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LETTER

Changes in leaf functional traits of rainforest canopy trees associated with an El Niño event in Borneo

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Abstract

El Niño events generate periods of relatively low precipitation, low cloud cover and high temperature over the rainforests of Southeast Asia, but their impact on tree physiology remains poorly understood. Here we use remote sensing and functional trait approaches—commonly used to understand plant acclimation to environmental fluctuations—to evaluate rainforest responses to an El Niño event at a site in northern Borneo. Spaceborne measurements (i.e. normalised difference vegetation index calculated from Moderate Resolution Imaging Spectroradiometer data) show the rainforest canopy greened throughout 2015, coinciding with a strengthening of the El Niño event in Sabah, Malaysia, then lost greenness in early 2016, when the El Niño was at its peak. Leaf chemical and structural traits measured for mature leaves of 65 species (104 branches from 99 tree canopies), during and after this El Niño event revealed that chlorophyll and carotenoid concentrations were 35% higher in mid 2015 than in mid 2016. Foliar concentrations of the nutrients N, P, K and Mg did not vary, suggesting the mineralisation and transportation processes were unaffected by the El Niño event. Leaves contained more phenolics, tannins and cellulose but less Ca and lignin during the El Niño event, with concentration shifts varying strongly among species. These changes in functional traits were also apparent in hyperspectral reflectance data collected using a field spectrometer, particularly in the shortwave infrared region. Leaf-level acclimation and leaf turnover could have driven the trait changes observed. We argue that trees were not water limited in the initial phase of the El Niño event, and responded by flushing new leaves, seen in the canopy greening trend and higher pigment concentrations (associated with young leaves); we argue that high evaporative demand and depleted soil water eventually caused leaves to drop in 2016. However, further studies are needed to confirm these ideas. Time-series of vegetation dynamics obtained from space can only be understood if changes in functional traits, as well as the quantity of leaves in canopies, are monitored on the ground.

Introduction

El Niño events bring periods of low rainfall and reduced cloud cover to tropical rainforests that are typically supplied with plentiful water (Lopes *et al* 2016), but the responses of tropical rain forests to these events remain poorly understood. The Southern Oscillations responsible for El Niño events have

occurred for at least 130 000 years (Tudhop *et al* 2001) suggesting ample opportunity for natural selection to enhance the capability of trees to tolerate irregular drought events (Harrison 2000, Detto *et al* 2018). However, climate change is increasing the severity and frequency of El Niño events (Breshears *et al* 2005, Allen *et al* 2010, Thirumalai *et al* 2017, Wang *et al* 2017, Freund *et al* 2019); and higher than average temperatures recorded across Southeast Asia in 2015 and early 2016 were attributed to a climate-change amplified El Niño event (Thirumalai *et al* 2017, Susskind *et al* 2019). Higher temperatures increase evaporative demand and therefore exacerbate the severity of drought events (Adams *et al* 2009). Recent research has demonstrated a variety of biotic responses to El Niño-induced droughts (e.g. O'Brien *et al* 2017, Qie *et al* 2017, Detto *et al* 2018, Santos *et al* 2018). While there is evidence of increased mortality in the Amazon (Phillips *et al* 2009, Doughty *et al* 2015), West African forests appear more resilient due to a gradual shift in species composition toward drought-tolerant species (Fauset *et al* 2012). There is also evidence of greening of tropical tree canopies during dry periods in the Amazon based on optical remote sensing (Saleska *et al* 2007). One explanation for this greening is that trees continue to access water through deep root systems (Huete *et al* 2006) and acclimatise to greater direct solar irradiance (i.e. reduced cloud cover) by up-regulating photosynthetic and protective pigments (Saleska *et al* 2007, Saleska *et al* 2016). An alternative explanation is that greening during dry periods is related to the flush of new leaves (Lopes *et al* 2016, Wu *et al* 2016, Wagner *et al* 2017). However, interpretation of remotely sensed data is challenging and there is continued debate over tropical forest responses to variability in temperature, irradiance and precipitation (Samanta *et al* 2010, Morton *et al* 2014, Bi *et al* 2015).

Plant functional traits provide a way of predicting tropical forest responses to short- and long-term climate changes in terms of physiological mechanisms (Reich 2012, Reich 2014, Doughty *et al* 2018). Traits help explain differences in growth and survival across resource gradients; for example, plant trait diversity might act as an insurance against climate change impacts on Amazon forests biomass, and considering the possible plasticity of traits, fast shifts of functional dominance enhance biomass resilience (Sakschewski *et al* 2016). Nevertheless, repeated trait measurements on the same plants are infrequent. Recent studies have measured traits over time to investigate leaf aging impacts (Chavana-Bryant *et al* 2017), but this approach has not been used previously to track traits changes in response to fluctuating environmental conditions such as an El Niño event.

If variation in leaf traits result in changes to leaf spectral reflectance, then these changes should be observable using remote sensing methods. Reflectance signatures are affected by the optical properties of leaves in a range of wavelengths; the visible (400–750 nm) portion of the spectrum is mainly driven by pigments (Sims and Gamon 2002), the near infrared (751–1300 nm) and shortwave infrared (1301–2400 nm) driven by internal and external leaf structure (Slaton *et al* 2001), including water content (Tucker 1980, Ustin *et al* 2004), phenolics (Kokaly *et al* 2009) and organic constituents (Petisco *et al* 2006, Asner *et al* 2011). The diversity of leaf reflectance signatures within a community arises from the functional and evolutionary divergence among the constituent species, and may be used to predict ecosystem function (Schweiger *et al* 2018). Remote sensing studies using Moderate Resolution Imaging Spectroradiometer (MODIS) satellite spectroscopy have reported positive impacts of dry seasons on EVI—an enhanced vegetation index which is a combination of chlorophyll content and leaf area that does not saturate in dense forests—indicating a 'greening up' phenomenon associated with increased irradiance during dry seasons (Huete *et al* 2006, Saleska *et al* 2007). However, it remains controversial whether trees are actually investing in photosynthetic apparatus or whether this phenomenon is an artefact of optical sensors (Morton *et al* 2014). We propose that leaf-level reflectance obtained from proximal sensing using field spectroscopy can provide an accurate method for monitoring short-term climate fluctuations, on the basis that trait variation affects reflectance in different portions of the spectrum that can be captured using field measurements.

This paper presents observations of changing leaf traits in a Bornean tropical forest associated with the 2015/16 E Niño drought, and tests whether those changes can be detected from leaf spectroscopy and *in situ* sampling. In terms of drought stress, there may be species-specific responses at the leaf level (Maréchaux *et al* 2015). Changes in leaf functional traits could indicate a combination of leaf physiological and structural responses to drought, but no studies have previously reported such acclimation from repeated measurements in tropical forests. We investigate changes in 17 foliar traits and leaf spectral reflectance in response to the El Niño event to address the following questions: (1) how do foliar traits change with El Niño events? (2) Can responses to El Niño be detected from leaf spectral properties? Leaf samples and field spectroscopy data were acquired in two field campaigns, one during the El Niño event (September 2015) and one after the rains had returned (October 2016). By taking repeated measurements of physico-chemical and spectral properties on the same trees, this is the first study to measure leaf-level responses to an El Niño event, providing a unique perspective on the acclimation response of tropical rain forest trees to short-term climatic variation.

Material and methods

Description of field site and environmental time-series

The study was conducted in a lowland mixed dipter-ocarp forest (Fox 1972) on clay soils (Wright 1975) in the Danum Valley Conservation Area in the Malaysian state of Sabah, Borneo (Reynolds *et al* 2011). Data collection was carried out within two 1 ha plots located in an old growth forest (plot coordinates 4.951 °N, 117.796 °E and 4.953 °N, 117.793 °E) characterised by high species richness and tall emergent trees without evidence of logging or recent human disturbance (Riutta *et al* 2018).

Daily rainfall, temperature and sunshine duration data were systematically recorded at a weather station located at Danum Valley Field Centre, which is located adjacent to the Conservation Area. These data are freely available and can be downloaded from the South-East Asian Rainforest Research Partnership (www.searrp.org/scientists/available-data/) and were used to derive time-series of meteorological variables during the study period. Normalised difference vegetation index (NDVI) time-series were computed from the MODIS Multi-Angle Implementation of Atmospheric Correction Daily Land Surface (MCD19A1) product (Lyapustin *et al* 2011a, 2011b, 2018). Detailed methods and an overview of environmental conditions before, during and after the 2015/2016 El Niño event in Danum Valley are provided in supplementary information is available online at stacks.iop.org/ERL/14/085005/mmedia.

Leaf litterfall occurs throughout the year in these forests and South-East Asia rainforests. To investigate whether leaf litter was higher during the El Niño, leaf litter was collected from 25 traps, measuring 0.25 m^2, placed in the two plots, over collection intervals ranging from 7 to 29 d (Riutta *et al* 2018). Leaf litter dry mass was divided by the collection interval and multiplied by 30 to get a monthly estimate in MgC h^{-1}. Leaf litter carbon content was assumed to be 50%.

Sampling design and field data collection

Seventeen functional traits were measured on 38 sunlit and 66 shaded branches (104 branches in total) from 99 individual trees $\geqslant$ 10 cm diameter at breast height, representing 65 species from 44 genera in 24 families and tree height ranging from 2.3 to 73.7 m. The first measurements were conducted in September 2015, during a dry period, and the second measurements were taken a year later, after the rains had returned (figure 1(b)). The sampling design, analysis of leaf biochemistry and extraction of other traits were carried out in accordance with previous trait campaigns, as described by Both *et al* (2019) and more fully described in the SI.
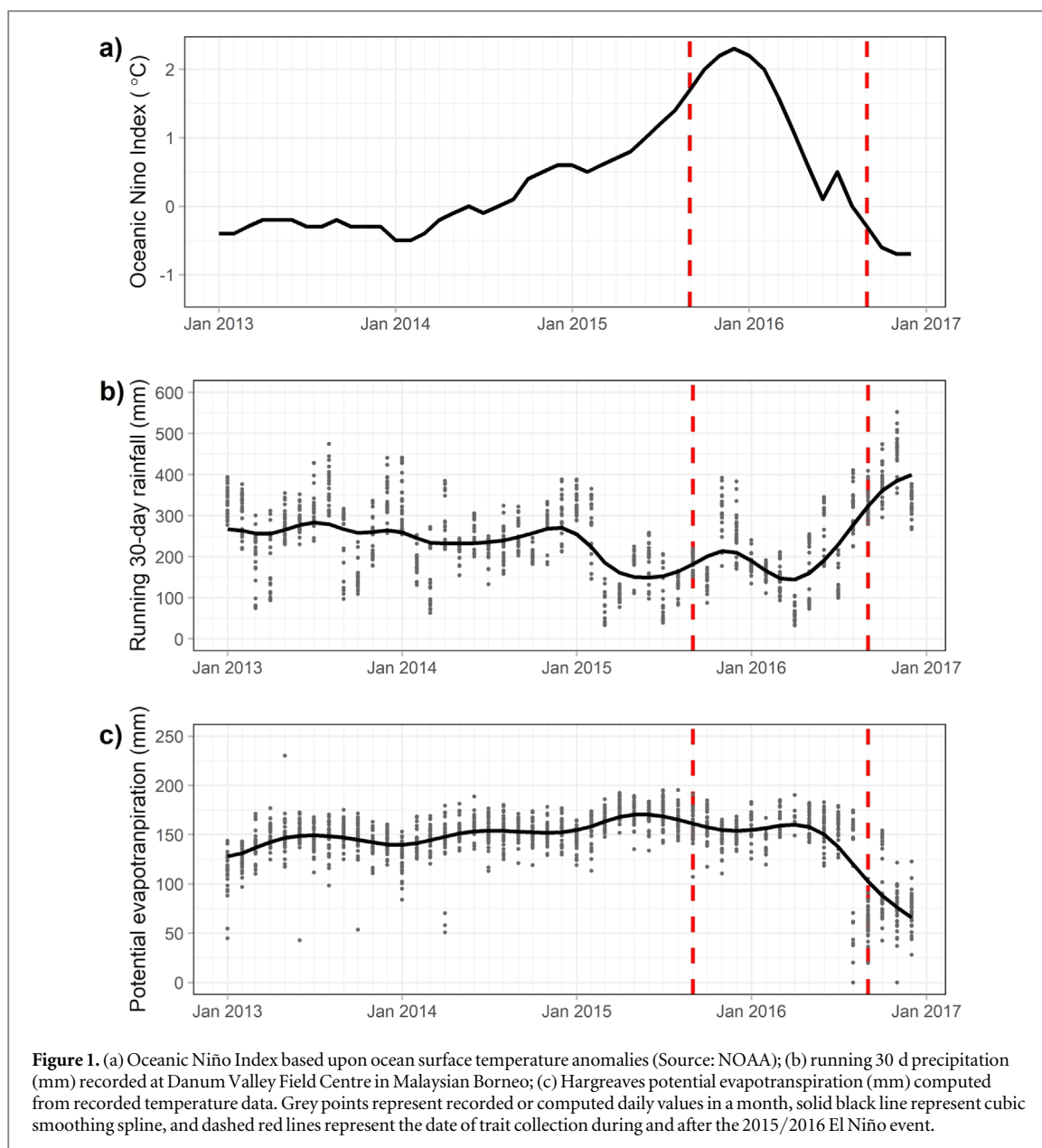
Analyses were performed within the R statistics framework (R Core Team 2018). We conducted analyses that considered the hierarchical structure of the data, and analyses focussing on species-level responses. First, to examine the influence of El Niño at the canopy level, we fitted linear mixed effects model to the change of each trait using the *lme*4 package in R, with species identity as a random effect (i.e. a grouping variable allowing 'paired comparisons' to be made; Messier *et al* 2010). Secondly, to evaluate the relative influence of the drought, shading and taxonomic level on each trait, we developed hierarchical models using the *lme*4 package in R. We included the phylogenetic levels of family, genus nested within family, species nested within genus, and branch type (shaded or sun-lit) nested within species, as well as a temporal effect. All effects were treated as random. In each model, the response variable (y) is any chemical trait for each canopy sample. The total variance of the mean for a given trait was quantitatively separated into variance explained by each taxonomic level, El Niño and unexplained variance was treated as a residual comprised of micro-environment, sample selection and measurement errors associated with laboratory analyses.

Spectroscopy collection

For both surveys, five leaves attached to the branches were selected at random, avoiding damaged and young leaves. Reflectance spectra (350–2500 nm) were acquired using a FieldSpec 4, produced by Analytical Spectral Devices (ASD, Boulder, Colorado, USA). The spectroradiometer's contact probe was mounted on a clamp and firmly pushed down onto the sample against a black background so that no extraneous light was included in the measurement. The spectral measurements were taken at the midpoint between the main vein and the leaf edge, approximately halfway between the petiole and leaf tip, with the abaxial surface pointing towards the probe. The readings were calibrated against a Spectralon white reference panel every five samples. In all statistical analyses, the spectral data were trimmed to the 400–2500 nm range, and the mean reflectance values of the five spectra per branch were used.

Partial least squares regression (PLSR) was initially used to predict leaf traits from spectral reflectance. There is strong autocorrelation in reflectance values, so PLSR involves dimensionality reduction, to produce orthogonal uncorrelated latent vectors containing the maximum explanatory power in relation to the trait data (Wold *et al* 2001). To avoid overfitting the calibration models, the number of latent variables was chosen according to the 'one standard error' rule that selects the least complex model with the average cross-validated accuracy within one standard error from that in the optimal model (Breiman *et al* 1984). We determined the contribution of individual ASD wavebands within the visible (VIS; 400–750 nm), near infrared (NIR; 751–1300) and shortwave infrared (SWIR; 1301–2400 nm) to the model performance

Figure 1. (a) Oceanic Niño Index based upon ocean surface temperature anomalies (Source: NOAA); (b) running 30 d precipitation (mm) recorded at Danum Valley Field Centre in Malaysian Borneo; (c) Hargreaves potential evapotranspiration (mm) computed from recorded temperature data. Grey points represent recorded or computed daily values in a month, solid black line represent cubic smoothing spline, and dashed red lines represent the date of trait collection during and after the 2015/2016 El Niño event.
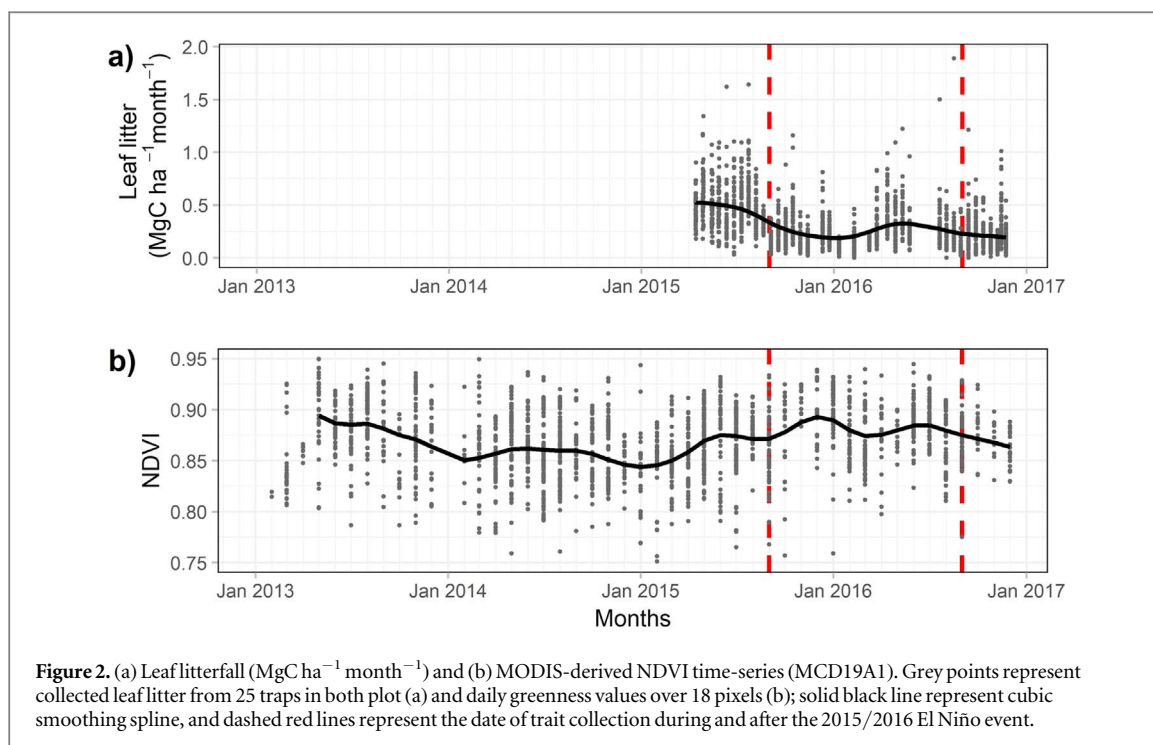
(Serbin *et al* 2014, Nunes *et al* 2017). We also combined two or more spectral regions to evaluate performance. In general, previous research indicates that the SWIR contains absorption features for most traits (Curran 1989, Kokaly *et al* 2009, Nunes *et al* 2017), with the visible being useful for pigments (Curran *et al* 1991, Sims and Gamon 2002), and the NIR for leaf mass per area (LMA; Asner *et al* 2011). Performance of the final models was evaluated using an 80/20 split of the data for calibration/validation, respectively, over 100 randomised permutations of the dataset. For each such permutation, we tracked the model fit (R^2) and the percentage root-mean-square error over the data range (%RMSE). These analyses generated a distribution of model coefficients and fit statistics and allowed for the assessment of model stability as well as uncertainty in predictions. Models were built using the packages *caret* and *vegan* in R (www.r-project.org). Additionally, we explored whether the data collected

using spectroscopy could be used as a surrogate for the validation data to determine the effect of El Niño on leaf traits. To test this question, we used calculated the variation with 95% confidence intervals for both reference and predicted data.

Results

Time-series of environmental change

Borneo experiences variability in climate due to influences from both the Pacific and Indian Oceans. The National Oceanic and Atmospheric Administration (NOAA) considers El Niño conditions to be present when the Oceanic Niño Index is +0.5 or higher. The strong El Niño of 2015–16 (figure 1(a)) coincided with a period of higher diurnal range in surface air temperatures across the island, peaking during the months November 2015–April 2016 which were on average 0.6°–1.2° higher than average seasonal

Figure 2. (a) Leaf litterfall (MgC ha^{-1} month^{-1}) and (b) MODIS-derived NDVI time-series (MCD19A1). Grey points represent collected leaf litter from 25 traps in both plot (a) and daily greenness values over 18 pixels (b); solid black line represent cubic smoothing spline, and dashed red lines represent the date of trait collection during and after the 2015/2016 El Niño event.

temperatures (Whitfield *et al* 2019). Precipitation during 2015 and 2016 varied considerably across the region, but in North-eastern Borneo seasonal total rainfall in May to October 2015 was between 75% and 100% of the 1981–2010 seasonal average, reducing to 50%–75% of normal rainfall for the period November 2015–April 2016, returning to long-term seasonal average amounts for May to October 2016 (typically 900–1000 mm) (Colledge 2017). At Danum Valley Conservation Area itself, mean daily rainfall (mm) in the latter half of 2015 and early 2016 was lower than typically recorded for the site (figure 1(b)), before increasing rapidly in the latter half of 2016. In the months immediately preceding the two surveys (May–August) the average number of days when no rain was recorded was 16 in 2015 and 10 in 2016, whilst the longest run of consecutive days without rain was 10 in 2015, and just 3 in 2016. Coupled with reduced rainfall, an increase in sunshine duration was also recorded at Danum Valley, with mean daily sunshine of 5.9 h in May–August 2015, reducing to 5.4 h for the same months in 2016. Thus, at Danum Valley Conservation Area, the forest experienced a period of relatively low rainfall (figure 1(b)) and high potential evapotranspiration (figure 1(c)) before and during the first survey (September 2015).

Leaf loss was greater in the period running up to the first field campaign and increased again toward the end of the El Nino in April 2016 (figure 2(a)). NDVI values increase in the early El Niño period in 2015 (figure 2(b)), and then a sharp decrease late in the El Niño. By the time of the second field survey, NDVI is similar to the first survey despite evidence of major upheavals in the interim.

The influence of the El Niño event on traits

Pigment concentrations, and several other traits, varied between field campaigns that sampled species during and after the 2015/2016 El Niño event (table 1). Pigment concentrations, namely chlorophyll $a + b$ and carotenoids, were about a third higher during the El Niño event than afterwards, when heavy rain and low irradiance conditions had returned (figure 3); the El Niño effect was much stronger than the position of the branch within the canopy, or species identity (figure 4). Phenolic and tannin concentrations were 18% and 16% higher during the El Niño, while δ^{13} C, cellulose, LMA and water were 9%, 5%, 4% and 3%. higher, respectively. Calcium and lignin were the only leaf traits that increase in concentration after the El Niño by 17% and 13%. The other carbon fractions, including soluble and hemicellulose, as well as N, δ^{15} N and the rock-derived nutrients P, K and Mg did not change between sampling periods. Correlation analysis (figure S1) indicates that plants with higher LMA have more phenolics and pigments but less water and lower N concentrations.

Organisation of traits by taxonomy, light exposure and El Niño

Using hierarchical models for variance partitioning to analyse the dataset, we found evidence for strong taxonomy organisation of multiple traits operating independently of variation in climate (figure 4). Our analysis also incorporated branch type (sunlit or shaded branches) to test whether traits were variable within canopies. Residual variation may result from variation in micro-environment, sample selection and analytical error. High trait diversity among coexisting trees is driven by differences between taxa rather than by environmental conditions. Water content,
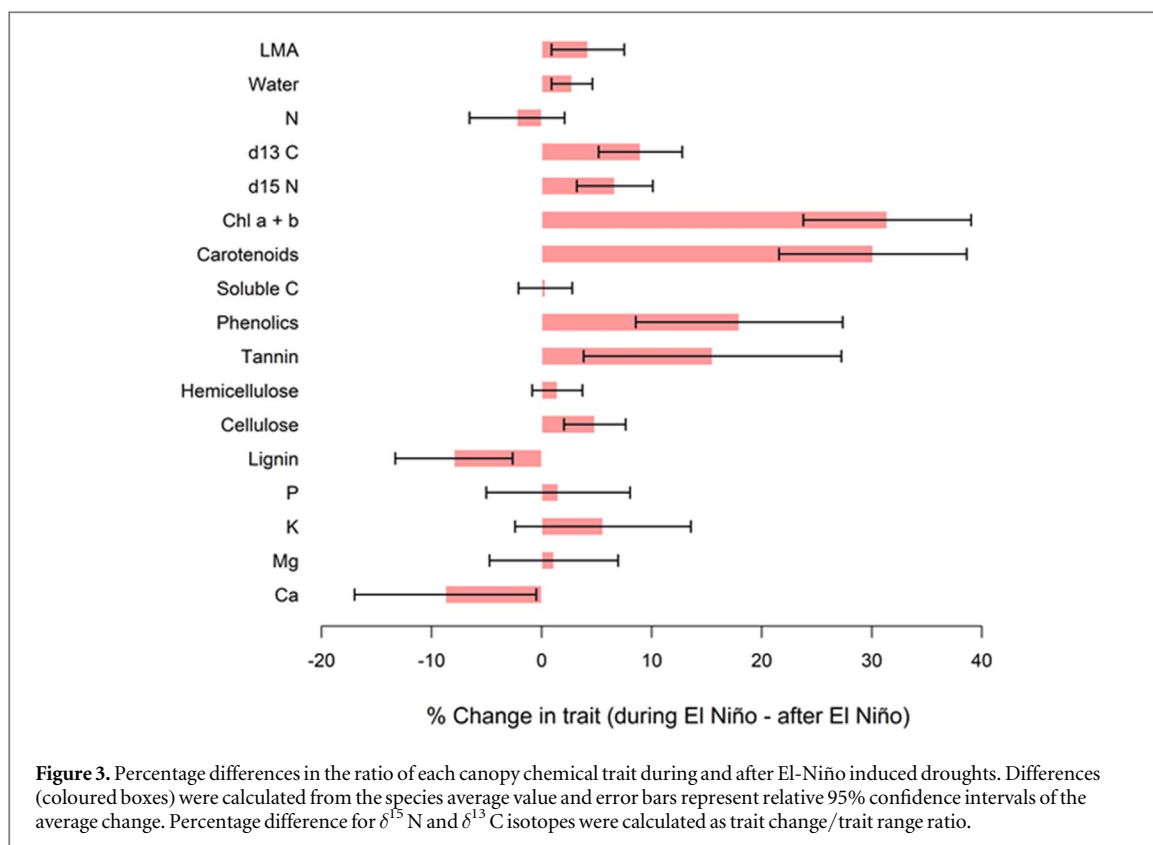
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Figure 3. Percentage differences in the ratio of each canopy chemical trait during and after El-Niño induced droughts. Differences (coloured boxes) were calculated from the species average value and error bars represent relative 95% confidence intervals of the average change. Percentage difference for δ^{15} N and δ^{13} C isotopes were calculated as trait change/trait range ratio.

Table 1. Comparison of foliar trait of 65 species of Bornean rainforest tree, sampled during during and after an El Niño event. Mean traits value (with 95% confidence interval) are given. Mixed effects modelling, with species identity as a grouping variable, was used to assess the statistical significance of trait changes (95% CIs predicted by model; bold indicates significance at $P < 0.05$), adjusted for multiple comparisons using approach of Benjamini and Hochberg (1995).

Foliar trait	During El Niño	After El Niño	Change (During–After)	*P*-value
LMA (g cm^{-2})	95.8 (91.0–100.7)	90.4 (86.5–94.3)	**4.03 (1.08–6.98)**	**0.010**
Water content (%)	58.8 (57.5–60.2)	57.2 (55.8–58.7)	**1.62 (0.70–2.54)**	**0.001**
N (%)	1.79 (1.70–1.89)	1.85 (1.76–1.94)	−0.04 (−0.10 to 0.02)	0.176
δ^{13} C (‰)	−32.0 (−32.3 to 31.8)	−32.5 (−32.8 32.3)	**0.49 (0.28–0.70)**	**< 0.001**
δ^{15} N (‰)	1.16 (0.72–1.60)	0.73 (0.50–0.97)	0.42 (0.0–0.84)	0.052
Chl $a + b$ (mg m^{-2})	323.2 (307.1–339.5)	225.1 (206.8–243.3)	**101.5 (81.4–121.6)**	**< 0.001**
Car (mg m^{-2})	58.8 (55.5–62.0)	42.1 (38.6–45.6)	**17.7 (13.7–21.7)**	**< 0.001**
Sol. carbon (%)	50.2 (48.3–52.0)	50.2 (48.4–52.1)	0.17 (−1.12 to 1.46)	0.790
Phenolics (mg g^{-1})	36.2 (32.4–39.9)	29.7 (26.0–33.3)	**6.5 (3.5–9.5)**	**< 0.001**
Tannin (mg g^{-1})	8.5 (7.5–9.6)	7.3 (6.4–8.2)	**1.32 (0.42–2.22)**	**0.005**
Hemicellulose (%)	11.9 (11.2–12.6)	11.7 (11.1–12.4)	0.17 (−0.11 to 0.45)	0.251
Cellulose (%)	21.3 (20.4–22.1)	20.0 (19.2–20.8)	**1.03 (0.41–1.65)**	**0.001**
Lignin (%)	16.7 (15.5–17.8)	17.9 (16.7–19.2)	**−1.33 (−2.22 to −0.44)**	**0.005**
P (mg g^{-1})	1.33 (1.23–1.42)	1.28 (1.21–1.35)	0.02 (−0.06 to 0.10)	0.555
K (mg g^{-1})	10.4 (9.0–11.7)	9.7 (8.6–10.7)	0.58 (−0.25 to 1.41)	0.180
Mg (mg g^{-1})	4.5 (3.8–5.1)	4.4 (3.8–5.0)	0.05 (−0.19 to 0.29)	0.652
Ca (mg g^{-1})	12.7 (11.2–14.3)	14.1 (12.6–15.6)	**−1.11 (−2.16 to −0.06)**	**0.043**

rock-derived nutrient concentrations, lignin, phenolics and tannin were all strongly phylogenetically conserved; species-level differences were usually greater than family- or genus-level differences, although K, water, tannins, N, Mg and lignin had strong family-level effects. Pigments had the highest impact by El Niño and δ^{15} N was the least taxonomically organised trait with the highest unexplained variation. For most traits, branch type accounted for more variance than the El Niño event, in particular LMA, N, δ^{13} C and carbon fractions. LMA was conspicuously variable within canopies, indicating the dependence of environmental attributes associated with the vertical canopy profile, and is less affected by short-term climatic variation. Our analysis suggests that sun exposed leaves can have variable responses to El Niño.
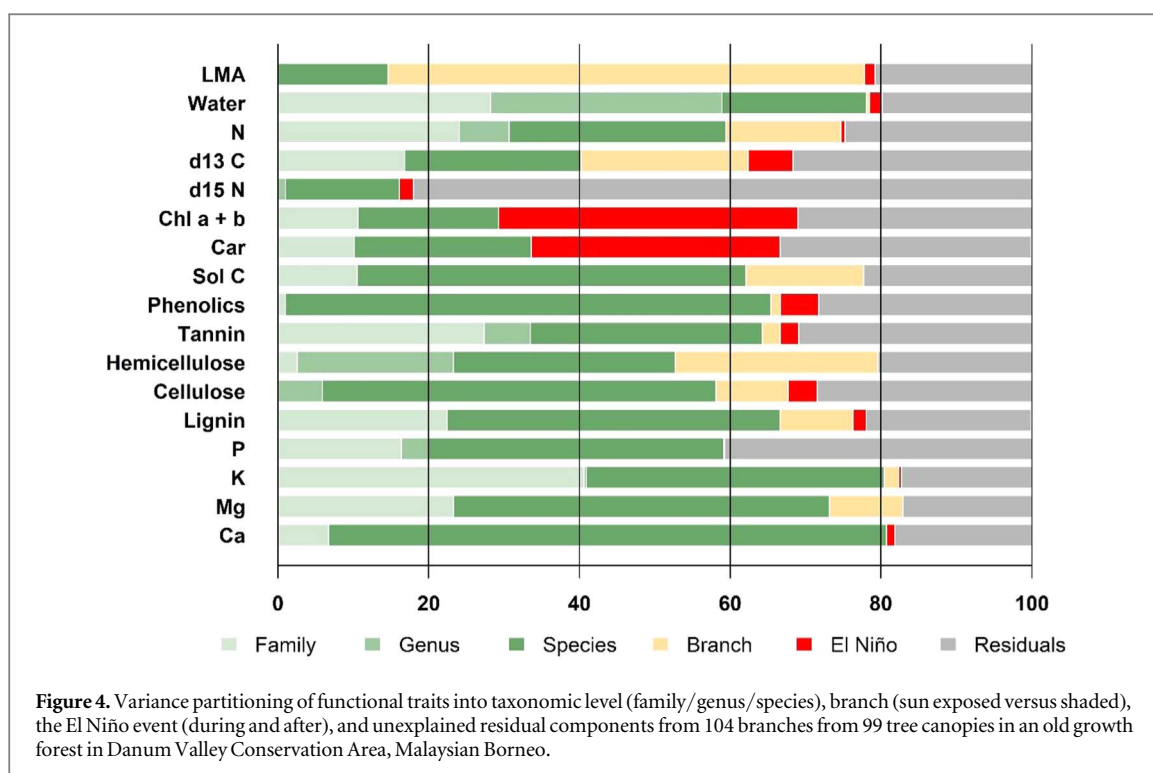
Figure 4. Variance partitioning of functional traits into taxonomic level (family/genus/species), branch (sun exposed versus shaded), the El Niño event (during and after), and unexplained residual components from 104 branches from 99 tree canopies in an old growth forest in Danum Valley Conservation Area, Malaysian Borneo.

Table 2. Spectroscopy estimation of leaf chemical and structural properties using leaf spectral reflectance of 104 trees in Malaysian Borneo during and after an El Niño event. NComp is the number of latent components using partial least square regression and the average $\pm$ standard deviation of metrics to assess the predictive power. Performance of the final models was evaluated using an 80/20 split of the data for calibration/validation, respectively, over 100 randomized permutations of the dataset. Regions of the spectrum selected for hyperspectral analyses were the visible (VIS; 400–750 nm), near infrared (NIR; 751–1300) and shortwave infrared (SWIR; 1301–2400 nm); different regions were selected for each trait, based on comparisons of the performance of alternative PLSR models.

Trait	Region	ncomp	R^2	%RMSE
LMA $(g\,cm^{-2})$	VIS–NIR–SWIR	10	59.2 ± 9.4	14.1 ± 1.4
Water content (%)	SWIR	5	67.3 ± 8.0	7.1 ± 0.9
N (%)	SWIR	16	58.8 ± 8.8	17.4 ± 2.7
$\delta^{13}C$ (‰)	SWIR	14	32.6 ± 10.7	17.1 ± 1.6
$\delta^{15}N$ (‰)	SWIR	1	3.2 ± 3.1	7.5 ± 2.5
Chl $a + b$ $(mg\,m^{-2})$	VIS–SWIR	8	40.0 ± 12.5	28.4 ± 2.6
Car $(mg\,m^{-2})$	VIS–SWIR	7	41.2 ± 12.7	28.3 ± 2.9
Soluble carbon (%)	SWIR	18	38.8 ± 10.8	14.2 ± 1.6
Phenolics $(mg\,g^{-1})$	NIR–SWIR	9	53.8 ± 10.1	40.3 ± 4.6
Tannin $(mg\,g^{-1})$	SWIR	11	42.9 ± 9.9	47.6 ± 4.8
Hemicellulose (%)	SWIR	12	45.1 ± 9.7	21.3 ± 2.3
Cellulose (%)	SWIR	19	53.3 ± 10.1	15.2 ± 1.7
Lignin (%)	SWIR	17	34.8 ± 11.9	30.0 ± 4.3
P $(mg\,g^{-1})$	NIR–SWIR	10	27.7 ± 14.6	27.9 ± 6.1
K $(mg\,g^{-1})$	SWIR	9	24.5 ± 10.7	50.4 ± 7.0
Mg $(mg\,g^{-1})$	SWIR	13	43.0 ± 11.3	57.8 ± 7.6
Ca $(mg\,g^{-1})$	SWIR	11	36.7 ± 9.3	47.1 ± 6.6

Spectral analyses of leaf trait responses to El Niño

Several foliar traits were successfully estimated from leaf spectral reflectance (table 2). Variation in water content, LMA, and concentrations of N, phenolics and cellulose was estimated particularly well, while concentration of P, K, $\delta^{13}C$ and $\delta^{15}N$ were poorly estimated. In general, the highest absolute spectral sensitivity was observed in the SWIR portion between 1301 and 2400 nm, with all traits influencing this spectral region. The visible portion of the spectrum (400–750 nm) was influenced only by chlorophyll $a + b$, carotenoids and LMA, while the near infrared (751–1300 nm) was influenced only by LMA, phenolics and P.

Differences in leaf traits between the two surveys could generally be detected with hyperspectral

Table 3. Temporal changes in foliar trait values predicted from spectral reflectance compared with temporal changes observed in traits significantly affected by El Niño. Partial-least square regression was used to generate models relating leaf traits measured during and after an El Niño event to spectral reflectance data collected by field spectroscopy. Regression analyses did not include sampling date in model calibration, so the predicted during and after El Niño values indicate predictive power to detect El Niño influences on each trait. Mean (and 95% CI) of each spectranomic trait change is provided.

Foliar trait	Predicted change	Observed change
LMA (g cm^{-2})	3.44 (1.02–5.86)	4.03 (1.08–6.98)
Water content (%)	−0.72 (−1.47 to 0.03)	1.62 (0.70–2.54)
δ^{13}C (‰)	0.41 (0.24–0.58)	0.49 (0.28–0.70)
Chl a + b (mg m^{-2})	79.8 (70.1–89.5)	101.5 (81.4–121.6)
Car (mg m^{-2})	15.2 (13.5–16.9)	17.7 (13.7–21.7)
Phenolics (mg g^{-1})	9.0 (7.4–10.6)	6.5 (3.5–9.5)
Tannin (mg g^{-1})	1.71 (1.28–2.14)	1.32 (0.42–2.22)
Cellulose (%)	1.03 (0.62–1.44)	1.03 (0.41–1.65)
Lignin (%)	−1.53 (−2.07 to −0.99)	−1.33 (−2.22 to −0.44)
Ca (mg g^{-1})	−0.61 (−1.26 to 0.04)	−1.11 (−2.16 to −0.06)

reflectance data (table 3): changes predicted by PLSR of spectral data are similar to laboratory-measured differences for all traits except water content and calcium (figure 5). However, the residuals are mostly negative in the upper half of *x*-axe values for some traits, e.g. pigments, indicating that spectroscopy underestimate pigment concentrations of leaves with high concentrations. However, the influence of El Niño on pigment concentrations is apparent in the separation of during- and after-classes, indicating the ability to detect the leaf-greening phenomenon from spectral data.

Discussion

Changes in rainfall and temperature observed during the the El Niño event of 2015/2016 varied markedly across South-East Asia (Thirumalai *et al* 2017). Even on the island of Borneo there were significant differences in both the duration and severity of reduced rainfall and increased temperatures (Colledge 2017, Whitfield *et al* 2019). This paper provides the first analysis of how rainforest leaf traits respond to El Niño events at a single site within this region, and uses trends in satellite-derived canopy greenness to interpret these changes. Measurements of leaf functional traits reveal that pigment concentrations were consistently higher during the El Niño event than afterwards, and a number of other traits varied to lesser extents. There are two non-exclusive explanations for these trait changes: that trees exchanged leaves in response to changing conditions and that the new leaf cohort had different traits to those that had been discarded, and/or that individual leaves acclimatised to the new environmental conditions brought about by the El Niño event. With functional trait data from just two points in time, it is challenging to distinguish between these two mechanisms. We start by looking at the NDVI trends, then explore possible ecophysiological explanations for the leaf-level trait changes, before returning to the question of whether leaf turnover or leaf acclimation or both contributed to the changes observed.
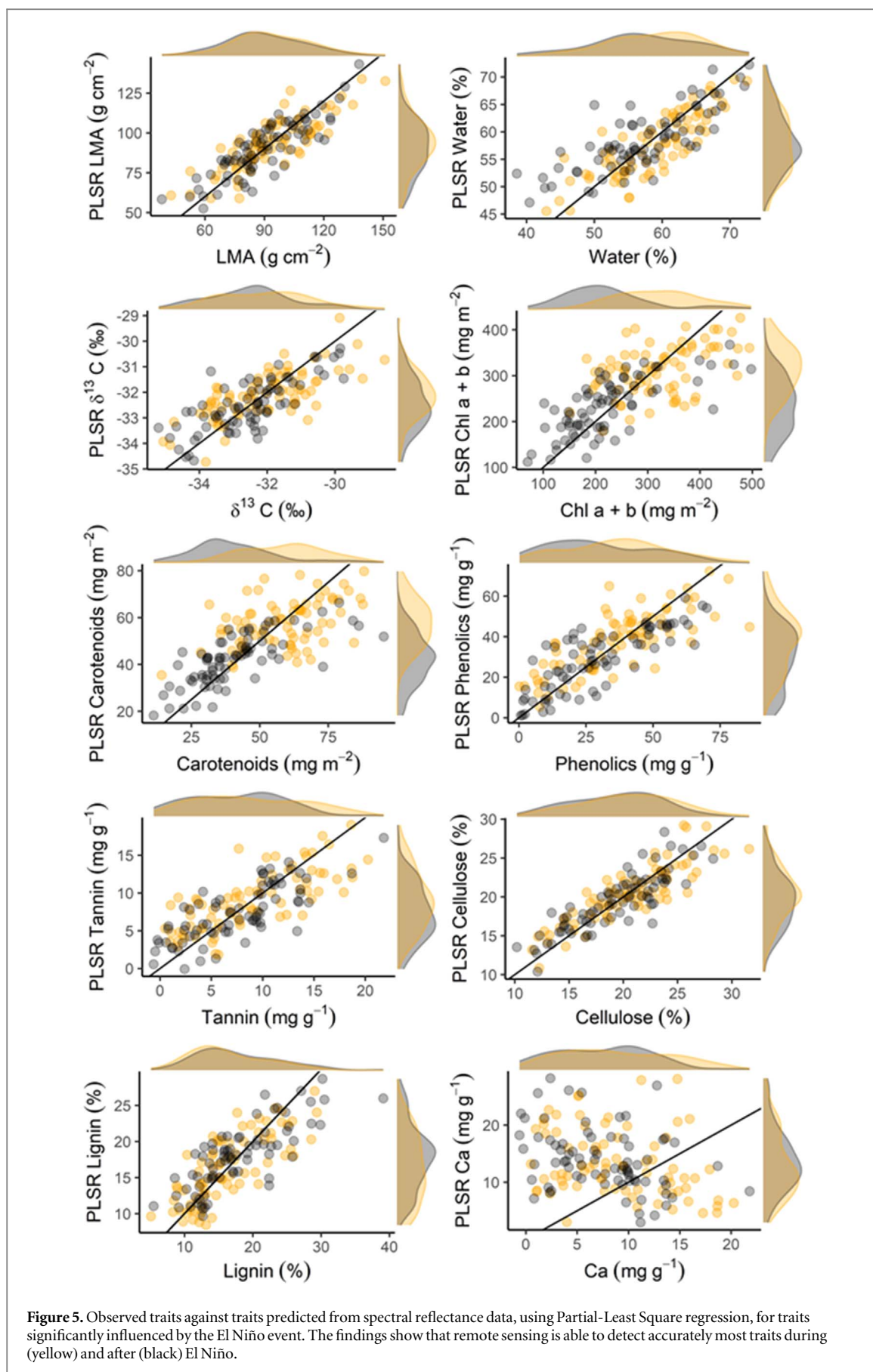
Ecophysiological explanations for functional trait shifts in response to El Niño

Pigment concentrations were about a third higher during the El Niño event than afterwards, which suggests that trees responded to having more light by upregulating photosynthetic processes. Greater foliar chlorophyll concentrations ensures that more photosynthetically active radiation is utilised for electron transport (Poorter *et al* 2009). Increased light availability during the relative dry phase of the El Niño cycle can result in high rates of photosynthesis (Guan *et al* 2015). However, it remains unclear whether higher rates of photosynthesis occur in Sabah, as N and P concentrations are similar during and after the El Niño, suggesting that the total concentration of leaf proteins (including Rubisco) remain unchanged (Evans 1989); this is a topic in need of further research. Carotenoids protect leaves from photoinhibition (i.e. damage caused by solar radiation when supply outstrips demand) by releasing excess energy as heat via the xanthophyll cycle (Ustin *et al* 2009). The ratio of carotenoids to chlorophyll remains similar between surveys, suggesting leaves retain similar commitment to protection against photoinhibition.

Leaves had higher δ^{13}C values during the El Niño event, consistent with greater water use efficiency in a period of increased evaporative demand. Water-use efficiency can be effectively measured with foliar δ^{13}C values (Farquhar *et al* 1989) because changes in stomatal conductance in response to leaf water balance changes intercellular/ambient CO_2 ratios and discrimination against the heavier isotope in metabolic processes.

The observed increases in phenolic compounds are consistent with other studies showing increased production in response to heat stress and higher irradiation (Rivero *et al* 2001, Caldwell *et al* 2007, Poorter *et al* 2009). Phenolic compounds are secondary metabolites with antioxidant effects in plants exposed to

Figure 5. Observed traits against traits predicted from spectral reflectance data, using Partial-Least Square regression, for traits significantly influenced by the El Niño event. The findings show that remote sensing is able to detect accurately most traits during (yellow) and after (black) El Niño.

oxidative stress (Olsson *et al* 1998, Tattini *et al* 2004, Tatinni *et al* 2005, Mansori *et al* 2015). Phenolic compounds accumulate in large quantities in the vacuoles of epidermal cells and effectively attenuate the UV component of sunlight with minimal change in the visible region of the spectrum.

The ecophysiological responses outlined above could have resulted from rapid acclimation of existing leaves or from the production of new leaves with different properties in response to the El Niño environment. The next section considers evidence supporting the latter hypothesis.

Evidence for increased leaf turnover

Shedding of leaves has been observed as a response to both intense short and long period droughts in the north of Borneo (Ichie *et al* 2004) and most trees flush new young leaves with the end of drought and increase in rainfall (Itioka and Yamauti 2004). If leaf loss was greater in the period running up to the first field campaign, and if new leaves were flushed almost immediately, then we could have inadvertently sampled younger leaves in the first campaign which are known to have higher concentrations of photosynthetic pigments (Doughty and Goulden 2008, Hilker *et al* 2017). Recent studies have demonstrated strong relationships of leaf traits and spectra with leaf age (Chavana-Bryant *et al* 2017, Wu *et al* 2017). By selecting what appeared to be mature leaves on each branch we attempted to minimise any effects of leaf turnover, but leaf age was not determined.

Our NDVI time series is likely as a result of both leaf biochemistry and canopy structure (i.e. leaf area, crown geometry and leaf demography) (Wu *et al* 2016, 2017, 2018). We see greening in the early El Niño period in 2015 (figure 2(b)), probably because there was more PAR and sufficient water, which resulted in more chlorophyll and increased LAI. We see a sharp decrease in greeness late in the El Niño which possibly indicates loss of leaves associated with strong evaporative demand and depleted soil water (figure 2(b)). By the time of the second field survey, the NDVI is similar to the first survey despite evidence of major upheavals in the interim.

Some—but not all—functional trait responses vary among species

By concentrating on functional traits without reference to species identities or individuals, we are able to account for intra-specific variability, often neglected when functional diversity is indirectly calculated from taxonomic data. Strong taxonomic organisation probably indicates low plasticity within species (Asner and Martin 2011). Our results suggest that most traits have strong phylogenetic signals; among those traits that do not have strong taxonomic contribution to the overall variance partitioning, changes in LMA and δ^{13}C

concentration are primarily driven by sun/shade branch conditions whereas pigments are primarily driven by the El Niño event. LMA has a tight relationship with the photosynthetic capacity of plants (Poorter *et al* 2009), and is highly modulated by the total photon irradiance over the day (Niinemets *et al* 2004) and the vertical light-gradient and light quality along plants play a crucial role in determining LMA (Niinemets 2007). Our results suggest that variation in irradiance may be the underlying mechanism behind changes in LMA between the two sampling events, especially if the onset of drier conditions was associated with reduced cloud cover and lower irradiance during the El Niño event. On the other hand, nutrients and water content had particularly strong taxonomic organisation. Although plants can quickly adjust investment in the photosynthetic machinery and water-use efficiency (δ^{13}C), nutrients stored in tissues may be reused and changes in those traits may take longer to manifest. The strong taxonomic pattern in water content may indicate selective pressure among coexisting species.

A clearer sense of the diversity and organisation of canopy chemical traits may help us to forecast the species that will suffer or gain from an increasing frequency of El Niño events. Some old growth forests of Borneo have high levels of interspecific variability associated with high biological diversity (Asner *et al* 2012). The rapid shift in water-use efficiency indicates the ability of plants to adapt to these short-term climate variation, but may also suggest that more frequent droughts could increase selection for species with greater intrinsic water-use efficiency (Cernusak *et al* 2009).

Application of spectroscopy to predict trait variation

To our knowledge, our study is the first to analyse the morphological (LMA) and a range of chemical traits along with spectral reflectance of leaves of emergent canopies and tropical tree species during and after El Niño. Many previous studies have shown that leaf reflectance can predict the morphological and chemical leaf traits in the tropics that are commonly used for determining functional diversity (Asner *et al* 2012, Asner *et al* 2014, Doughty *et al* 2017) and also capture variation that is not traditionally measured (Schweiger *et al* 2018). We evaluated the variation of 17 leaf traits using spectral reflectance and were able to validate these measurements against field data. In particular, the variation of traits affected by El Niño such as pigments, δ^{13}C and phenolics were successfully detected, which suggests that repeated reflectance measurements can also predict physiologically relevant variation of the El Niño effects at the leaf level. The effects of El Niño on leaves accompanied by high pigment concentrations were detected from the visible

(400–750 nm) portion of the spectra, as expected from previous studies (Curran *et al* 1991, Sims and Gamon 2002, Serbin *et al* 2014). From a remote sensing perspective, a potential leaf-level greening phenomenon during El Niño could be then a factor contributing to the greening observed during the dry season.

Concluding thoughts

Greening of forest canopies during short and long-term drought have been reported previously in the Amazon basin, using satellite remote sensing (Saleska *et al* 2007, Manoli *et al* 2018). Ground-based spectral data and NDVI trends measured by spaceborne spectroradiometers in this study suggest canopy-level greening in response to the initial phase of the El Niño drought, similar to those observed in several studies and attributed to greater irradiance when cloud cover is reduced and/or to leaf demography (Nemani *et al* 2003, Huete *et al* 2006, Wu *et al* 2016). Manoli *et al* (2018) recreated dry-season greening in the Amazon using an eco-hydrological model, providing further support for the idea that leaf development and synchronised dry season litterfall and dry conditions are in agreement with evolutionary strategies aimed at increasing the efficiency of photosynthesis and water consumption during periods of abundant light but potentially low water availability. We observed the greening with both ground-based sensor and spaceborne analyses in the early part of the El Niño, quite possibly because plants were not initially droughted despite increased evaporative demand, but then towards its climax forest greeness reduced, presumably because of leaf shedding in response to water availability.

The short and long-term impacts of El Niño may differ and are likely to depend on species (Slik 2004) and tree age and height (Giardina *et al* 2018). Despite the greening observed, plot-based estimates demonstrated that a previous 2005 drought negatively affected forest carbon through increased mortality (Phillips *et al* 2009). Although our study provides evidence of a rapid shift to maximise water use efficiency, as well as a large investment in photosynthetic and defensive machineries, we cannot infer information about mortality and productivity of trees from our data. Leaf-level traits do not account for all important aspects of functional traits that do not interact with light (e.g. rooting depth) or canopy-level functional traits such as LAI, canopy height or tree architecture hence the difficulties to predict future responses to El Niño events. However, these events have been documented for at least 130 000 years (Tudhop *et al* 2001), which allows abundant time for selection on plant functional responses to El Niño and supporting the idea that the ability to change traits over short time frames is adaptive. More integrative work is needed to link remote

sensing time-series with ground-based surveys of trait and population-level changes.

Our results demonstrate that trees do increase chlorophyll concentration in their leaves during El Niño and this change can be detected from spectral reflectance. In our analysis we have analysed the spectral information at specific wavelengths within broad regions of the electromagnetic spectrum, i.e. visible, near infrared and shortwave infrared regions of the spectrum. Future work will examine changes in spectral response associated with specific absorption and reflectance features within each spectra. This will likely yield better predictive and explanatory models of changing leaf traits with hyperspectral remote sensing in an era when airborne spectrometers are mapping large areas of the Earth (e.g. Asner *et al* 2017) and new spaceborne hyperspectral missions (e.g. ESA's EnMap) are being developed, thus paving the way for changing leaf and canopy traits to be observed at landscape-scales. The implication of this study thus extends beyond the Borneo region and suggests that remote sensing-based observations will soon enable vegetation and ecosystem function, and their responses to short-term climate changes, to be characterised at the global scale. Providing evidence that plant strategies during short-term climate change can be accurately predicted using spectrometers paves the way for new research on tropical forest responses to a changing climate using sensors in space.

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References

Adams H D, Guardiola-Claramonte M, Barron-Gafford G A, Villegas J C, Breshears D D, Zou C B, Troch P A and Huxman T E 2009 Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought *Proc. Natl Acad. Sci.* **106** 7063–6

Allen C D *et al* 2010 A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests *Forest Ecol. Manage.* **259** 660–84

Asner G P and Martin R E 2011 Canopy phylogenetic, chemical and spectral assembly in a lowland Amazonian forest *New Phytol.* **189** 999–1012

Asner G P, Martin R E, Carranza-Jiménez L, Sinca F, Tupayachi R, Anderson C B and Martinez P 2014 Functional and biological diversity of foliar spectra in tree canopies throughout the Andes to Amazon region *New Phytol.* **204** 127–39

Asner G P, Martin R E, Knapp D E, Tupayachi R, Anderson C B, Sinca F, Vaughn N R and Llactayo W 2017 Airborne laser-guided imaging spectroscopy to map forest trait diversity and guide conservation *Science* **355** 385–9

Asner G P, Martin R E and Suhaili A B 2012 Sources of canopy chemical and spectral diversity in lowland Bornean forest *Ecosystems* **15** 504–17

Asner G P, Martin R E, Tupayachi R, Emerson R, Martinez P, Sinca F, Powell G V, Wright S J and Lugo A E 2011 Taxonomy and remote sensing of leaf mass per area (LMA) in humid tropical forests *Ecol. Appl.* **21** 85–98

Benjamini Y and Hochberg Y 1995 Controlling the false discovery rate: a practical and powerful approach to multiple testing *J. R. Stat. Soc.* B **57** 289–300

Bi J *et al* 2015 Sunlight mediated seasonality in canopy structure and photosynthetic activity of Amazonian rainforests *Environ. Res. Lett.* **10** 064014

Both S *et al* 2019 Logging and soil nutrients independently explain plant trait expression in tropical forests *New Phytol.* **221** 1853–65

Breiman L, Friedman J H and Olshen R A 1984 *Classification and Regression Trees* (Wadsworth, CA: CRC)

Breshears D D, Myers O B, Meyer C W, Barnes F J, Zou C B, Allen C D, McDowell N G and Pockman W T 2009 Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements *Frontiers Ecol. Environ.* **7** 185–9

Breshears D D 2005 Regional vegetation die-off in response to global-change-type drought *Proc. Natl Acad. Sci. USA* **102** 15144

Caldwell M M, Bornman J F, Ballaré C L, Flint S D and Kulandaivelu G 2007 Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors *Photochem. Photobiol. Sci.* **6** 252–66

Cernusak L A *et al* 2009 Why are non-photosynthetic tissues generally 13C enriched compared with leaves in C3 plants? Review and synthesis of current hypotheses *Funct. Plant Biol.* **36** 199–213

Chavana-Bryant C *et al* 2017 Leaf aging of Amazonian canopy trees as revealed by spectral and physiochemical measurements *New Phytol.* **214** 1049–63

Colledge F 2017 *Summary of the 2015/2016 El Niño Wet and Dry Season Climatology for: Ethiopia, Ghana, Malawi, Colombia, Papua New Guinea and Indonesia* Leeds University and Natural Environment Research Council

Curran P J 1989 Remote sensing of foliar chemistry *Remote Sens. Environ.* **30** 271–8

Curran P J, Dungan J L, Macler B A and Plummer S E 1991 The effect of a red leaf pigment on the relationship between red edge and chlorophyll concentration *Remote Sens. Environ.* **35** 69–76

Detto M, Wright S J, Calderón O and Muller-Landau H C 2018 Resource acquisition and reproductive strategies of tropical forest in response to the El Niño–southern oscillation *Nat. Commun.* **9** 913

Doughty C E and Goulden M L 2008 Seasonal patterns of tropical forest leaf area index and CO_2 exchange *J. Geophys. Res.: Biogeosci.* **113** G00B06

Doughty C E *et al* 2015 Drought impact on forest carbon dynamics and fluxes in Amazonia *Nature* **519** 78

Doughty C E *et al* 2017 Can leaf spectroscopy predict leaf and forest traits along a peruvian tropical forest elevation gradient? *J. Geophys. Res.: Biogeosci.* **122** 2952–65

Doughty C E *et al* 2018 Tropical forest leaves may darken in response to climate change *Nat. Ecol. Evol.* **2** 1918

Evans J R 1989 Photosynthesis and nitrogen relationships in leaves of C 3 plants *Oecologia* **78** 9–19

Farquhar G D, Hubick K T, Condon A G and Richards R A 1989 Carbon isotope fractionation and plant water-use efficiency *Stable Isotopes in Ecological Research* (New York: Springer) pp 21–40

Fauset S, Baker T R, Lewis S L, Feldpausch T R, Affum-Baffoe K, Foli E G, Hamer K C and Swaine M D 2012 Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana *Ecol. Lett.* **15** 1120–9

Fox J E D 1972 The natural vegetation of the Sabah and natural regeneration of the dipterocarp forests *Doctoral Dissertation* University of Wales, Bangor

Freund M B, Henley B J, Karoly D J, McGregor H V, Abram N J and Dommenget D 2019 Higher frequency of central pacific El Niño events in recent decades relative to past centuries *Nat. Geosci.* **12** 450

Giardina F, Konings A G, Kennedy D, Alemohammad S H, Oliveira R S, Uriarte M and Gentine P 2018 Tall Amazonian forests are less sensitive to precipitation variability *Nat. Geosci.* **11** 405–9

Guan K *et al* 2015 Photosynthetic seasonality of global tropical forests constrained by hydroclimate *Nat. Geosci.* **8** 284

Harrison R D 2000 Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo *Proc. R. Soc.* B **267** 911–5

Hilker T *et al* 2017 Vegetation chlorophyll estimates in the Amazon from multi-angle MODIS observations and canopy reflectance model *Int. J. Appl. Earth Obs. Geoinf.* **58** 278–87

Huete A R, Didan K, Shimabukuro Y E, Ratana P, Saleska S R, Hutyra L R, Yang W, Nemani R R and Myneni R 2006 Amazon rainforests green-up with sunlight in dry season *Geophys. Res. Lett.* **33** L06405

Ichie T, Hiromi T, Yoneda R, Kamiya K, Kohira M, Niñomiya I and Ogino K 2004 Short-term drought causes synchronous leaf shedding and flushing in a lowland mixed dipterocarp forest, Sarawak, Malaysia *J. Tropical Ecol.* **20** 697–700

Itioka T and Yamauti M 2004 Severe drought, leafing phenology, leaf damage and lepidopteran abundance in the canopy of a Bornean aseasonal tropical rain forest *J. Tropical Ecol.* **20** 479–82

Kokaly R F, Asner G P, Ollinger S V, Martin M E and Wessman C A 2009 Characterizing canopy biochemistry from imaging spectroscopy and its application to ecosystem studies *Remote Sens. Environ.* **113** S78–91

Lopes A V, Chiang J C H, Thompson S A and Dracup J A 2016 Trend and uncertainty in spatial-temporal patterns of hydrological droughts in the Amazon basin *Geophys. Res. Lett.* **43** 3307–16

Lyapustin A, Martonchik J, Wang Y, Laszlo I and Korkin S 2011a Multiangle implementation of atmospheric correction (MAIAC): 1. radiative transfer basis and look-up tables *J. Geophys. Res.* **116** D03210

Lyapustin A, Wang Y, Korkin S and Huang D 2018 MODIS Collection 6 MAIAC algorithm *Atmos. Meas. Tech.* **11** 5741

Lyapustin A, Wang Y, Laszlo I, Kahn R, Korkin S, Remer L, Levy R and Reid J S 2011b Multiangle implementation of atmospheric correction (MAIAC): 2. Aerosol algorithm *J. Geophys. Res.* **116** D03211

Manoli G, Ivanov V Y and Fatichi S 2018 Dry-season greening and water stress in Amazonia: the role of modeling leaf phenology *J. Geophys. Res.: Biogeosci.* **123** 1909–26

Mansori M, Chernane H, Latique S, Benaliat A, Hsissou D and El Kaoua M 2015 Seaweed extract effect on water deficit and antioxidative mechanisms in bean plants (*Phaseolus vulgaris* L.) *J. Appl. Phycol.* **27** 1689–98

Maréchaux I, Bartlett M K, Sack L, Baraloto C, Engel J, Joetzjer E and Chave J 2015 Drought tolerance as predicted by leaf water potential at turgor loss point varies strongly across species within an Amazonian forest *Funct. Ecol.* **29** 1268–77

Messier J, McGill B J and Lechowicz M J 2010 How do traits vary across ecological scales? A case for trait-based ecology *Ecol. Lett.* **13** 838–48

Morton D C, Nagol J, Carabajal C C, Rosette J, Palace M, Cook B D, Vermote E F, Harding D J and North P R 2014 Amazon forests maintain consistent canopy structure and greenness during the dry season *Nature* **506** 221

Nemani R R *et al* 2003 Climate-driven increases in global terrestrial net primary production from 1982 to 199 *Science* **300** 1560

Niinemets U 2007 Photosynthesis and resource distribution through plant canopies *Plant, Cell Environ.* **30** 1052–71

Niinemets Ü, Kull O and Tenhunen J D 2004 Within-canopy variation in the rate of development of photosynthetic capacity is proportional to integrated quantum flux density in temperate deciduous trees *Plant, Cell Environ.* **27** 293–313

Nunes M H, Davey M P and Coomes D A 2017 On the challenges of using field spectroscopy to measure the impact of soil type on leaf traits *Biogeosciences* **14** 3371–85

O'Brien M J, Reynolds G, Ong R and Hector A 2017 Resistance of tropical seedlings to drought is mediated by neighbourhood diversity *Nat. Ecol. Evol.* **1** 1643

Olsson L C, Veit M, Weissenböck G and Bornman J F 1998 Differential flavonoid response to enhanced UV-B radiation in Brassica napus *Phytochemistry* **49** 1021–8

Petisco C, García-Criado B, Mediavilla S, De Aldana B V and Zabalgogeazcoa I 2006 Near-infrared reflectance spectroscopy as a fast and non-destructive tool to predict foliar organic constituents of several woody species *Anal. Bioanal. Chem.* **386** 1823–33

Phillips O L *et al* 2009 Drought sensitivity of the Amazon rainforest *Science* **323** 1344–7

Poorter H, Niinemets Ü, Poorter L, Wright I J and Villar R 2009 Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis *New Phytol.* **182** 565–88

Qie L *et al* 2017 Long-term carbon sink in Borneo's forests halted by drought and vulnerable to edge effects *Nat. Commun.* **8** 1966

Reich P B 2012 Key canopy traits drive forest productivity *Proc. R. Soc. B* **279** 2128

Reich P B 2014 The world-wide 'fast–slow' plant economics spectrum: a traits manifesto *J. Ecol.* **102** 275–301

Reynolds G, Payne J, Sinun W, Mosigil G and Walsh R P 2011 Changes in forest land use and management in Sabah, Malaysian Borneo, 1990–2010, with a focus on the Danum valley region *Phil. Trans. R. Soc. B* **366** 3168–76

Riutta T *et al* 2018 Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests *Glob. Change Biol.* **24** 2913–28

Rivero R M *et al* 2001 Resistance to cold and heat stress: accumulation of phenolic compounds in tomato and watermelon plants *Plant Sci.* **160** 315–21

Sakschewski B, Von Bloh W, Boit A, Poorter L, Peña-Claros M, Heinke J, Joshi J and Thonicke K 2016 Resilience of Amazon forests emerges from plant trait diversity *Nat. Clim. Change* **6** 1032

Saleska S R, Didan K, Huete A R and Da Rocha H R 2007 Amazon forests green-up during 2005 drought *Science* **318** 612–612

Saleska S R, Wu J, Guan K, Araujo A C, Huete A, Nobre A D and Restrepo-Coupe N 2016 Dry-season greening of Amazon forests *Nature* **531** E4

Samanta A, Ganguly S, Hashimoto H, Devadiga S, Vermote E, Knyazikhin Y, Nemani R R and Myneni R B 2010 Amazon forests did not green-up during the 2005 drought *Geophys. Res. Lett.* **37** L05401

Santos V A H F D, Ferreira M J, Rodrigues J V F C, Garcia M N, Ceron J V B, Nelson B W and Saleska S R 2018 Causes of reduced leaf-level photosynthesis during strong El Niño drought in a Central Amazon forest *Glob. Change Biol.* **24** 4266–79

Schweiger A K, Cavender-Bares J, Townsend P A, Hobbie S E, Madritch M D, Wang R, Tilman D and Gamon J A 2018 Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function *Nat. Ecol. Evol.* **2** 976

Serbin S P, Singh A, McNeil B E, Kingdon C C and Townsend P A 2014 Spectroscopic determination of leaf morphological and biochemical traits for northern temperate and boreal tree species *Ecol. Appl.* **24** 1651–69

Sims D A and Gamon J A 2002 Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages *Remote Sens. Environ.* **81** 337–54

Slaton M R, Raymond Hunt E Jr and Smith W K 2001 Estimating near-infrared leaf reflectance from leaf structural characteristics *Am. J. Bot.* **88** 278–84

Slik J W F 2004 El Niño droughts and their effects on tree species composition and diversity in tropical rain forests *Oecologia* **141** 114–20

Susskind J, Schmidt G A, Lee J N and Iredell L 2019 Recent global warming as confirmed by AIRS *Environ. Res. Lett.* **14** 044030

Tattini M, Galardi C, Pinelli P, Massai R, Remorini D and Agati G 2004 Differential accumulation of flavonoids and hydroxycinnamates in leaves of Ligustrum vulgare under excess light and drought stress *New Phytol.* **163** 547–61

Tattini M, Guidi L, Morassi-Bonzi L, Pinelli P, Remorini D, Degl'Innocenti E, Giordano C, Massai R and Agati G 2005 On the role of flavonoids in the integrated mechanisms of response of Ligustrum vulgare and Phillyrea latifolia to high solar radiation *New Phytol.* **167** 457–70

Team, R C 2018 *R: A Language and Environment for Statistical Computing* (Vienna: R Foundation for Statistical Computing)

Thirumalai K, DiNezio P N, Okumura Y and Deser C 2017 Extreme temperatures in Southeast Asia caused by El Niño and worsened by global warming *Nat. Commun.* **8** 15531

Tucker C J 1980 Remote sensing of leaf water content in the near infrared *Remote Sens. Environ.* **10** 23–32

Tudhope A W, Chilcott C P, McCulloch M T, Cook E R, Chappell J, Ellam R M, Lea D W, Lough J M and Shimmield G B 2001 Variability in the El Niño-Southern Oscillation through a glacial-interglacial cycle *Science* **291** 1511–7

Ustin S L, Gitelson A A, Jacquemoud S, Schaepman M, Asner G P, Gamon J A and Zarco-Tejada P 2009 Retrieval of foliar information about plant pigment systems from high resolution spectroscopy *Remote Sens. Environ.* **113** S67–77

Ustin S L, Roberts D A, Gamon J A, Asner G P and Green R O 2004 Using imaging spectroscopy to study ecosystem processes and properties *AIBS Bull.* **54** 523–34

Wagner F H, Hérault B, Rossi V, Hilker T, Maeda E E, Sanchez A, Lyapustin A I, Galvão L S, Wang Y and Aragão L E 2017 Climate drivers of the Amazon forest greening *PLoS One* **12** e0180932

Wang G, Cai W, Gan B, Wu L, Santoso A, Lin X, Chen Z and McPhaden M J 2017 Continued increase of extreme El Niño frequency long after 1.5 °C warming stabilization *Nat. Clim. Change* **7** 568

Whitfield S *et al* 2019 Exploring temporality in socio-ecological resilience through experiences of the 2015/16 El Niño across the tropics *Glob. Environ. Change* **55** 1–14

Whitmore T C and Burnham C P 1975 *Tropical Rain Forests of the Far East* (Oxford: Clarendon)

Wold S, Sjöström M and Eriksson L 2001 PLS-regression: a basic tool of chemometrics *Chemometr. Intell. Lab. Syst.* **58** 109–30

Wright P S 1975 *Western Parts of Tawau and Lahad Datu Districts. The Soils of Sabah* (Land Resource Study vol 20) vol 5 (Surbiton: Land Resources Division)

Wu J *et al* 2016 Leaf development and demography explain photosynthetic seasonality in Amazon evergreen forests *Science* **351** 972–6

Wu J *et al* 2017 Convergence in relationships between leaf traits, spectra and age across diverse canopy environments and two contrasting tropical forests *New Phytol.* **214** 1033–48

Wu J *et al* 2018 Biological processes dominate seasonality of remotely sensed canopy greenness in an Amazon evergreen forest *New Phytol.* **217** 1507–20