to partition light gradients in the forest canopy and on the forest floor (Kitajima & Poorter 2008).

Small-statured tree species benefit little from investment in stem bark defence because their crowns remain within reach of ground fires, and they should therefore follow a reseeder or resprouter strategy. For individuals of tall-statured species, in contrast, it may pay off to invest heavily in bark defence because, as adults they have their crowns high up in the canopy and because they are likely to experience fire during their long life spans.

Light-demanding forest species tend to be fast growing, and for them, the opportunity costs of resource investments in structural defences (such as bark) are high (Coley 1987) because it comes at the expense of a reduced investment in leaves, which curtails potential growth rates. In contrast, shade-tolerant species regenerate in the low-resource environment of the forest understory where there is a premium on survival rather than potential growth. They do so by high investment in structural stem and leaf defences (Kitajima & Poorter 2010).

Several studies have compared bark thickness of species, but most considered a relative limited number of species (<15, e.g. Romero, Bolker & Edwards 2009; but see Roth 1981; Hoffmann, Orthen & Do Nascimento 2003; Brando *et al.* 2012). Some studies considered species from geographically widely different communities so that it is difficult to separate acclimation from adaptation (Jackson, Adams & Jackson 1999). Other studies considered the whole tree community but included only few individuals per species (e.g. Paine *et al.* 2010), making it difficult to remove the confounding effect of tree size on bark thickness. Moreover, for tropical forest trees, it is largely unknown how bark thickness is related to other important life-history axes of variation, such as shade tolerance or adult stature. This information is needed to predict how the structure and composition of tropical forest communities will shift after fire (Gould *et al.* 2002; Van Nieuwstadt & Sheil 2005), especially, because fire frequencies will increase even further with ongoing climate- and land use change (Alencar *et al.* 2011).

AIMS AND HYPOTHESES

We evaluate how size-dependent changes in bark thickness relate to other bark traits, wood characteristics and life-history strategies of 50 species from a dry tropical forest and 50 species from a moist tropical forest in Bolivia. We address four questions: first, does bark thickness differ between dry- and moist-forest species? Second, how does bark thickness change with increases in stem diameter of trees of different species, and at what stem diameter (and hence bark thickness) are trees safe from fire? Third, how is bark thickness associated with species life-history strategies such as adult stature and regeneration light requirements? Fourth, how are bark and wood traits related? We hypothesized that (i) for individuals of the same size, dry-forest species have thicker bark than moist-forest species because they are adapted to frequent fires, (ii) bark thickness increases with tree diameter and all species attain a stem diameter at which they are safe from fire, (iii) size-corrected bark thickness increases with adult stature of the species because long-lived species are more likely to be exposed to fire, whereas bark thickness decreases with regeneration light requirements because the opportunity costs of structural stem defence are high for fast-growing pioneers, and (iv) across species, there is a positive relationship between densities of bark and wood because they are components of the same stem defence syndrome.

Materials and methods

RESEARCH SITES

Field work was carried out in the tropical moist semi-evergreen forest of La Chonta (15°47′S, 62°55′W) and the dry deciduous forest of Inpa (16°1′S, 61°4′W) in lowland Bolivia. Henceforth, they are referred to as moist forest and dry forest, respectively. According to the Köppen–Geiger classification system, both sites are in the equatorial savanna climate zone with dry winters and hot summers (Awa; Kottek *et al.* 2006). Annual precipitation in La Chonta is 1580 mm, with a dry season (potential evapotranspiration > rainfall) of 1 month. The forest has a mean canopy height of 27 m, tree density of 367 ha^{-1}, basal area of 19·7 m^2 ha^{-1} and species richness of 59 ha^{-1} [all data for trees >10 cm diameter at breast height over bark (d.b.h.), Peña-Claros *et al.* 2012]. About a third of the trees in the canopy are deciduous in the dry season. Inpa is drier, with only 1160 mm of precipitation annually and a 3-month dry season. The forest has a mean canopy height of 20 m, tree density of 420 ha^{-1}, basal area of 19·3 m^2 ha^{-1} and species richness of 34 ha^{-1} (Peña-Claros *et al.* 2012). Nearly all trees in the canopy are dry season deciduous, but many understory saplings are evergreen. In general, the moist forest is more fertile than the dry forest (Peña-Claros *et al.* 2012). The absolute rainfall difference between the two forests is not large, but it results in striking differences in floristic composition, structure and phenology (Peña-Claros *et al.* 2012; see also Killeen *et al.* 2006). During the past decade, fires were more frequent in dry forest (where Inpa is situated) than in wetter Bolivian forests (Rodriguez Montellano 2012).

SPECIES SELECTION

In total, 50 woody species were selected from the moist forest and 50 woody species from the dry forest, with eight species common to both sites (see Table S1, Supporting Information). The selected species were the most abundant species at each site. To relate species traits to shade tolerance and adult stature, we used this full species data set, as it encompasses a wide range of life-history strategies and tree sizes. To compare the two forest types, we used only the subset of species that attain 10-cm d.b.h. (47 species from the moist forest, 44 species from the dry forest).

A continuous and objective measure of the regeneration light requirements of each species was obtained from Poorter & Kitajima (2007) who calculated for each species the average population-level crown exposure at a standardized height of 2 m (juvenile crown exposure, CE$_{juv}$, see their article for more details). A low CE$_{juv}$ of 1 indicates that a species regenerates mainly in the shaded understory (i.e. a shade-tolerant species), whereas a high CE$_{juv}$ of ≥2·5 indicates that it mainly regenerates in the bright light conditions of canopy gaps (i.e. a light-demanding species). The adult stature of the species was described using the 'average' maximum height (H_{max}) of a species (sensu Thomas 1996). The H_{max} was calculated based on the diameter of the third thickest tree of the species in the 420 ha of permanent sample plots of Instituto Boliviano de Investigación Forestal (IBIF) and species-specific regression equations relating tree height to stem diameter (Poorter, Bongers & Bongers 2006). The third thickest tree was used to avoid rare large individuals or trees with unduly large diameter due to measurement errors.

BARK MEASUREMENTS

For each species, individuals were selected over the full diameter range, from 1-cm basal stem diameter up to the largest sizes found. On average, 14 individuals were selected per species (range, 8–21) with a total of 1508 trees. The diameters of each tree's stem were measured at heights of 0·5 m and at 1·3 m. Bark thickness was measured at 0·5 m from the ground because most tropical forests suffer from low-flame-height ground fires rather than crown fires. For larger trees, a 3 × 3 cm piece of bark was removed to the vascular cambium with a chisel from the northern side of each tree, and from saplings, a smaller piece of bark was removed. The minimum and maximum bark thickness were measured to the closest mm with a calliper and averaged.

In a separate study, bark and wood samples were taken from three individuals per species (Poorter 2008). Data were collected for 34 dry-forest species and 40 (bark) to 47 (wood) moist-forest species. The trees were 20–50-cm d.b.h. for the tall-statured species and close to their maximal sizes for small-statured species. The bark sample included inner and outer bark; the wood sample contained mostly sapwood and was taken just interior to the cambium up to 2 cm depth. Fresh mass was determined with a balance with a precision of 0·01 g, and fresh volume was measured using the water displacement method with a precision of 0·01 cm^3, after which the samples were oven-dried for at least 48 h at 70 °C and reweighed. Densities of wood and bark were calculated by dividing dry mass by fresh volume. Water contents of the wood and bark were calculated as $100 \times$ ([fresh mass − dry mass]/fresh volume).

DATA ANALYSIS

Ontogenetic trends in bark thickness were described for each species as the power relation between bark thickness and stem diameter over bark at 0·5 m height. Two types of regression were performed with different aims. First, to evaluate the allometric coefficient (cf. Jackson, Adams & Jackson 1999), log$_{10}$-transformed bark thickness was regressed against log$_{10}$-transformed stem diameter, using standard major axis regression (i.e. a type II regression), with the program SMATR (Warton *et al.* 2006). Using the 95% confidence intervals, we evaluated whether the allometric slopes differ significantly from 1. Second, to predict bark thickness from stem diameter, log$_{10}$-transformed bark thickness was also regressed against log$_{10}$-transformed stem diameter using a type I regression. These regression equations might then be used in combination with permanent sample plot data to estimate bark thickness from tree diameter as a predictor of vulnerability to fire (e.g. Brando *et al.* 2012) and to estimate timber volume from over-bark measurements. Species may show crossovers in bark thickness with increasing tree size (i.e. a species with a thick bark as sapling may have in larger size classes a relatively thin bark compared to other species), which can confound interspecific comparisons. Bark thickness of each species was therefore also calculated at a standardized reference diameter of 1 cm and for subsequent 10-cm-diameter intervals up to 80 cm diameter using the species-specific regression equations.

To evaluate whether dry-forest trees are thicker barked than moist-forest trees, the bark thickness of dry- and moist-forest species was compared at each of the nine reference diameters, using *t*-tests with species as replicates. We calculated the stem diameters at which individuals of each species are expected to attain a bark thickness of 10 mm, which we assume protects them from lethal stem damage by fire: this bark thickness is intermediate between the results from studies in the region that estimated bark thickness values that lead to ca. 50% mortality after fire (Hoffmann *et al.* 2009: 6 mm; Brando *et al.* 2012: somewhere between 5 and 17 mm) or the bark thickness values at which trees did not attain a lethal cambium temperature of 60 °C when subjected to the experimental wick-fire technique (Pinard & Huffman 1997: 18 mm).

To evaluate whether species with thicker bark invest more biomass in bark, we calculated the bark biomass of a 1-cm-thick cross-sectional stem segment of 10-cm d.b.h. trees. Using the species-specific regression equations, we calculated the cross-sectional bark area, used this value to calculate the volume of a 1-cm-wide band of bark, and multiplied this volume by bark density to get the biomass of the bark ring. To evaluate how bark and stem traits are associated, a principle component analysis (PCA) was carried out using species as data points. Variables included in the PCA were bark thickness at 1-, 10-, 20- and 30-cm d.b.h., the allometric coefficient of the bark–stem diameter relationship, the densities and water contents of wood and bark, bark ring mass and

whether a species has a deciduous leaf habit (1 = yes, 0 = no), produces exudates (latex or resins, 1 = yes, 0 = no), or has spines or thorns on its stem or branches (1 = yes, 0 = no). For this analysis, species were only included if they attain 30-cm d.b.h. and for which data on densities of bark and wood were available (27 dry-forest species, 37 moist-forest species, seven species in common). To evaluate whether bark investment is related to life-history strategy, bark thickness at a standardized diameter of 1 cm was correlated with H_{max} and CE_{juv}, using Pearson correlation. All statistical analyses were carried out using PASSW 17 (SPSS Inc., Chicago, IL, USA).

Results

ONTOGENETIC CHANGES IN BARK THICKNESS

Trees generally show a strong ontogenetic increase in bark thickness with stem diameter (Fig. 1), with very similar relationships and explained variances for dry-forest ($r^2 = 0.67$, $N = 750$, $P < 0.001$) and moist ($r^2 = 0.68$, $N = 681$, $P < 0.001$)-forest trees. Nonetheless, relative investments in bark thickness decline rapidly with stem diameter; bark constituted 13% of the stem diameter for 1-cm-thick trees, 7% for 10-cm-thick trees and 3% for 150-cm-thick trees (Fig. 1). Power relationships describe ontogenetic trends in bark thickness of individual species very well, with an average r^2 across species of 0·82 (range, 0·37–0·99; Table S1, Supporting Information). The allometric coefficient of the slope relating bark thickness and stem diameter did not differ between dry- and moist-forest species (*t*-test, $t = -0.48$, d.f. = 89, $P = 0.63$). The allometric coefficient averaged 0·74 (range 0·38–1·20) across species, and for 65 of the 91 evaluated species, it was significantly <1, which indicates that while bark thickness increases with stem diameter, trees invest relatively less in bark thickness at larger diameters.

Species show ontogenetic crossovers in bark thickness; that is, some species have, compared with other species, a thin bark when small and a relatively thick bark at larger tree diameters (Fig. 2). In both forest types, coexisting species show large variation in bark thickness: when compared at a reference diameter of 40 cm, moist-forest species show an eightfold variation in bark thickness (range 2·9–23·0 mm) and dry-forest species a 15-fold variation (range 1·7–25·7 mm).

DO DRY- AND MOIST-FOREST SPECIES DIFFER IN BARK THICKNESS AND FIRE SAFETY MARGINS?

When species of dry- and moist-forest trees are 1 cm in over-bark diameter, they have a statistically similar bark thickness (*t*-test, $t = 0.50$, $P = 0.62$, d.f. = 89). The same applies at each of the larger reference stem diameters (Fig. 3a). Although dry-forest species tend to have a thicker bark than moist-forest species at the largest reference sizes, this difference is not significant, at least partially because few species attain such large (i.e. ≥70 cm d.b.h.) sizes and can be included in the analysis.

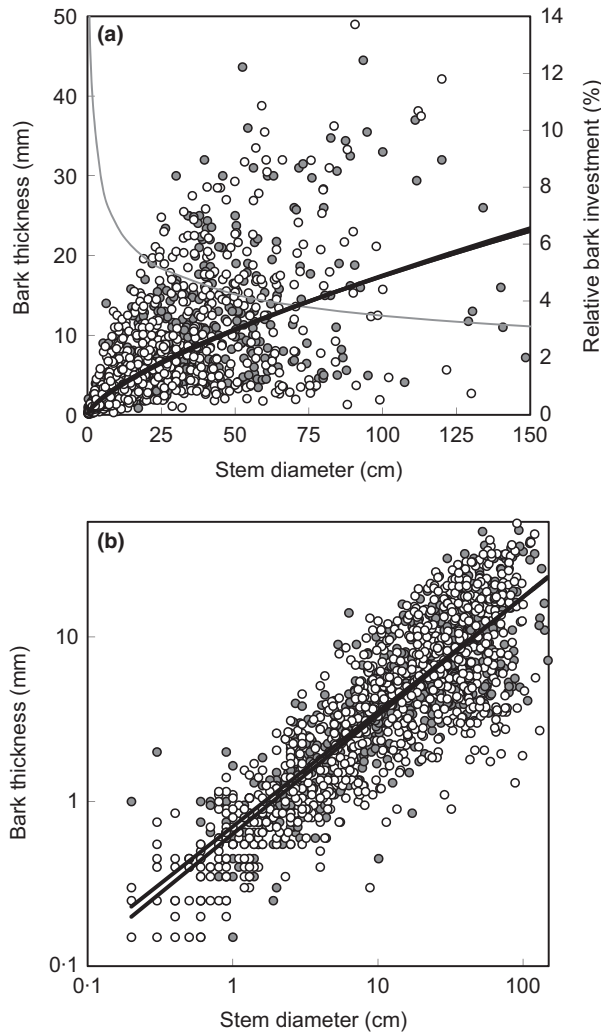Assuming that trees are safe from lethal stem damage by fire if their bark is >10 mm thick, we found that 49% of

Fig. 1. (a) Untransformed and b) log–log relationships between bark thickness and stem diameter at 50 cm height for dry-forest trees (open symbols, $n = 826$) and moist-forest trees (filled symbols, $n = 738$). Regression lines are shown for trees belonging to dry-forest ($\log[BT] = -0.1552 + 0.6938 \times \log[d.b.h.]$; $r^2 = 0.67$, $n = 750$) and moist-forest species ($\log[BT] = -0.1448 + 0.6917 \times \log[d.b.h.]$; $r^2 = 0.68$, $n = 681$) that can attain >10-cm d.b.h. The relative investment in bark thickness (as a percentage of stem diameter) is indicated by the grey line.

moist-forest species and 47% of dry-forest species never attain this minimum thickness. This finding suggests that whole populations of thin-barked species are at risk from fire in both forests. The remaining species only reach a safe bark thickness when they are 12–72-cm d.b.h. (Fig. S1, Supporting Information), and these 'safe' diameter sizes did not differ between dry- and moist-forest species (*t*-test, $t = 0.91$, $P = 0.369$, d.f. = 42).

BARK THICKNESS VS. LIFE-HISTORY STRATEGIES

Trees run the largest risk of fire damage to their stems when small, which is also when investments in thick bark are most appropriate (unless they invest in below-ground storage and follow a resprouter strategy instead). Species

differed largely in their bark thickness as saplings (i.e. at 1-cm stem diameter), and in both forests, the bark thickness of species was positively related to their adult stature, but not related to their juvenile crown exposure (Fig. 4).

ASSOCIATIONS BETWEEN BARK AND WOOD TRAITS

To evaluate whether species that produce thicker bark also invest more biomass in bark, we calculated for each species the bark biomass of a 1-cm-tall band of bark of a 10-cm d.b.h. tree. In both the dry- and moist-forest, there was a strong positive relationship between bark mass and bark thickness of the species (Fig. 5a), and the two forest communities did not differ significantly in their slopes and intercepts (smatr analysis, $P = 0.515$ for slopes, $P = 0.402$ for intercepts). Only in the dry forest was bark thickness negatively correlated with species-specific wood density, indicating that soft-wooded species were protected by thick bark (Fig. 5b).

For species in both forests, bark density was strongly positively correlated with wood density (Fig. 5c), implying that species with dense wood make also dense bark (and hence have a low water content of bark). The two forest communities did not differ in the slopes of this relationship, but they differed in their intercepts (smatr analysis, $P = 0.668$ for slopes and 0.0006 for intercepts); when compared at the same wood density, dry-forest species had lower bark density than moist-forest species (Fig. 5b). Most species fall below the 1 : 1 line, indicating that their wood is denser than their bark, but several species (*Jacaratia spinosa*, *Cavanillesia hylogeiton* and *Ceiba pentandra*) make denser bark than wood. In both forests, species showed a strong negative relationship between bark density and bark water content (Fig. 5d) and the two communities did not differ in the slopes and intercepts of this relationship (smatr analysis, $P = 0.128$ for slopes, $P = 0.251$ for intercepts). This negative relationship indicates that species fill up most of their bark volume either with solid material or with water.

The associations between stem and bark traits were analysed with a principal component analysis (PCA). The first PCA axis explained 36% of the variation and shows a trade-off between high densities of bark and wood on the left vs. thick bark and high water contents of bark and wood on the right (Fig. 6a). The second PCA axis explained 26% of the variation and shows a trade-off between a high bark biomass investment at the top of the second PCA axis vs. a high water content of bark and wood at the bottom. Exudate production, leaf habit and spines showed low loadings on these two axes. High water content of wood tended to be associated with spines ($P = 0.051$). The same relationships and trade-offs were found when using bivariate Pearson correlations (Table 1). Dry- and moist-forest species showed largely overlapping positions in their multivariate trait characteristics (Fig. 6b) and did not differ significantly in their regression scores on the first and second PCA axis.
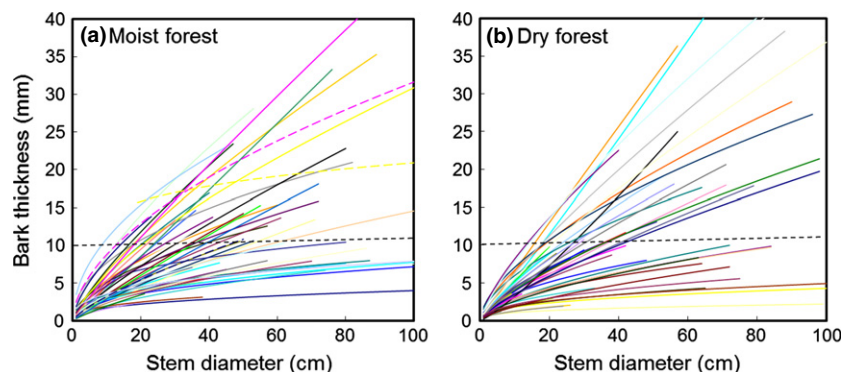
Fig. 2. Allometric power relationships between bark thickness and stem diameter at 50 cm height for moist-forest species (left panel, $N = 47$) and dry-forest species (right panel, $N = 44$). Regression lines are shown for each species. The *x*-axis and *y*-axis are truncated to obtain an optimal resolution for most species. The horizontal dashed line indicates the bark thickness of 10 mm, at which species are safe from lethal stem damage by fire.
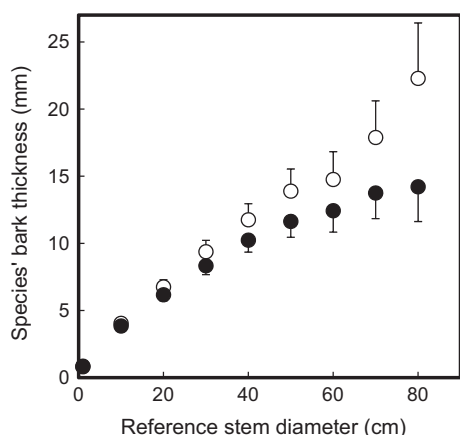

Fig. 3. Bark thickness vs. stem diameter for dry-forest species ($N = 44$, open symbols) and moist-forest species ($N = 47$, filled symbols). Species are used as replicates, and bark thickness is compared at several stem diameters. Dry- and moist-forest species have similar bark thickness for each of the standardized sizes (*t*-tests, $P > 0.05$ in all cases).

Discussion

We evaluated size-dependent changes in bark thickness for 92 woody species and related this to forest type and life-history strategies. Contrary to our expectations, the bark of dry- and moist forest tree species is similar in thickness and other properties. Coexisting species in each forest community showed large variation in bark investment strategies and up to 15-fold differences in bark thickness. This interspecific variation in size-corrected bark thickness is partially explained by adult stature, with large-statured species having thicker bark, but is not related to the regeneration light requirements of the species.

ONTOGENETIC CHANGES IN BARK THICKNESS

All species showed a strong absolute increase in bark thickness with increased stem diameter (Fig. 2). For 71%

of the species, the allometric coefficient was significantly smaller than 1, which indicates that species invest relatively less in bark thickness at larger diameters possibly because they have sufficient phloem for sugar transport and sufficiently thick bark for protection. Alternatively, large trees invest carbon in other competing plant functions, such as reproduction (Thomas 2011), and thus can allocate less carbon to bark growth.

Power functions describe the bark thickness–stem diameter relationships well, with an average r^2 of 0·68 for the forest-wide relationships, and an r^2 of 0·82 across species. In contrast, forest-wide allometric relationships reported for other tropical forests explain substantially less variation in bark thickness [r^2 = 0·38 for a French Guianan forest (Paine *et al.* 2010), 0·35–0·38 for Amazonian rain forest (Uhl & Kauffman 1990; Barlow, Lagan & Peres 2003)] possibly because they included few trees with small stem diameters (<10–20 cm) and thin bark or because they reported maximum bark thickness rather than the average as we did. Such forest-wide allometric relationships are often used to predict tree mortality after fire, and our results suggest that the predictions can be improved by using species-specific equations (cf. Brando *et al.* 2012).

DO DRY- AND MOIST-FOREST SPECIES DIFFER IN BARK THICKNESS AND FIRE SAFETY MARGINS?

We hypothesized that dry-forest species have thicker bark than moist-forest species because they are adapted to more frequent fires. Instead, we found that dry- and moist forest trees had a surprisingly similar allometric bark coefficients and bark thickness at the species level and a similar proportion of species that can attain 'fire-safe' stem diameters. It is clear that each forest harbours a range of species with different bark investment strategies (Figs 2 and 6).

Perhaps the historical fire regimes in both forests are more similar than we presumed, or the higher fire frequency in dry forests is offset by lower fire intensity. Fire intensity can be lower in dry forest due to lower
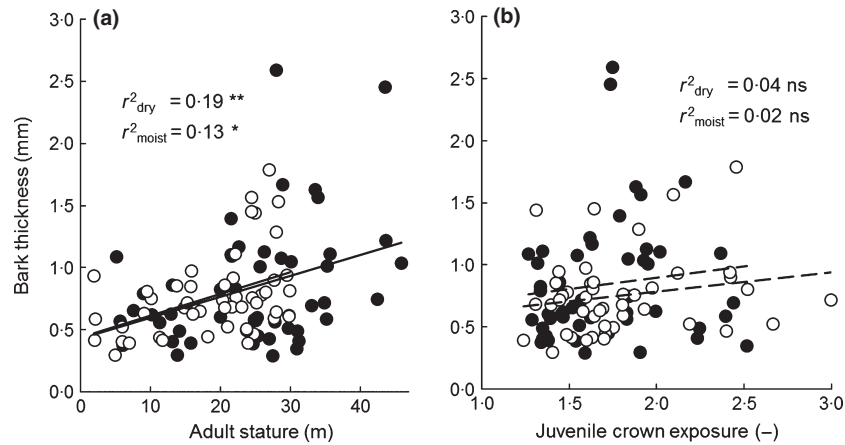
Fig. 4. Bark thickness of dry-forest (open symbols, N = 45–49) and moist-forest (filled symbols, N = 50) tree species at the standardized stem diameter of 1 cm in relation to (a) maximum adult stature and (b) regeneration light requirements (i.e. juvenile crown exposure index values). Regression lines, coefficients of determination (r^2) and significance levels are shown.*P < 0·05; ***P < 0·001; ns P > 0·05. Significant regressions are represented by continuous lines, and nonsignificant regressions are represented by broken lines.
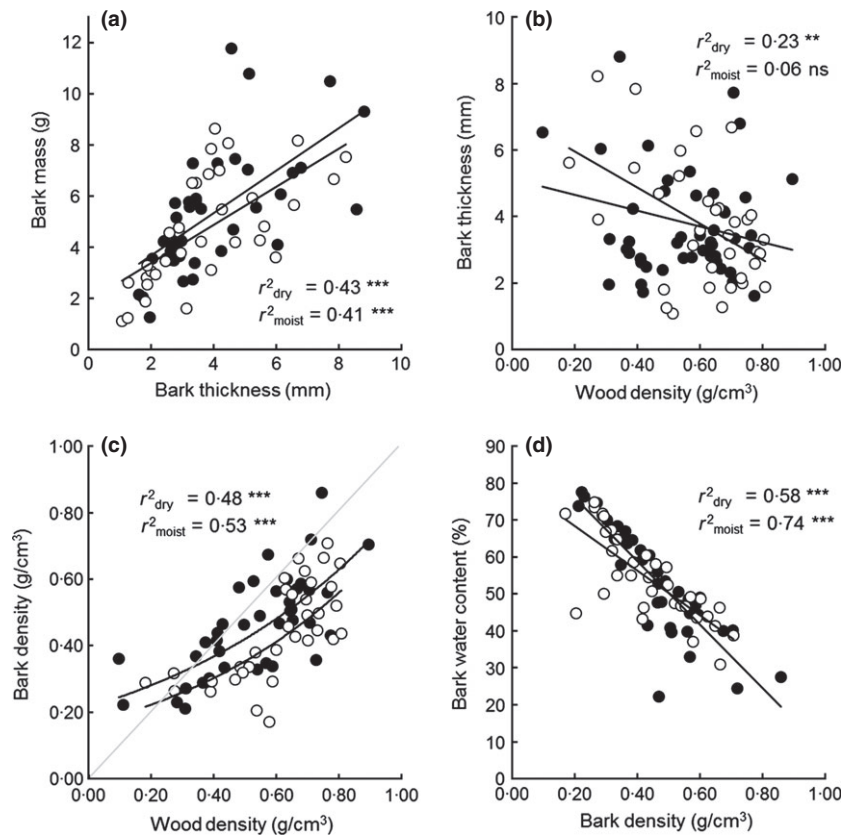

Fig. 5. Bark properties of dry-forest species (open symbols) and moist-forest species (filled symbols). (a) bark dry mass vs. bark diameter, (b) bark thickness vs. wood density, (c) bark density vs. wood density and (d) bark water content vs. bark density. Bark mass was calculated for a 1-cm-tall band of bark for trees 10-cm d.b.h. Regression lines, coefficients of determination (r^2) and significance levels are shown.*P < 0·05; **P < 0·01; **P < 0·001. N varies from 40 to 47 for moist-forest species and N = 34 for dry-forest species.

productivity (Toledo *et al.* 2011) and lower tree mortality rates in dry forest, resulting in less combustible material on the forest floor. This argument is obviously untenable for dry forests with open canopies and abundant understory grasses, but this is not the case in our dry forest where understory grasses are absent. Frequent fires may also prevent the buildup of a large pool of organic material on the forest floor, leading to lower fire intensity. Indirect evidence for low fire intensity in dry forests comes from a study by Hoffmann *et al.* (2009) who reported that fire-induced tree mortality was much lower in dry than in wet forests. Where we found little differences in bark thickness between dry and wet forest, other studies do show that bark thickness differs among species from different vegetation types. Scattered trees in Brazilian savannas where fires are frequent have, for example, thicker bark than trees in neighbouring gallery forests where fires are less frequent or in Amazonian forests where fires are
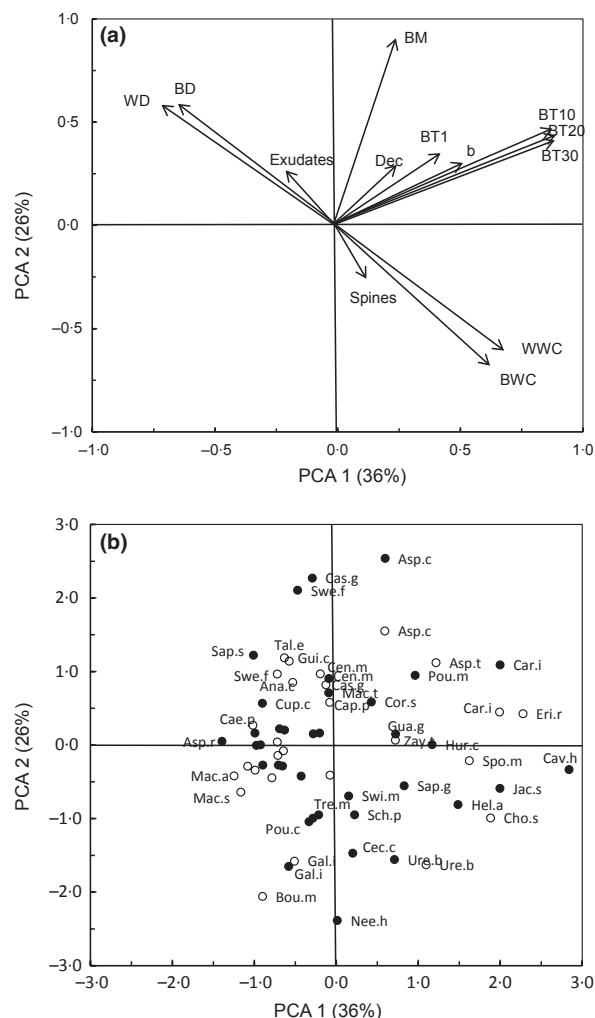
Fig. 6. (a) Associations between bark and stem traits and (b) regression scores of tropical dry- and moist-forest tree species as analysed with a principle component analysis (PCA). Axis loadings are shown for bark thickness for trees with 1-cm (BT1), 10-cm (BT10), 20-cm (BT20) and 30-cm (BT30) stem diameter, bark mass of a bark slice of trees of 10-cm stem diameter (BM), the slope (b) of the bark–stem diameter power relationship, and wood density (WD), wood water content (WWC), bark density (BD), bark water content (BWC), exudates, spines and deciduous leaf habit (Dec). Regression scores are shown for dry-forest species (open symbols, $N = 27$) and moist-forest species (filled symbols, $N = 37$). Species abbreviations refer to the first three letters of the genus name, followed by the first letter of the species name. For full species names, see Table S1 (Supporting Information).

extremely rare (Hoffmann, Orthen & Do Nascimento 2003; Hoffmann *et al.* 2009).

In both forests we studied in Bolivia, about half of the tree species never attain a fire-safe bark thickness, which means that their whole population is susceptible to lethal fire damage from stem heating. During the past decade, fire frequency and extent have increased sixfold in Bolivia (Rodriguez Montellano 2012), and this is only likely to increase in the future. As a result, potentially large fire impacts on forest structure and composition are expected.

Nevertheless, the reality is that fire occurrence and intensity are spatially highly variable, and many trees in forests that are largely burned do escape fire. The remaining species do attain a safe bark thickness and do so at very similar stem diameters in dry- and moist-forest species. As tree diameter growth rates are 2·3-fold higher in the moist compared with the dry forest (Dauber, Fredericksen & Peña-Claros 2005), this also means that it takes dry-forest species more than twice as long to attain a safe (bark) diameter. The risk of severe cambial damage or topkill is therefore much higher in dry forest and it is perhaps for this reason that dry-forest species are far better resprouters than moist-forest species; they have a higher survival and grow substantially faster after stem damage (Poorter *et al.* 2010). Postfire resprouting ability depends largely on below-ground reserves, and these are likely to be higher for dry-forest species, because they invest relatively more biomass in roots (Markesteijn & Poorter 2009). Other studies also found that fire-adapted species have typically higher below-ground carbohydrate concentrations (Bond & Midgley 2003) and/or pool sizes (Hoffmann, Orthen & Do Nascimento 2003).

BARK THICKNESS VS. LIFE-HISTORY STRATEGIES

Within each forest, tree species showed up to 15-fold differences in bark thickness when compared at a standardized stem diameter. We hypothesized that this interspecific variation is positively related to the adult stature of the species because trees of long-lived species are more likely to experience fire during their life spans. This hypothesis was supported in both forest types, as saplings of large-statured species produce thicker bark (Fig. 4a). For small and short-lived species, it may not pay off to invest heavily in bark, and they may follow a resprouter strategy instead.

We also hypothesized that bark thickness decreases with species-specific regeneration light requirements because the opportunity costs of structural stem defence are higher for fast-growing pioneers. This hypothesis was rejected because there was no apparent relationship between bark thickness and average juvenile crown exposure in any of the forest types (Fig. 4b). Light-demanding pioneer species do perhaps invest in thick bark for other reasons, such as structural support or defence against herbivores or pathogens that otherwise might attack their soft wood. Indeed, soft-wooded species in the dry forest produced thick bark, although no such a relationship was observed in the moist forest (Fig. 5b).

Light-demanding tropical pioneer tree species are typically poor resprouters (Putz & Brokaw 1989; Poorter *et al.* 2010) and employ after fire a reseeder strategy instead. They may recruit massively after forest fires (Slik *et al.* 2010) because of their copious seed production, effective long-distance seed dispersal (Muller-Landau *et al.* 2008) and high abundance in the soil seedbank (Putz 1983).

Table 1. Pearson correlation between bark and stem traits across species. Above the diagonal correlations are presented for species with complete trait data that were included in the principal components analysis (*N* = 64). Below the diagonal correlations are presented for all species (*N* = 64–100). For explanation of trait abbreviations, see Fig. 6

	BT1	BT10	BT20	BT30	b	WD	BD	WWC	BWC	BM	Spines	Exudates	Dec
BT1		**0·66**	**0·47**	**0·37**	**−0·30**	−0·10	−0·21	0·08	−0·03	**0·44**	−0·10	0·01	0·16
BT10	**0·68**		**0·97**	**0·93**	**0·44**	**−0·33**	**−0·33**	**0·29**	0·21	**0·61**	−0·03	−0·05	0·20
BT20	**0·52**	**0·97**		**0·99**	**0·62**	**−0·36**	**−0·33**	**0·31**	**0·26**	**0·58**	−0·01	−0·05	0·18
BT30	**0·40**	**0·94**	**0·99**		**0·69**	**−0·37**	**−0·33**	**0·31**	**0·27**	**0·55**	−0·01	−0·04	0·17
b	**−0·39**	**0·34**	**0·51**	**0·63**		−0·21	−0·03	0·17	0·12	**0·36**	0·03	−0·03	0·00
WD	−0·13	**−0·34**	**−0·36**	**−0·37**	−0·16		**0·71**	**−0·92**	**−0·79**	**0·29**	−0·22	**0·28**	0·09
BD	−0·16	**−0·31**	**−0·33**	**−0·33**	−0·08	**0·64**		**−0·69**	**−0·82**	**0·51**	−0·12	0·19	−0·07
WWC	0·12	**0·29**	**0·30**	**0·32**	0·12	**−0·92**	**−0·62**		**0·79**	**−0·29**	0·25	**−0·29**	−0·07
BWC	−0·03	0·21	**0·26**	**0·27**	0·14	**−0·76**	**−0·81**	**0·75**		**−0·47**	0·19	−0·22	0·01
BM	**0·48**	**0·64**	**0·61**	**0·55**	0·31	**0·23**	**0·49**	**−0·24**	**−0·45**		−0·12	0·11	0·11
Spines	0·01	0·01	0·00	−0·01	0·03	−0·18	−0·08	0·19	0·15	−0·07		0·06	0·14
Exudates	0·04	0·03	0·00	−0·05	−0·06	0·17	0·17	−0·17	−0·18	0·19	0·01		0·01
Dec	**0·25**	**0·25**	**0·24**	**0·23**	−0·09	−0·04	−0·03	0·04	0·01	0·15	**0·23**	0·03	

WD, wood density; WWC, wood water content; BD, bark density; BWC, bark water content; BM, bark mass.

Significant correlations (*P* < 0·05) are given in bold, and correlations with *P* < 0·001 are bold and underlined.

TRADE-OFFS AND THE SPECTRUM OF BARK AND WOOD TRAITS

We hypothesized that species-specific bark and wood traits are closely associated because they form part of the same stem defence syndrome (cf. Baraloto *et al.* 2010). Overall, we found that bark and wood traits were closely associated, showing a trade-off between species with tough tissues (high densities of bark and wood) on the one hand vs. species with watery tissues (high water contents of bark and wood) and thick bark on the other hand (Fig. 6). Other defence strategies (exudates, spines) and a deciduous leaf habit were only loosely associated with these spectra (Fig. 6, Table 1). Stem bark and wood fulfil many functions, and the observed trade-off may reflect different plant strategies to deal with fire, avoidance and repair of stem damage, and avoidance and resistance of drought stress.

THICK BARK PROTECTS AGAINST FIRE

Thick bark with high water contents could be advantageous during fires, as much of the heat is absorbed by warming and vaporizing the water. In a fire experiment in a moist forest in Amazonian Brazil, Brando *et al.* (2012) found that until all bark water is volatilized, cambium temperatures do not exceed 100 °C, even if the fire adjacent to the outer bark is several times higher. Despite this buffering effect of water, they also found that increased water content of bark was associated with an increased heat transfer rate, probably because of the high thermal conductivity of water. The best and most realistic combination of bark properties for heat insulation could therefore be a combination of low water content of bark and high tissue density (i.e. the species in the lower right corner of Fig. 5d), as dense tissues have low thermal diffusivity. Yet, the relationship between heat insulation and bark traits is complicated, as many of these bark traits are associated (cf. Fig. 6). Brando *et al.* (2012) reported that when comparing different models to explain the protection of vascular cambia from fire damage, bark thickness was the best and only predictor of heat transfer rates and that water content and density of bark did not explain anything in addition.

DAMAGE AVOIDANCE VS. DAMAGE REPAIR

Wood and bark traits are also crucial for damage avoidance and repair. Trees are long-lived organisms that rely on well-defended stems for continued mechanical support, conduction and storage. Densities of bark and wood were tightly coupled in both the dry and the moist forests (Fig. 5c), and species with dense tissues may avoid damage as they produce small cells with thick cell walls that deter herbivores and pathogens. Species with high wood density also tend to produce exudates such as latex or resins, which clog the mouthparts of chewing insects, and rapidly seal fresh stem wounds against pathogen intrusion. In our study, exudates were not significantly associated with bark thickness, whereas other studies from wetter forest found that thick-barked species have more copious latex production, probably because they produce numerous latex channels in their inner bark (Paine *et al.* 2010). Dense-wooded species are also efficient in compartmentalization of damage, thus reducing pathogen spread and, hence, decay penetration (Romero & Bolker 2008). Species with soft and watery tissues, in contrast, have a range of defence strategies; they may benefit from spines to avoid large mammals (Tomlinson *et al.* unpublished data) and thick (outer) bark (Fig. 5b), which provides a first barrier against phloem sucking, cambium eating and xylophagous insects, as well as pathogens. Thick barks are also advantageous in terms of damage repair partially because their widely dilated parenchyma rays facilitate rapid wound closure (Romero & Bolker 2008).

DROUGHT AVOIDANCE VS. DROUGHT RESISTANCE

Stem and bark traits influence whole-tree water balance and phenology (cf. Borchert 1994; Méndez-Alonzo *et al.* 2012). Across species in our dry and moist forest, there was a strong negative relationship between bark (and wood) density and bark (and wood) water content (Fig. 5d and 6), indicating that species fill their bark and wood volumes either with solid material or with water and only to a lesser extent with gas. Parenchyma cells in the sapwood and inner bark store large volumes of water that is available as a water source for transpiring leaves when water uptake by roots lags (Scholz *et al.* 2007); water stored in the stem contributes as much as 10–50% of the daily transpiration (Scholz *et al.* 2007 and references therein). Stored water also enables flowering or flushing of new leaves during the dry season when soil water is in short supply (Borchert 1994), although in our data set deciduousness and tissue water content were uncoupled (Table 1). The amount of water stored in wood and bark tissues is indicated by their relative water contents, but the amount of water that actually can be released is controlled by tissue properties (Scholz *et al.* 2007). Sapwood capacitance increases with a decrease in wood density, indicating that wood physical properties are important for helping plants function in dry environments.

Borchert (1994) distinguished several plant functional types of tropical dry-forest trees based on leaf phenology, stem water content and dry-season leaf water potential. Deciduous softwood species (like *Chorisia* in our case) with wide vessels drop their leaves early in the dry season to avoid cavitation and use stored water reserves to flower massively during the dry season. Because of low mechanical strength of their low-density wood, they must be stout to be stable, leading to the typical fat or bottle-like stems that store large amounts of water (Méndez-Alonzo *et al.* 2012). Such trees usually have very thick bark, either to store water or to reduce stem water evaporation. In contrast, deciduous hardwood species (like *Tabebuia* and *Acosmium* in our case) usually have dense wood with narrow vessels that are resistant to cavitation (cf. Markesteijn *et al.* 2011a), which helps them withstand low water potentials and tolerate drought (Markesteijn *et al.* 2011b) and, as a result, they typically drop their leaves late in the dry season (Borchert 1994; Méndez-Alonzo *et al.* 2012). Because of the mechanical rigidity conferred by high wood density, such trees have relatively slender stems (cf. Iida *et al.* 2012). Evergreen species with intermediate-to-high wood density (like *Capparis* and *Guibourtia*) are reasonably drought tolerant and are found in less exposed and more mesic microsites. In general, there is therefore a stem spectrum that runs from deciduous, drought avoiding species with stout stems and low-density wood, thick bark and large water capacitance, to more dense wooded, brevideciduous or evergreen drought-tolerant species with slender stems, thin bark and low water capacitance (cf. Méndez-Alonzo *et al.* 2012).

In sum, bark characteristics of the dry- and moist-forest communities are surprisingly similar, whereas bark characteristics of coexisting species are surprisingly different. Apart from fire insulation, bark fulfils many other functions, such as the reduction in evaporation and defence against pests and pathogens, and these manifold functions may lead to large differences in bark characteristics among coexisting tree species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Minimum stem diameters at which trees are expected to be safe from fire damage to their vascular cambium for (a) moist-forest species, and (b) dry-forest species.

Table S1. Overview of bark characteristics of 50 moist- and 50 dry tropical forest tree species.