BRIEF COMMUNICATIONS ARISING

Dry-season greening of Amazon forests

ARISING FROM D. C. Morton *et al. Nature* **506,** 221–224 (2014); doi:10.1038/nature13006

Evidence from ecological studies[1,2], eddy flux towers[3–5], and satellites[3,6] shows that many tropical forests 'green up' during higher sunlight annual dry seasons, suggesting they are more limited by light than water. Morton *et al.*[7] reported that satellite-observed dry-season green up in Amazon forests is an artefact of seasonal variations in sun-sensor geometry. However, here we argue that even after artefact correction, data from Morton *et al.* show statistically significant increases in canopy greenness during the dry season. Integrating corrected satellite with ground observations indicates that dry-season forest greening is prevalent in Amazonia, probably reflecting large-scale seasonal upregulation of photosynthesis by canopy leaf dynamics. There is a reply to this Brief Communication Arising by Morton, D. C. *et al. Nature* **531,** http://dx.doi.org/10.1038/nature16458 (2016).

Variations in sun-sensor geometry induce artefacts in remotely sensed vegetated surfaces[8]. Satellite studies thus typically use models to correct artefacts (for example, Moderate Resolution Imaging Spectroradiometer (MODIS) leaf area index[9], and multiangle implementation of atmospheric correction (MAIAC) enhanced vegetation index[10] (EVI)) or compositing algorithms designed to minimize artefacts (standard MODIS EVI[11]). Morton *et al.*[7] used a modelling approach to correct MODIS satellite data, which they state removed seasonal changes in surface reflectance, and redefined debates over how climate controls forest productivity in the Amazon. Setting aside arguments that the remote sensing analysis by Morton *et al.* is faulty[12], we take their correction[7] at face value, and ask two questions.

First, we ask whether the corrected results support their core conclusion that dry-season green up, previously observed by MODIS EVI, is eliminated. The hypothesis that Amazon forests green up in the dry season[3] can be rigorously evaluated by formal statistical tests. Morton *et al.*[7] showed that their correction reduces estimated dry season green up, ΔEVI (the EVI change during the dry season, ΔEVI = October EVI − June EVI; figure 3 in ref. 7 and Fig. 1). As the corrected mean ΔEVI was smaller than an *a priori* estimate of error for individual EVI observations, they concluded that the corrected mean ΔEVI was indistinguishable from zero. We find that this comparison, however, is not appropriate for assessing whether corrected EVI can resolve a basin-wide green up. The correct comparison, of mean ΔEVI to the error of the mean of the whole population of observations, is accomplished with standard statistical tests that lever the probability theory 'law of large numbers'[13]. For example, the 95% confidence interval[13] for basin-wide mean of corrected ΔEVI significantly excludes zero (Fig. 1). Alternatively, the corrected ΔEVI distribution[7] can be compared to the binomial distribution generated by the null hypothesis that pixels are equally likely to exhibit positive or negative ΔEVI (Fig. 1), which is analogous to treating 'green up' or 'brown down' as the outcome of the flip of a fair coin.

These standard tests show that corrected ΔEVI[7], though substantially smaller in magnitude than uncorrected, nonetheless shows a highly significant increase in forest greenness.

Second, we ask whether the smaller, but statistically significant, green up seen in the data from Morton *et al.* (Fig. 1) is biologically meaningful in terms of consistency with mechanisms and magnitude of seasonal changes in canopy-scale biophysics observed on the ground. We find that at an intensively measured site, significant dry-season increases in leaf area index are driven by coordinated flushing of new leaves, which have higher near-infrared reflectance (Fig. 2a) (mechanisms that Morton *et al.*[7] hypothesized could drive true increases in satellite-observed EVI). Leaf flushing is followed, after 1 to 2 months, by increases in photosynthetic capacity derived from CO_2 fluxes measured at eddy flux towers (Fig. 2a). This correlation—1-month-lagged photosynthetic capacity with leaf area index, $r = +0.90$, and with MAIAC EVI, $r = +0.89$, where r is Pearson's correlation coefficient, and the time lag is for new leaves to develop their photosynthetic capacity[14]—establishes a link between eddy flux measurements and biophysical properties observable from satellites.

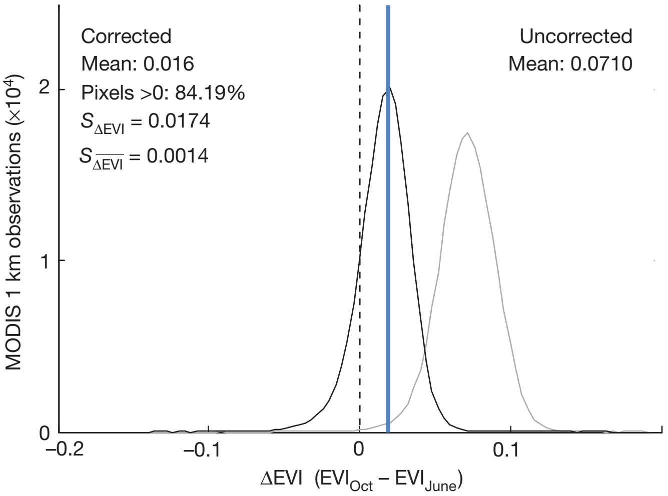

Figure 1 | Distribution of uncorrected and corrected ΔEVI. Reproducing figure 3b of ref. 7, with 95% confidence interval (shaded blue region), significantly excluding zero. We conservatively assume that only relatively large areas (1° × 1°, or $\sim 10^4$ MODIS pixels) are independent, giving 158 independent 1° × 1° patches that include valid pixels, and 95% confidence interval: $\overline{\Delta EVI} \pm Z S_{\overline{\Delta EVI}} = 0.016 \pm 0.0027$, where Z is 1.96 (the 95% Z-score), and $S_{\overline{\Delta EVI}}$ is the standard error of $\overline{\Delta EVI}$ (derived from ΔEVI standard deviation as $S_{\Delta EVI} / \sqrt{158}$). The probability of observing 84.2% positive values (or heads from fair coin flips) out of 158 observations is $P < 10^{-15}$ (binomial test).

On the basis of this link, we find that increases in dry-season greenness seen by corrected EVI products (whether those of ref. 7 or the MAIAC EVI of Lyapustin *et al.*[10]; Fig. 2b) are real and consistently correlated with photosynthetic capacity increases seen at towers within the region analysed by Morton *et al.* (including adjustment for possible sun-angle effects on canopy illumination). This suggests that even the smaller corrected ΔEVI[7] reflects mechanisms of canopy changes actually observed on the ground, and is therefore biologically meaningful.

The analysis in Morton *et al.*[7] is, notably, stimulating a productive re-examination of the methodology, meaning and magnitude of remote sensing indices, their artefacts, and their relation to field studies on the ground[6,12]. However, we believe that the primary substantive finding of Morton *et al.* of consistent canopy structure and greenness is incorrect. Both satellite remote sensing and ground-based observations show dry-season increases in greenness and biophysical properties associated with canopy photosynthesis across scales, from individual leaves to ecosystems to regions, in support of the conclusion that Amazon forests green up with sunlight in the dry season[3,14].

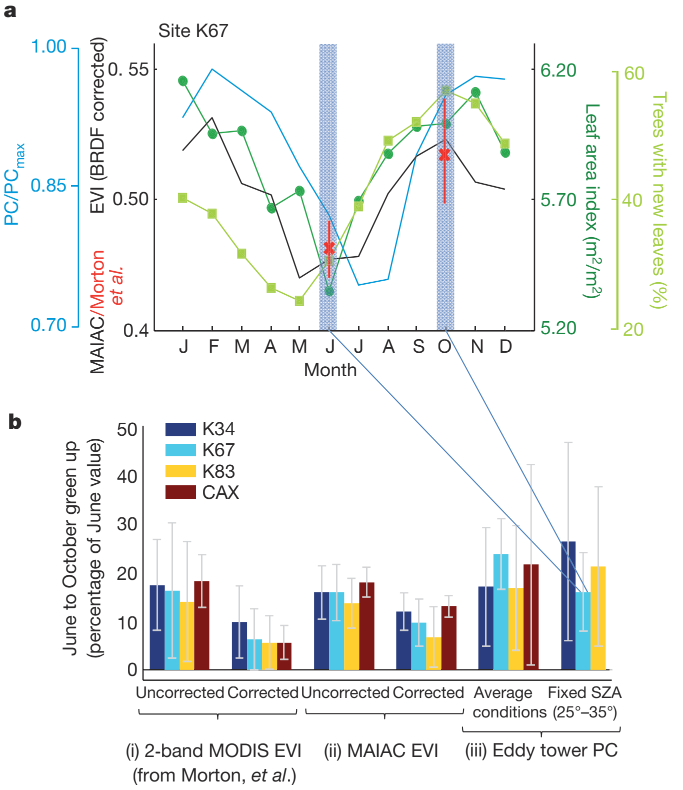

Figure 2 | Seasonality of vegetation metrics. a, Corrected EVI (from extended data figure 7 of ref. 7; red 'X' in June and October), and average cycle of corrected MAIAC EVI, a product that also corrects sun-sensor geometry (to nadir view, and 45° sun angle; black line)[10]; leaf area index (dark green)[15]; percentage of trees with new leaves (light green)[15]; and tower-derived photosynthetic capacity (PC/PC$_{max}$, blue line; see Methods), all from site K67 (ref. 4). BRDF, bidirectional reflectance distribution function. **b**, Green up at four tower sites for (i) EVI (corrected as in **a** and uncorrected); (ii) MAIAC EVI (corrected and uncorrected); and (iii) tower-derived photosynthetic capacity (with and without fixed solar zenith angle (SZA), showing potential effects of changing solar illumination). Sites: K34 (Manaus), K67 and K83 (Santarém), and CAX (Caxiuanã National Forest, near Belém (CAX had insufficient data for fixed SZA analysis))[4]. All uncertainties are 95% confidence intervals.

Methods

For basin-wide analysis, we analysed ΔEVI, corrected on a per-pixel basis, in 197,651 valid pixels (from figure 3 of ref. 7, data courtesy of D. C. Morton). For tower comparisons, we averaged valid pixels from both extended data figure 7 of ref. 7 (corrected with a simplified approach that retrieved ΔEVI for more area, $\sim 2 \times 10^6$ pixels, including around towers), and from the independent sun-sensor geometry corrected MAIAC EVI product[10], in 5 km grids around towers (11 km around CAX, to obtain sufficient data; Fig. 2b). Tower-based 95% confidences are boot-strapped June–October changes in photosynthetic capacity. Photosynthetic capacity is eddy-flux-derived gross primary productivity (from ref. 4) averaged under reference environmental conditions, an estimate of photosynthetic infrastructure independent of environment and (with additional binning) sun angle. Reference bins were: light ($1{,}350 \pm 200\,\mu$mol m^{-2} s^{-1}), vapour pressure deficit (980 ± 200 Pa), relative irradiance (observed/clear-sky expected $= 0.6 \pm 0.1$), and solar zenith angle (25°–35°).

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Author Contributions S.R.S. designed the statistical analysis and wrote the initial draft of the paper; J.W. implemented the statistical analysis; K.G. provided MAIAC EVI data and analysis; A.C.A. contributed eddy flux data; A.H. contributed analysed EVI data; A.D.N. contributed eddy flux data and insights; and N.R.C. integrated the multi-tower datasets. All authors contributed to writing the final version.

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Morton *et al.* reply

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Multiple mechanisms could lead to upregulation of dry-season photosynthesis in Amazon forests, including canopy phenology and illumination geometry. We specifically tested two mechanisms for phenology-driven changes in Amazon forests during dry-season months, and the combined evidence from passive optical and lidar satellite data[1] was incompatible with large net changes in canopy leaf area or leaf reflectance suggested by previous studies[2–5]. We therefore hypothesized[1] that seasonal changes in the fraction of sunlit and shaded canopies, one aspect of bidirectional reflectance effects in Moderate Resolution Imaging Spectroradiometer (MODIS) data, could alter light availability for dry-season photosynthesis and the photosynthetic capacity of Amazon forests without large net changes in canopy composition. Subsequent work supports the hypothesis that seasonal changes in illumination geometry and diffuse light regulate light saturation in Amazon forests[6,7]. These studies clarify the physical mechanisms that govern light availability in Amazon forests from seasonal variability in direct and diffuse illumination. Previously, in the debate over light limitation of Amazon forest productivity, seasonal changes in the distribution of light within complex Amazon forest canopies were confounded with dry-season increases in total incoming photosynthetically active radiation[2,3,8]. In the accompanying Comment[9], Saleska *et al.* do not fully account for this confounding effect of forest structure on photosynthetic capacity.

Saleska *et al.*[9] investigated one of the three lines of evidence in our paper to argue that near-zero seasonal changes in corrected MODIS enhanced vegetation index (EVI) are actually non-zero (figure 1 in ref. 9; 0.071 to 0.016, a 77% reduction). Following this logic, our data also show a small but statistically significant decrease in normalized difference vegetation index (NDVI; extended data figure 4 in ref. 1), a pattern that we attributed to residual artefacts from changes in sun-sensor geometry, as no leaf-level mechanism for increased forest productivity generates opposing responses in these vegetation indices (see supplementary discussion in ref. 1). Indeed, the comparison between NDVI and EVI responses is a useful diagnostic tool[1] that could have been used to investigate residual bidirectional reflectance effects in multiangle implementation of atmospheric correction (MAIAC) data (figure 2 in ref. 9).

In isolation, MODIS data provide limited insight into the mechanisms for seasonal changes in Amazon forests[9]. MODIS EVI is primarily sensitive to changes in near-infrared reflectance[1,4,10], not photosynthetically active radiation absorption that drives forest productivity. Saleska *et al.* misrepresent data from extended data figure 7 of ref. 1 as fully corrected in their figure 2 (ref. 9), and further confound seasonal changes through spatial averaging of 1 km^2 data over large regions (25–121 km^2). A previous study using 1 km^2 data for these same tower sites shows little or no seasonality in MAIAC EVI[11] (see supplementary figure 5 in ref. 1).

One of the key messages from our study was the need for careful attention to uncertainty in satellite-based measurements of forest seasonality. The presentation of *in situ* and satellite data by Saleska *et al.* (figure 2a in ref. 9), and the MAIAC product in general, could be improved with quantitative estimates of uncertainty to support assertions of forest seasonality.

Subtle variability in canopy structure and reflectance properties of Amazon forests remains a key area for further study, particularly with large-scale field studies[12], to better understand the spatial and temporal heterogeneity of leaf phenology strategies in Amazonia[13]. Other mechanisms for seasonal changes in photosynthetic capacity also merit further investigation, including how diurnal and seasonal variability in illumination alter the distribution of photosynthetically active radiation at the leaf level[1,6,7,14]. NASA satellite data remain an important foundation for future research on tropical forest dynamics, within the limits of calibration, measurement, and model uncertainty that can be realistically achieved with space-based sensors.

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