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Fire frequency filters species by bark traits in a savanna–forest mosaic

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Bark growth rate; Bark Thickness; Ecology; Environmental filtering; Fire; Forest; Root sucker; Savanna

Nomenclature
Coates-Palgrave (2002)

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Abstract

Aims: Savanna and forest biomes co-occur across many subtropical landscapes in Africa, and can be differentiated by their fire regime: fires are more frequent in savannas compared to forests. Bark thickness is a key trait of savanna trees, promoting their survival in this context. The rate of bark production (increment·yr^{-1}) should therefore be critical for determining how quickly a developing sapling would be protected or bark could regenerate between two fires. Despite this, the rate of bark production has seldom been measured in studies of fire-tolerant vs fire-intolerant species.

Location: Hluhluwe-iMfolozi Game reserve, South Africa.

Methods: We examined the distribution of woody species in a South African park over 253 sites, stratified by biome. We described the bark traits of the 63 most abundant species and related them to the fire frequencies of the sites where they occur.

Results: Bark growth rate was a good predictor of woody plant persistence in fire-prone savanna ecosystems. A key exception was root-suckering species, which have their structure physically protected underground and can thus survive frequent fires while producing little bark.

Conclusion: Species of different forest types and savanna have different bark characteristics, highlighting the important role played by fire in shaping biome distribution.

Introduction

Remote sensing technology has provided convincing evidence that multiple biomes, defined here as areas of vegetation characterized by the same dominant life forms, can occur within the same climatic envelope (Woodward et al. 2004; Staver et al. 2011). In the tropics and subtropics, grasses, especially C_4 grasses, can alter the fire regime and maintain a grassy environment or a savanna where the climate can potentially support forests (Woodward et al. 2004; Bond 2008; Staver et al. 2011). Fire plays an important role in shaping savannas by burning extensive areas at frequent intervals (Bond & Keeley 2005; van der Werf et al. 2010; Lehmann et al. 2011). Savanna fires occur several times per decade and, in some regions, twice in a year, but burn with a relatively low intensity. In these surface fire regimes, fire frequency has been shown to control ecosystem structure by top-killing juvenile trees before they become resistant (Higgins et al. 2000, 2012; Bond 2008; Hoffmann et al. 2009; Midgley et al. 2010).

To survive frequent fires, plants can complete their life cycle faster than the period separating two successive fires and protect their seeds or resist flame impact at every fire event (Pyke et al. 2010; Keeley et al. 2011). Trees and shrubs have developed many strategies to avoid the negative impact of fire on their perennial structures. They can survive damage by having good resprouting abilities after fire (Bond & Midgley 2001; Lawes & Clarke 2011; Clarke et al. 2013; Charles-Dominique et al. 2015a). Some savanna plants escape fire by developing as underground trees that have their perennial structures buried under the soil surface (White 1976; Simon & Pennington 2012;

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Maurin et al. 2014). Taller trees in frequently burned savannas have pole-like juveniles with a long trunk overtopping the flame height before branching (Archibald & Bond 2003; Staver et al. 2012). With the exception of underground trees, however, trees and shrubs lose a large part of their biomass if their above-ground structure is not protected when exposed to fire. The role played by bark in protecting plants against fire has been the subject of much research, highlighting the importance of bark thickness and bark quality for tree survival (for tropical systems: Uhl & Kauffman 1990; Gignoux et al. 1997; Hoffmann et al. 2009, 2012; Lawes et al. 2011; Dantas & Pausas 2013; Hempson et al. 2014; Rosell et al. 2014).

If one of the most important attributes for plants surviving frequent fire regimes is thick bark, then the growth rate of bark should be high in such systems. However bark growth rate (bark production per year) has, as yet, been little investigated (Schafer et al. 2015). Bark growth rate is important in determining (1) the period required for a juvenile tree to develop protection against fire; and (2) how quickly a mature tree can renew its bark between two fire events and protect cambium and buds against fire (Charles-Dominique et al. 2015a). Three main approaches have been adopted by researchers quantifying bark thickness: measuring bark thickness on undamaged adult trees (Perez-Harguindeguy et al. 2013), measuring bark thickness on juvenile trees in a given diameter class (Staver et al. 2012; Dantas & Pausas 2013) and measuring bark thickness and dividing it by stem radius to obtain relative bark thickness (Rosell et al. 2014; also referred to as bark investment: Perez-Harguindeguy et al. 2013). The first approach measures the combined result of bark production and bark shedding (due to active shedding by the plant, weathering, losses from fire, abrasion from animals, etc.). It is inappropriate for assessing species response to fire frequency as a species with both high production and high bark shedding could be immediately protected and renew its bark rapidly between two fire events, but will always have a relatively thin layer of bark (Fig. 1); similarly, a species with low bark production and no bark shedding will have thick bark on adult undamaged individuals but would be poorly protected against repeated fires or fire early in life (Fig. 1). Measuring bark thickness for a given diameter or dividing it by stem radius to obtain relative bark thickness provides meaningful information when analysing size-dependent stem mortality. However, the diameter of stems cannot be translated directly into stem age (Dantas & Pausas 2013), especially for comparisons among tree species since they may differ widely in their rate of wood accumulation (Fig. 1). Bark growth rate allows direct comparison of the rate at which species develop protection against fire, which is potentially crucial for determining species performance when they are exposed to frequent fires of low intensity.

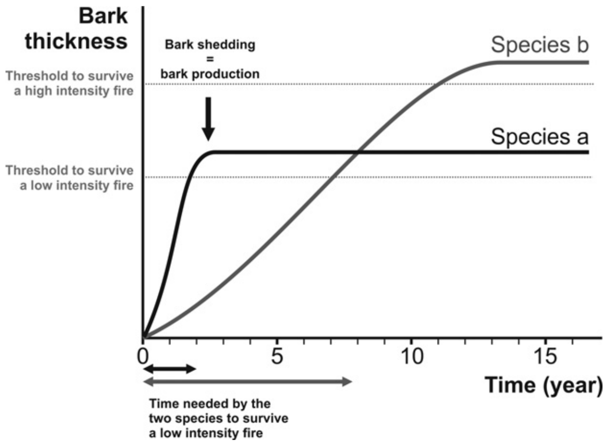

Fig. 1. Schematic diagram showing bark thickness accumulation curves through time for two theoretical species. Species a has a fast bark growth rate and early bark shedding (determining the position of the plateau of bark accumulation), while species b has a slow bark growth rate and a late bark shedding. In this example, species a would perform well in a surface fire regime (low fire intensity; high fire frequency) but poorly in a canopy fire regime (high fire intensity; low fire frequency). Species b would perform poorly in a surface fire regime but well in a canopy fire regime. Both species could have the same relative bark thickness (ratio bark/diameter) before their bark starts shedding if species a has fast growth rates of both bark and wood and species b has slow growth rates of both bark and wood.

In this paper we investigated bark growth rate as a predictor of the distribution of each of the 63 most abundant tree species in 253 sites with contrasting fire frequencies in Hluhluwe-iMfolozi park, South Africa. Thick bark would be less important for species propagating from underground structures insulated by soil. We therefore tested the hypothesis that the bark growth rate of plants is less constrained by fire frequencies when they are capable of clonal spread by underground propagation structures, such as stems or adventitious buds on roots. Lastly, we compared bark protection of savanna and forest trees.

Methods

Vegetation description

This study was performed in Hluhluwe-iMfolozi Park (HiP), South Africa. Vegetation includes 16 vegetation types (Whateley & Porter 1983), distributed in three main biomes (Charles-Dominique et al. 2015b): tall forest (Fig. 2a) with no C_4 grass layer; thicket (Fig. 2b) composed of shrubs and treelets and with a discontinuous C_4 grass layer; and savanna (Fig. 2c), a mixture of trees and grass and with a continuous layer of C_4 grasses. Forest can be discriminated from thicket by the

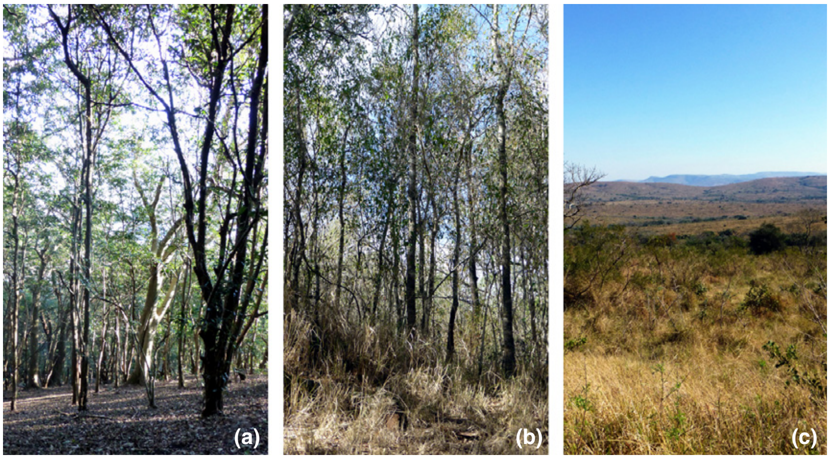

Fig. 2. Examples of the three sampled biomes. (**a**) Forest; (**b**) thicket; (**c**) savanna. [Colour figure can be viewed at wileyonlinelibrary.com]

presence of a multi-layered structure with mid-storey shade-tolerant trees. We selected 253 sites (Fig. 3) with a stratified sampling proportional to the relative spatial extent of each biome in HiP (202 savanna sites; 14 forest sites; 37 thicket sites).

We used 40 m × 10 m transects where every woody plant taller than 50 cm was attributed to a height class: >0.5, >2.0, >5.0 and >10.0 m. Species abundance were described using cumulated heights (class midpoints), transformed using Hellinger transformation (Legendre & Legendre 2012), which reduces the contribution of the most abundant species. Species nomenclature follows Coates-Palgrave (2002).

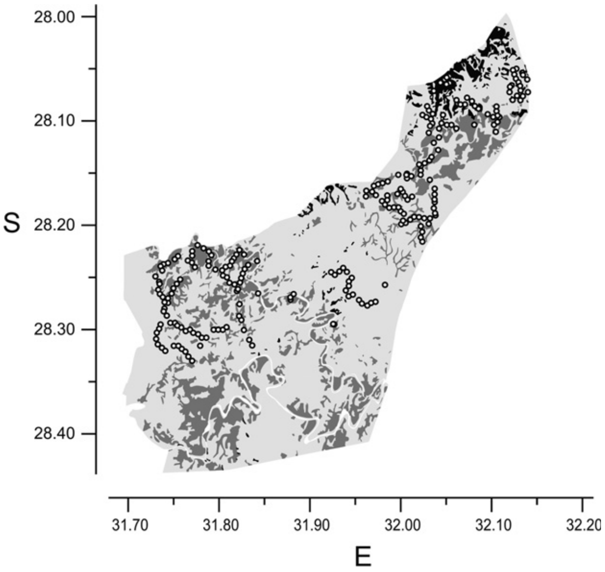

Fig. 3. Location of the 253 study sites. White points indicate site locations. Latitude and longitude coordinates are shown in the margins. Black colour is for forest, dark grey for thicket and light grey for savanna.

Fire records

Hluhluwe iMfolozi Park records include the location of all fires over the period 1992–2012.

Fire frequencies of the two decades (1992–2002 and 2002–2012) are strongly correlated with each other (Charles-Dominique et al. 2015a). We used the fire frequency for the last decade only (Table 1) as we were interested in fire frequency experienced by the trees described.

Bark description and sampling

We analysed bark properties of 63 trees species accounting for 93.5% of the total tree abundance recorded in the transects. We collected three individuals per species that were 2- to 3-m tall, except for small species such as *Coddia rudis*. Fire effect should be strongest on trees at this life stage as their whole structure is exposed to flames. Second, measuring bark on young trees reduced the problem of confounding bark gains from growth with losses from bark shedding. To ensure that no bark had been shed, we checked that dead epidermis was visible at the location on the trunk where bark was measured. Identifying the epidermal layer can easily be done by looking at young stems. Most measurements were performed at the base of the trunk. Bark growth was obtained by dividing bark thickness (transverse sections photographed under a binocular microscope and measured using ImageJ) by age of the stem at the cutting location. Bark is used in this paper to describe all tissues external to the wood (Perez-Harguindeguy et al. 2013). We divided bark thickness by stem radius of each sample to estimate relative bark thickness (Rosell et al. 2014), also referred to as bark investment (Perez-Harguindeguy et al. 2013). In addition to bark measurements, we recorded the ability of species to spread vegetatively using underground specialized organs, either by underground

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modified stems or by true root-suckering (both referred to here as 'root suckers'; see Charles-Dominique et al. 2015a for methods).

Age determination

We estimated age of the cuttings with two methods. First we counted the number of growth units from the top of the plant to the cutting position using morphological markers: shortening of internodes, presence of bud scale leaves and events of branching for species with a 1-yr-delayed development of new shoots (Barthélémy & Caraglio 2007). The relationship between number of growth units and age was checked in sites where the age of plants was known. We then counted the number of wood rings on stem cross-sections. We used the mean of the age estimated using the two methods. When one of the two methods led to unclear estimation (absence of morphological markers or wood rings), we did not take it into account. Bark growth rate was calculated by dividing bark thickness by stem age.

Statistical analyses

We calculated the mean fire frequency at which each species occurred using relative abundances as weights. Linear regressions were used to assess the extent to which bark growth rate and bark thickness are associated with fire frequency and to test the hypothesis that the bark growth rate/thickness of root-suckering species is less constrained by fire frequency. Bark growth rate values were log-transformed to obtain normality of residuals (verified with a Shapiro–Wilk test with a significance threshold fixed at 0.1). We compared models including bark growth rate only, bark thickness only, bark growth rate and root suckering abilities, and bark thickness and root suckering using AIC scores. Complementary analyses (RLQ and fourth-corner analyses) were performed to test the environmental filtering exerted on trait distribution within communities by the fire frequency and biome distribution, and are presented in Appendix S1.

All analyses were processed using the R software (v 3.0.2; R Foundation for Statistical Computing, Vienna, AT).

Results

Bark growth rate was better correlated with the fire frequency at which species occur than bark thickness and relative bark thickness (Table 2). Species with a high bark growth rate were most common at sites with frequent fire (Fig. 4). Conversely, species occurring in places with infrequent fires or no fire had low bark growth rates. All models (with bark growth rate, bark thickness and relative bark thickness) were improved (lower AIC; Table 2) by considering the ability of species to develop root suckers. Root suckering species, although tolerant of frequent fires, generally had low bark growth rates (Fig. 4). The relationships between bark growth rate and fire frequencies were significantly different for root suckers and non-root suckers, as indicated by the significant interaction term (Table 2, Fig. 4).

Two species, *Dombeya rotundifolia* and *Ekebergia capensis*, had an extremely high bark growth rate, explained by extensive inner bark production (see Appendix S2: *D. rotundifolia*). They were excluded from the analysis as their production of inner bark, which is almost ten-fold higher than outer bark, is exceptional within the set of species. Most of the other species have an inner bark equivalent to, or thinner than, the outer bark. Contrary to the outer bark, the inner bark cells are not suberized and provide little protection against heat (Rosell 2016). We note that the exclusion of these outlier species did not affect the conclusions of the analyses (Appendix S3).

The mean fire frequencies differed between savanna and thicket and forest (Fig. 5). The high fire frequencies found in savanna were mirrored by significantly higher community mean bark growth rate and bark thickness (Fig. 5).

Discussion

Recent studies have confirmed the importance of bark protection as a key trait in fire-prone environments, especially those with surface fire regimes such as savannas (Lawes et al. 2011; Clarke et al. 2013; Hempson et al. 2014). In higher rainfall savannas, fires commonly occur at intervals of three or more fires per decade. This implies that plants face fire early in their development and repeatedly throughout their entire life. In this study we investigated the rate at which species produce bark and how bark growth rate influences their distribution and abundance in fire-prone environments.

Our results show that the bark growth rate (bark production per unit time) is critical in environments with frequent fires. The survival during the juvenile period (minimum time from germination to sapling release from

Table 1. Contingency table showing the number of sampled sites per fire class.

Number of fires between 2002 and 2012	0	1	2	3	4	5	6	7
Number of sites	78	28	33	33	36	27	14	10

Table 2. Parameter estimates for linear regression models.

Response Variable	Explanatory Variables	Estimate	SE	*t*-Value	*P*-Value	Adj R^2	AIC
Bark Growth Rate	Intercept	−2.21	0.11	−19.70	<0.001***	0.52	114.37
	Fire frequency	0.44	0.05	8.10	<0.001***		
	Root sucker	0.36	0.32	1.13	0.262		
	Interaction	−0.32	0.10	−3.21	0.002**		
Bark Growth Rate	Intercept	−2.11	0.11	−18.42	<0.001***	0.41	124.47
	Fire frequency	0.31	0.05	6.53	<0.001***		
Bark Thickness	Intercept	0.16	0.11	1.40	0.167	0.27	117.25
	Fire frequency	0.28	0.06	4.99	<0.001***		
	Root sucker	0.25	0.32	0.77	0.445		
	Interaction	−0.24	0.10	−2.28	0.026*		
Bark Thickness	Intercept	0.23	0.11	2.07	0.043*	0.20	120.93
	Fire frequency	0.18	0.05	4.00	<0.001***		
Relative Bark Thickness	Intercept	−3.13	0.09	−35.49	<0.001***	0.43	85.42
	Fire frequency	0.29	0.04	6.85	<0.001***		
	Root sucker	0.18	0.25	0.72	0.473		
	Interaction	−0.19	0.08	−2.44	0.018*		
Relative Bark Thickness	Intercept	−3.08	0.09	−35.48	<0.001***	0.37	90.62
	Fire frequency	0.21	0.04	5.96	<0.001***		

Note that the three response variables are not dimensionally homogeneous. The AICs are only shown for comparison of models using the same response variable. Significance levels are reported as follow: 0<***≤0.001<**≤0.01<*≤0.05<ns.

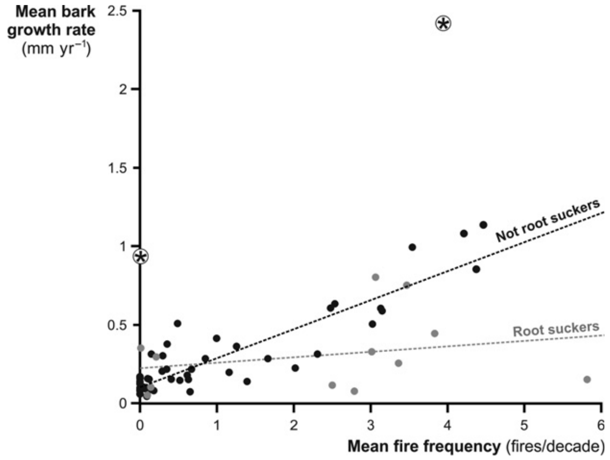

Fig. 4. Bark growth rate and fire frequency experienced by each species. Asterisks show outlier species (*Dombeya rotundifolia* and *Ekebergia capensis*) that were excluded in the analyses due to their exceptional inner bark production (see details in the text). Black dotted line = linear regression for species without root suckers (49 species; BGR = 0.18 × FF + 0.10; R^2 = 0.81; test on the slope: *P*-value < 0.001). Grey dotted line = linear regression for species with root suckers (12 species; BGR = 0.03 × FF + 0.22; R^2 = 0.06; test on the slope: ns).

the fire trap) depends on the species ability to grow a sufficiently thick bark layer to resist the first fire event. Using bark thickness measured on undamaged adult plants (Perez-Harguindeguy et al. 2013) might be more appropriate for predicting tree survival after fires of high intensity and low frequency (Fig. 1). The bark of trees exposed to infrequent and high-intensity fires would have time to recover and stabilize between two fire events: the measurement would then capture the species balance between bark production and bark shedding, which might be critical for surviving intense fires (Uhl & Kauffman 1990; Hoffmann et al. 2009; Dantas & Pausas 2013).

Fire frequency filters species in Hluhluwe-iMfolozi

The results from our analyses show that fire frequency is one of the main factors controlling species distribution in the vegetation in Hluhluwe-iMfolozi. It acts as an environmental filter on trait distribution, with species having good bark protection (produced by high bark growth rate and bark thickness) distributed where the fires are frequent. These results corroborate conclusions of other studies about the essential role of fire frequency for determining species and trait distribution in savanna (Peterson & Reich 2008; Staver et al. 2012; Charles-Dominique et al. 2015a). While bark thickness has been extensively analysed, we provide in this study one of the first direct quantifications of the importance of this trait for community composition where fire frequency is the selective filter (see also Appendix S1). An interesting point is that bark protection is low where fires are infrequent, suggesting that the cost of bark production would tend to exclude species with high bark protection in vegetation rarely exposed to fire (Lawes et al. 2013). This also means that bark growth rate could potentially be used as a predictor of surface fire frequency. The correlation of fire frequency with bark growth rate was always higher than with bark thickness, confirming that species performance is better described by this

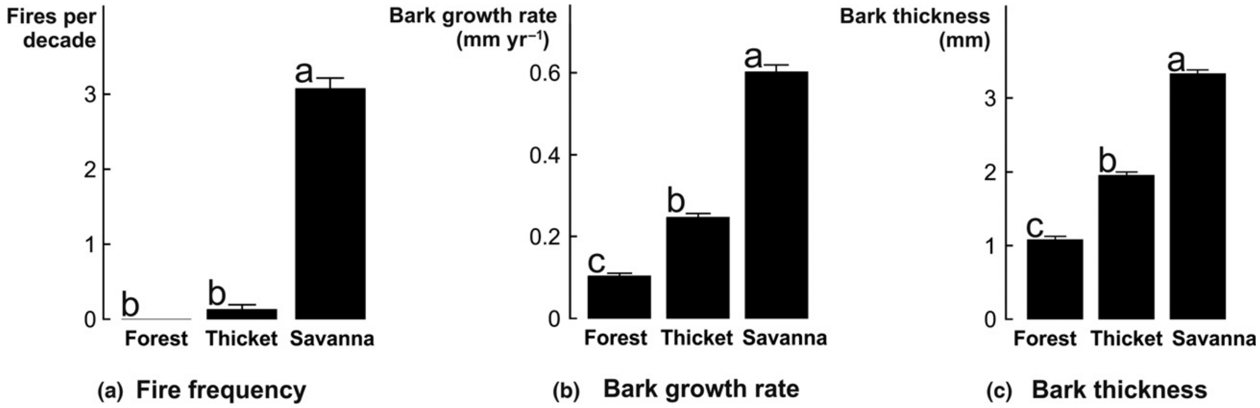

Fig. 5. Biome fire frequencies and bark protection. (**a**) Mean fire frequencies; community-weighted mean values of bark growth rates (**b**) and bark thickness (**c**) in forest, thicket and savanna. Values are Mean ± SE. Grouping letters show the result of a multiple Wilcoxon–Mann Whitney test with a Holm correction (0.95 CI).

trait. We can draw two hypotheses from this result: (1) either the rate at which saplings are producing bark; or (2) the rate of bark renewal between two fires is critical for species survival. The first hypothesis is consistent with the large importance of top-kill of juvenile trees by fire in determining species composition in savannas (Bond et al. 2008, 2012; Hoffmann et al. 2009; Midgley et al. 2010; Higgins et al. 2012). A high bark growth rate would then allow species to overcome this temporal bottleneck. The second hypothesis would explain fast changes in community composition, thus implying a high mortality of mature trees, after modification of the fire regime (Keeley et al. 2011), and, conversely, the better survival of mature trees when fire is excluded (N'Dri et al. 2014).

Root suckers are not as constrained by fire than non-root suckers

A larger proportion of root-suckering species was found at high fire frequency in Hluhluwe-iMfolozi park (Charles-Dominique et al. 2015a,b). An interesting point is that their bark growth rate is not as high as for other species. This suggests that having a spreading strategy based on underground organs partially releases the constraint exerted by fire on bark protection. Plants having an underground bud bank are less sensitive to fire impact as they have numerous sites for resprouting and a large part of their resources is buried and thus protected (Clarke et al. 2013). Various strategies adopted by plants involving hiding the regenerating structures below-ground have been described; e.g. the hide and resprout strategy (Gignoux et al. 1997), geoxyle or underground trees (White 1976; Simon & Pennington 2012; Maurin et al. 2014). An interesting extension of this study could be to investigate whether these growth forms are also characterized by a smaller bark growth rate compared to other species growing under the same fire frequency.

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Supporting Information

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

Appendix S1. Complementary analyses: RLQ and fourth-corner analyses.

Appendix S2. Photographs of stem cuttings of 16 species.

Appendix S3. Parameter estimates for linear regression models including outlier species.