Associate Editor Decision: Publish subject to minor revisions (Editor review) (08 Jul 2016) by Georg Wohlfahrt

Comments to the Author:

The authors have responded reasonably to the reviewer comments and revised their manuscript accordingly. I have a couple of more comments, which I ask the authors to take into account, before I can accept the manuscript. Please revised the manuscript accordingly and include a point-by-point reply with the revised manuscript. I apologize for these late comments, but as I had only recently taken over the manuscript, I had not chance make these comments at an earlier stage.

We greatly appreciate the thoroughly review and welcome all questions and comments as they will help us improve the clarity and scientific rigor of this study.

Editor comments:

p. 3, l. 23: break up sentence

Following the Editor's comments we broke up and reorganized the sentence as:

Past studies have focused on the relationship between the Moderate Resolution Imaging Spectroradiometer (MODIS) VIs, such as the enhanced vegetation index (*EVI*), and tower based measurements of gross ecosystem productivity (*GEP*) (Gamon et al., 2013; Huete et al., 2008, 2006; Maeda et al., 2014; Sims et al., 2006; Wang et al., 2004). In this studies, satellite derived vegetation indices (VIs) represented a community property of chlorophyll content, leaf area index (*LAI)*, and fractional vegetation cover.

p. 6, l. 21: no first objective formulated (at least not formally)

We reorganized the sentence in L11-15 to clarify our first objective as:

...Our first objective was to revisit the *GEP versus EVI,* and *GEP versus* GPP_{MOD} regressions at different sites to gain a better understanding of ecosystem behaviour, rather than simply to determine the “best performing model”...

p. 6, l. 24: explored instead of explore d

Corrected

p. 7, l. 2: maybe formulate this as a third objective

Corrected as:

Our third objective was to combine satellite-derived meteorology (radiation, precipitation and temperature) and biological drivers (vegetation phenology) to determine site specific and multi-biome *GEP* values using multiple regression models....

Figure 1: not all climate classes are explained; in case not all are present in the map – remove from figure legend; AU_How is hard to read and the dot would be better visible if a different color was used

We propose a modified version of Fig. 1 with a new flux location symbol and color scheme for the Köppen-Geiger climate classification map following Kottek et al. (2006). We similarly corrected the figure's legend to include only classes present across the continent.

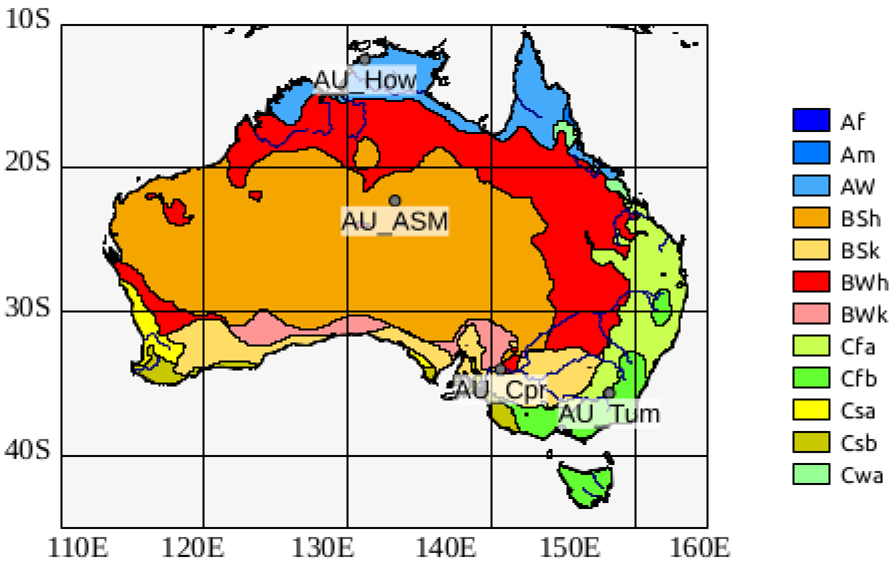

Figure 1. Location of four OzFlux eddy covariance tower sites included on this analysis: AU-How: Howard Springs (at Aw), AU-ASM: Alice Springs Mulga (at BSh and BWh boundary), AU-Cpr: Calperum-Chowilla (at Bwk), and AU-Tum: Tumbarumba (at Cfa and Cfb boundary). Köppen-Geiger climate classification as published by Kottek et al. (2006) and Rubel and Kottek (2010). Where Aw is equatorial winter dry climate, BSh is arid steppe, BWh is hot arid desert, BWk is cold arid desert, Cfb is warm temperate fully humid warm summer, Cfa is warm temperate fully humid hot summer and Cwa is warm temperate winter dry hot summer. Other climate classes are: Equatorial fully humid (Af) and monsoonal climate (Am), arid summer dry and cold desert (Bsk), and warm temperate hot summer (Csa) and warm summer (Csb) steppes.

p. 9, l. 22; u* - the star should be sub-scripted (i.e. u*) ; while -1 should be super-scripted in s-1

Corrected as:

Low turbulent missing periods were determined when friction velocity (u_* in m s^{-1}) was below a threshold value ($u_{*thresh}$) as described in Restrepo-Coupe et al. (2013). Table 1 presents site-specific $u_{*thresh}$ values and the corresponding upper and lower confidence bounds.

Similarly, we corrected p. 10 l. 5:

In order to determine the consistency of the Fourier regression method and the low friction velocity (u_*) filter on the modelled R_{eco} (directly dependent of night-time *NEE* values)

and p.10 l. 28:

We observed no statistically significant seasonal differences between calculating R_{eco} as the intercept of the light response curve (Falge et al., 2001) and *NEE* not subject to $u_{*thresh}$ correction ($R_{eco\ LRC}$), to calculating R_{eco} using the Fourier regression method (slope ~0.87 and R^2=0.94 linear regression between $R_{eco\ LRC}$ and R_{eco}).

p. 11, l. 1-18: this hinges critically on whether or not the chosen time windows (16 days in this case) includes the full range of environmental conditions, in particular PAR – clearly, if PAR values are restricted to the linear portion of the light response curve, e.g. GEPsat will be highly uncertain – I imagine this to be an issue during the rainy season

The Editor is correct to point out GEP_{sat} and other measures of photosynthetic potential depend on the selection of aggregation period (e.g. 16-days *versus* daily). Although, the fitted light response curve would be a function of seasonal levels of *PAR* -and GEP_{sat} is calculated independently of fixed radiation values (high *PAR* is not predefined), future work should address the above-mentioned seasonal uncertainty. This study relies on the assumption that the 16-day aggregation is representative of important ecological processes, in particular, leaf appearance to full expansion (Jurik, 1986; Varone and Gratani, 2009), greenup of soil biological crusts in response to precipitation events (Cleverly et al., 2016a), and changes in ecosystem water use efficiency (Shi et al., 2014). We added text to section 2.4 to address this comment, as follows:

...For analysis and presentation purposes, we averaged all existing 16-day values of EC and RS data to produce a single year, seasonal cycle. We understand measures of photosynthetic potential as to be dependent of the selection of aggregation period. However, the 16-day interval has been shown to be representative of important ecological processes, in particular, leaf appearance to full expansion (Jurik, 1986; Varone and Gratani, 2009), greenup of soil biological crusts in response to precipitation events (Cleverly et al., 2016a), and reported ecosystem-level changes in ecosystem water use efficiency (Shi et al., 2014).

Figures 5-6: axes should be scaled such that any within-plot panels do not overlap with or hide data points

We modified figures 5 and 6, as follows:

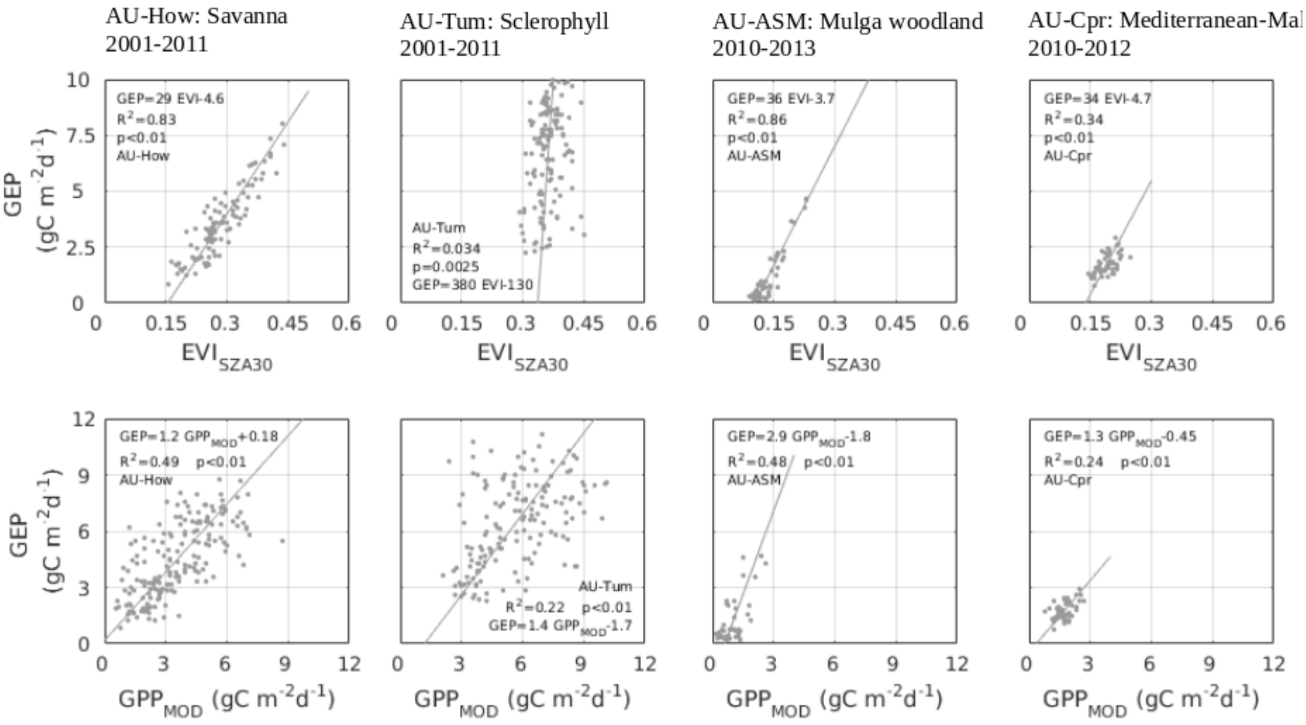

Figure 5. Top row: Linear regression between 16 and 8-day time series of measured gross ecosystem productivity (*GEP*; gC m^{-2} d^{-1}) (top row) and the MODIS fixed solar zenith angle of 30° enhanced vegetation index (EVI_{SZA30}) at (a) Howard Springs (AU-How) open woodland savanna, (b) Alice Springs Mulga (AU-ASM), (c) Tumbarumba (AU-Tum) wet sclerophyll forest eddy, and (d) Chowilla Mallee (AU-Cpr) covariance site. Lower row: Regression between *GEP* and MODIS gross primary productivity (GPP_{MOD}) (e) AU-How, (f) AU-Tum, (g) AU-ASM, and (h) AU-Cpr.

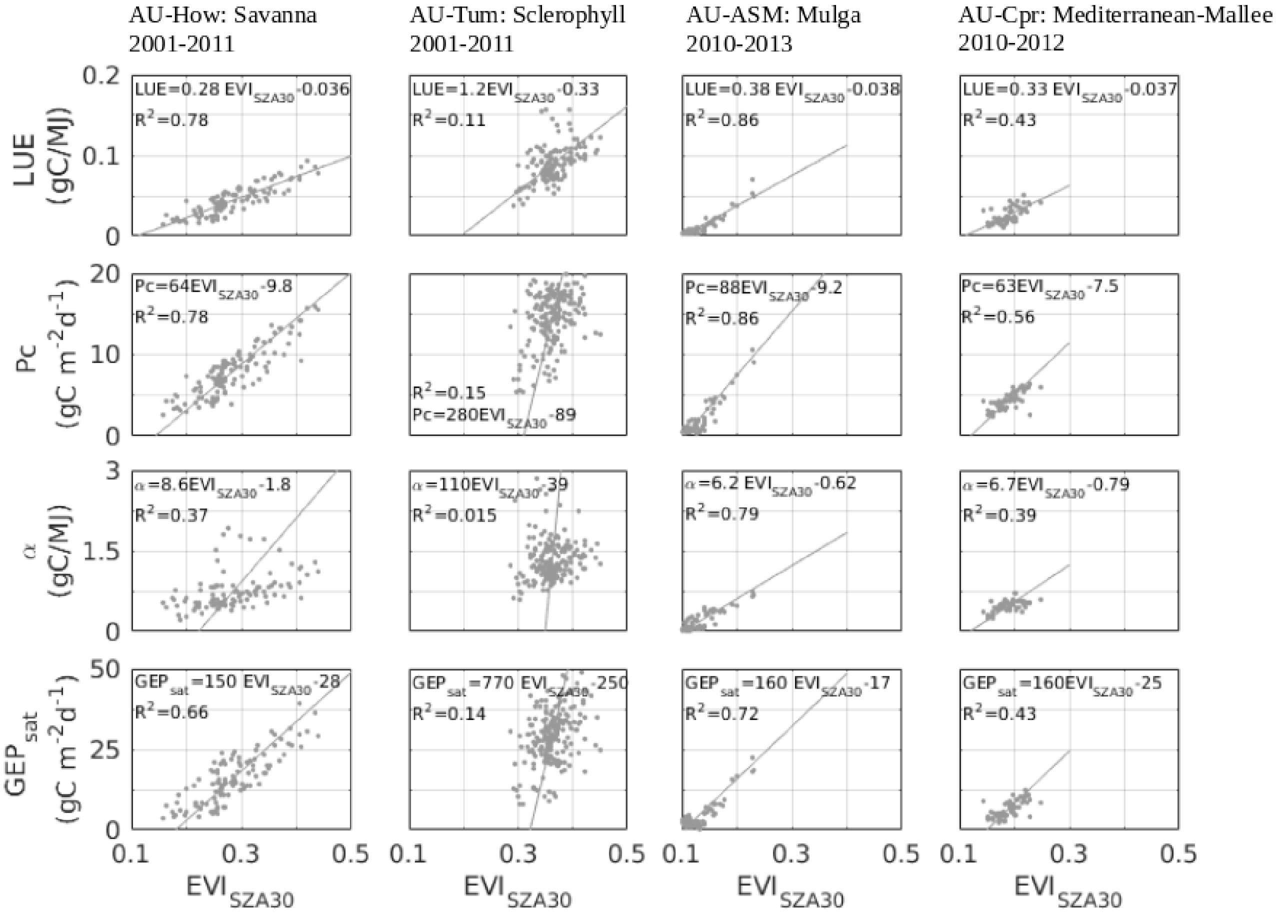

Figure 6. Relationships between 16-day mean values of (a) light use efficiency (*LUE*; gC MJ^{-1}), (b) photosynthetic capacity (*Pc*; gC m^{-2} d^{-1}), (c) ecosystem quantum yield (α; gC MJ^{-1}), and (d) *GEP* at

saturation light (GEP_{sat}; gC m^{-2} d^{-1}), and MODIS fixed solar zenith angle of 30˚ enhanced vegetation index (EVI_{SZA30}). Four key Australian ecosystem sites, from left to right (columns), AU-How savanna, AU-ASM Mulga, wet sclerophyll forest of AU-Tum and AU-Cpr Mallee

p. 22, l. 22-23: might be worth including a reference to earlier work where the same approach was followed, e.g. in Biogeosciences Wohlfahrt et al. (2010) or Balzarolo et al. (2015)

Modified as:

...Using the parameterization of the light response curve we derived different measures of vegetation photosynthetic potential (α, *LUE*, GEP_{sat} and *Pc*) (Balzarolo et al., 2015; Wohlfahrt et al., 2010)....

Balzarolo, M., Vescovo, L., Hammerle, A., Gianelle, D., Papale, D., Tomelleri, E. and Wohlfahrt, G.: On the relationship between ecosystem-scale hyperspectral reflectance and CO2 exchange in European mountain grasslands, Biogeosciences, 12(10), 3089–3108, doi:10.5194/bg-12-3089-2015, 2015.

Wohlfahrt, G., Pilloni, S., Hörtnagl, L. and Hammerle, A.: Estimating carbon dioxide fluxes from temperate mountain grasslands using broad-band vegetation indices, Biogeosciences, 7(2), 683–694, doi:10.5194/bg-7-683-2010, 2010.

section 4.1: cites only two references – I suggest to include more references to the literature, as otherwise the text appears overly descriptive

Corrected as:

... At seasonal time scales (e.g. 16-days, monthly), our analysis looks at the biotic drivers of productivity; whereas at shorter time scales (e.g. hourly, daily) photosynthetic potential can be limited or enhanced by meteorological controls, thus as linked to resource scarcity (i.e. high *VPD* or water constraints), or availability (e.g. increase radiation or access to soil water), and correspondent ecosystem responses (e.g. stomatal closure, CO_2 fertilization) will determine *GEP* (Ainsworth and Long, 2005; Doughty et al., 2014; Fatichi et al., 2014)....

... Seasonal values of GEP_{sat} at the semi-arid sites (AU-Cpr and AU-ASM) did not show a direct relationship with *VPD* or precipitation. This does not mean that there is no effect of atmospheric demand or soil moisture content on carbon fluxes at shorter time scales (hourly or daily) (Cleverly et al., 2016b). …

...The influence of other environmental factors apart from *PAR* and *VPD*, such as soil water content and T_{air}, is difficult to isolate from the derivation of vegetation descriptors as there may be a high degree of cross-correlation between different variables (e.g. *VPD versus* T_{air}). Moreover, to what degree it is feasible to untangle the relations between climate and vegetation is complex and not well understood, as the feedback processes are essential in ecosystem function (leaf flush, wood allocation, among other vegetation strategies respond to available resources), species competition, and herbivory cycles (Delpierre et al., 2015).....

...By contrast, implicit in the derivation of *LUE* were the day length and anomalous climatic conditions. This finding has important implications when using EC data for the validation of satellite derived phenology (Restrepo Coupe et al., 2015).

Ainsworth, E. A. and Long, S. P.: What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2, New Phytol., 165(2), 351–371, doi:10.1111/j.1469-8137.2004.01224.x, 2005.

Doughty, C. E., Malhi, Y., Araujo-Murakami, A., Metcalfe, D. B., Silva-Espejo, J. E., Arroyo, L., Heredia, J. P., Pardo-Toledo, E., Mendizabal, L. M., Rojas-Landivar, V. D., Vega-Martinez, M., Flores-Valencia, M., Sibler-Rivero, R., Moreno-Vare, L., Viscarra, L. J., Chuviru-Castro, T., Osinaga-Becerra, M. and Ledezma, R.: Allocation trade-offs dominate the response of tropical forest growth to seasonal and interannual drought, Ecology, 95(8), 2192–2201, doi:10.1890/13-1507.1, 2014.

Fatichi, S., Leuzinger, S. and Körner, C.: Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling, New Phytol., 201(4), 1086–1095, doi:10.1111/nph.12614, 2014.

Restrepo Coupe, N., Huete, A. R. and Davis, K.: Satellite Phenology Validation, in AusCover Good Practice Guidelines: A technical handbook supporting calibration and validation activities of remotely sensed data products, TERN, Canberra, ATC, Australia., 2015.

Associate Editor Decision: Publish subject to minor revisions (Editor review) (24 Jun 2016) by Georg Wohlfahrt

Comments to the Author:

First I would like to apologize for the delay with this manuscript. Due to lack of action by the handling guest editor I have now taken over the manuscript.

Based on the reply to the reviewer comments I invite the authors to submit a revised version of their manuscript. In addition I ask the authors to include my following comment when preparing a revised version:

p. 19223-19224: please make sure your definitions of carbon cycle terms are consistent with Wohlfahrt & Gu (2015; 10.1111/pce.12569) – actually your terminology left me pretty much confused

We thank the Associate Editor for his feedback and incorporated his suggestion on the revised version of the manuscript, as follows:

GEP and *GPP* (true photosynthesis minus photorespiration (Wohlfahrt and Gu, 2015)) have been used interchangeably in the literature. However, *GPP* in this study was distinguished from *GEP*, thus as *GEP* does not include CO_2 recycling at leaf-level (i.e. re-assimilation of dark respiration) or below the plane of the EC system (i.e. within canopy volume) (Stoy et al., 2006). Differences may be important when comparing tower-flux observations of *GEP* to the MODIS *GPP* (see next section).

We appreciate the comments and suggestions from two referees on our manuscript “MODIS vegetation products as proxies of photosynthetic potential: A look across meteorological and biologic driven ecosystem productivity”. These have greatly contributed to improved scientific rigor and clarity and have enriched the presented discussion. We have addressed all comments and proposed significant changes to the manuscript, in particular to the Introduction and Conclusion sections, details follow:

Reviewer 2.

General comments: The authors tested whether seasonality of GEP and photosynthetic potential could be captured by MODIS VIs, GPP, LAI and FPAR products across four Oz flux towers. Although this is an important topic to link satellite remote sensing data with in-situ land surface observations, I found this manuscript requires substantial improvements.

The authors should stress the novelty of this manuscript and make a compelling conclusion. The authors showed a series of figures and tables, which did not converge towards conclusion which is actually unclear. I think the conclusion is that MODIS V captured seasonality of GEP when key meteorological variables and vegetation phenology were synchronous. If this is the conclusion, this is not new as reported from a series of previous papers (e.g. Gamon et al., 1995 Ecological Applications). If this is not the conclusion, then the authors failed to deliver clear, compelling conclusion. Also I see there is no clear linkages between the title (MODIS VI as proxies of photosynthetic potential....) and conclusion.

R2C01: We propose changes to our Conclusions section (see at the end of this response) to stress the highlight the originality and emphasize the compelling nature of our research and findings of the manuscript, that include the following:

1. Our results revealed three different environmental conditions, to be viewed as a continuum, consisting of (1) primarily meteorological-driven (solar radiation, air temperature and/or precipitation) systems (e.g. sclerophyll forests), with no statistically significant relationship between *GEP* and satellite derived measures of greenness; (2) biologically-driven ecosystems, where changes in the vegetation status represented by tower based measures of photosynthetic capacity drive *GEP* (e.g. tropical savannas); and (3) locations where meteorology and vegetation phenology are synchronous (e.g. *Acacia* woodland).

2. In contrast to past and current literature --studies that link ecosystem productivity (*GEP*) and VIs at phenologically driven ecosystems (Chen et al., 2004; Guan et al., 2015; Huete et al., 2008; Maeda et

al., 2014; Rahman et al., 2005; Toomey et al., 2015), we argue that satellite derived biophysical measures and other greenness indexes are not a measure of *GEP*; but rather a proxy for ecosystem structure (e.g. leaf area index - quantity of leaves) and function (e.g. leaf level photosynthetic assimilation capacity - quality of leaves). Our results should extend to other greenness measurements from remote sensing sensors, including phenocams, satellites, and *in situ* spectrometers.

3. We propose the parameterization of the light response curve from EC fluxes as a novel tool to obtain measures of photosynthetic potential (a proxy for vegetation structure and function) as the appropriate link to satellite derived measures of greenness. We find VIs to be statistically correlated to long term measures of phenology such as *Pc* and *LUE* rather than to variables subject to the short term responses to environmental conditions (e.g. *GEP* at saturation, GEP_{sat} and quantum yield, α). This, having important implications for earth system models that rely on RS products to determine maximum *GEP* (GEP_{max} – the GEP_{sat} in our study) or quantum yield (α), as they may misrepresent vegetation seasonality and phenology.

4. We identified the main seasonal drivers of productivity over four key ecosystem types: vegetation structure and function, meteorology, or a combination of both. Moreover, we included ecosystems where the MODIS *GPP* product has been questioned for not being able to capture the absolute value at *GPP*, its annual cycle, or in getting the right answer for the right reasons (Kanniah et al., 2009; Leuning et al., 2005). We quantified how much of the *GEP* seasonality could be explained by different variables (incoming radiation, temperature precipitation, or vegetation status) and then presented seasonal profiles that showed when vegetation photosynthetic potential and climate were synchronous or out-of-phase.

5. We used satellite derived vegetation indices and meteorological variables rather than in situ measurements; therefore, our findings (e.g. regressions) can be extrapolated to regional and continental scales.

6. The Reviewer 2 in pointing out that our findings build upon previous work by Gamon et al. (1995) and others (Huete, 2012; Peng and Gitelson, 2012; Sims et al., 2006); however, there are clear differences between our approach and Gamon et al. (1995) (see Table 1 of this response for a cross-study comparison).

Table 1. Differences between Gamon et al. (1995) and Restrepo-Coupe et al. (2015)

	Gamon et al. (1995)	Restrepo-Coupe et al. (2015)
Time period	1-year	EC: 3+ years RS: 15+ years
Spatial scale	In situ measurements	250+ m
Proxy for photosynthetic potential and activity (method)	• Leaf-level photosynthetic activity (*A*): gas exchange • LAI, biomass: biometry	Parameterization of the EC light response curve
	Note that the leaf level *A* measurements presented by Gamon et al were scaled up to represent the ecosystem. Scaled *A* and *GEP* may or may not be related as other ecosystem components, different from leaves can contribute to GEP (e.g. soil biological crusts, branches), which can be significant (e.g. semi-arid ecosystems).	

	Methodologically, *A* is a time intensive measurement and requires a high sampling that includes leaves from different age cohorts, canopy levels (shaded versus full light) if been used to scale to ecosystem level.	
Vegetation indices and other photosynthetic potential drivers (method)	*NDVI* and simple ratio (*SR*) (portable spectroradiometer sampled to mimic AVHRR reflectances)	*NDVI*, *EVI*, LAI_{MOD}, and $fPAR_{MOD}$ (remote sensing -MODIS). Satellite derived meteorological variables: LST_{day}, SW_{down} and $Precip_{TRMM}$.
Measures of productivity	*NPP* (restricted to above ground primary productivity). Later scaled to represent green leaf fraction.	*GEP*: photosynthetic activity. Includes above and below ground primary productivity and CO_2 used on photorespiration (Waring and Running, 1998)
Findings	The ability of *NDVI* to predict *A* is linked to a *LAI* threshold. Where at sparse canopies, *LAI*<2, *NDVI* is highly correlated to A. In contrast, at high *LAI* ecosystems, *LAI*>2, *NDVI* was insensitive to canopy structure.	We argue the ability of VIs to represent *GEP* is restricted to those sites where phenology is synchronous to photosynthetic activity. Thus, sites where photosynthetic potential was asynchronous or aseasonal to meteorological drives, RS products were unable to explain *GEP* independently of site

		biomass or *LAI*.
	Highest correlation between *NDVI* and maximum daily photosynthetic rates.	We found the short term response of the ecosystem (e.g. restricted by high values of *VPD*) showed lower correlations (GEP_{sat} a proxy of maximum daily photosynthetic rates) compared to other measures of potential (*LUE* and *Pc*).

The role of photosynthetic potential is unclear. In Abstract, the authors stated "...through comparisons of ecosystem photosynthetic activity (GEP) and potential (e.g. ecosystem light use efficiency and quantum yield) with MODIS vegetation satellite products...";

however, the authors did not report anything related to photosynthetic potential in the abstract.

R2C02: We propose to modify the Abstract to distinguish ecosystem photosynthetic activity from measures of potential addressing the reviewer's comments (see at the end of this response).

We used the term photosynthetic potential to refer to four variables obtained from the light response curve parameterization: ecosystem light use efficiency (*LUE*), photosynthetic capacity (*Pc*), *GEP* at saturating light (GEP_{sat}), and quantum yield (α). These variables were calculated to remove the effect of day length, changes in radiation environment, cold/warm periods, among other non optimum meteorological conditions from *GEP* (*Pc* and *LUE*), or to normalize the conditions under which the measurements are made (e.g. α as indicator of vegetation response under diffuse radiation) –thus, they represent the canopy's ability to do photosynthesis independently of the meteorological conditions (see Section 2.2.3.).

In TBR site, EVI did not agree well with GEP (Figure 5). Then the authors compared EVI with photosynthetic potential in Figure 6, which again did not show correlation between EVI and photosynthetic potential in TBR site. Thus photosynthetic potential did not provide any insight to understand why EVI failed to capture seasonality of GEP in this site.

R2C03: At the evergreen wet sclerophyll forests, there were no relationships between *GEP* and satellite derived measures of greenness (e.g. *GEP* and EVI_{SZA30}, $R^2<0.01$ and $p=0.93$, Figure 5b). However, p-values showed that the regression between *Pc* and EVI_{SZA30} and $NDVI_{SZA30}$ were statistically significant and that the null hypothesis was false -the relationship is not the result of chance ($R^2= 0.16$, $p<0.01$; Figure 6 and Supplement Table 4). Low R^2 values can be explained by the small dynamic range of both seasonal measures of photosynthetic potential and EVI_{SZA30} (cf. Figure 4 and Figure 6). Moreover, we showed how at this site incoming solar radiation explained 60% and a multi-linear model driven by SW_{down} and EVI_{SZA30} explained 70% of the variability in *GEP,* indicating that this is a meteorological driven ecosystem.

Across sites we observed strong correlations among VIs and *Pc*. The positioning of each ecosystem along a continuum of MODIS-derived variables representing phenology confirms the usefulness of satellite products as representative of vegetation structure and function.

The title says “MODIS vegetation products as proxies of photosynthetic potential”; however, the abstract did not tell anything about photosynthetic potential and the conclusion included only a bit, which was marginal.

R2C04: We propose to modify the Abstract (in italics) to clearly define photosynthetic potential as parameters of the light response curve, thus, to address the reviewer's comment:

"... In this study, we re-evaluate the connection between satellite and flux tower data at four contrasting Australian ecosystems, through comparisons of ecosystem photosynthetic activity (*GEP*) and measures of potential (via parameterization of the light response curve: ecosystem light use efficiency (*LUE*), photosynthetic capacity (*Pc*), *GEP* at saturation (GEP_{sat}), and quantum yield (α)) with MODIS vegetation satellite products, including VIs, gross primary productivity (GPP_{MOD}), leaf area index (LAI_{MOD}), and fraction of photosynthetic active radiation ($fPAR_{MOD}$). We found that satellite derived greenness products constitute a measurement of ecosystem structure (e.g. leaf area index - quantity of leaves) and function (e.g. leaf level photosynthetic assimilation capacity - quality of leaves) *represented by Pc and LUE, rather than GEP*..."

Inconsistent terms should be corrected. I found photosynthetic potential is unclear and confusing.

R2C05: We propose to modify the Introduction text to address the reviewer's comment

"Our second objective was to derive using the light response curve different ground-based measures of vegetation photosynthetic potential: quantum yield (α), photosynthetic capacity (*Pc*), *GEP* at saturation light (GEP_{sat}), and ecosystem light use efficiency (*LUE*) in an attempt to separate the vegetation structure and function (phenology) from the climatic drivers of productivity. We explored the seasonality of the four measures of photosynthetic potential (α , *Pc, LUE,* GEP_{sat}) and aimed to determine if *EVI* was able to replicate absolute value and their annual cycle rather than photosynthetic activity (*GEP*), based on linear regressions....”

The authors used this term to indicate LUE and quantum yield (P2 L7-8) or LUE, quantum yield, GEPsat, and Pc (P11 L11). I think “potential” is not related to LUE; probably, it might be related to LUEmax. In P16 L6, the authors defined potential as “biophysical drivers of productivity”, which seems not related to GEPsat or Pc. Ecosystem photosynthetic activity is another confusing term. It corresponded to photosynthetic activity, productivity, or gross ecosystem productivity (GEP). I recommend using GEP consistently across the manuscript.

R2C06: *GEP* and photosynthetic activity are currently used synonymously in the literature. At times, in the text we used photosynthetic activity to differentiate the term from photosynthetic potential by indicating that one is the ability to do photosynthesis (potential) and differs from the activity (the result of radiation, H_2O, and CO_2 used by the vegetation to attain carbon uptake).

Uncertainty in photosynthetic potential should be incorporated. Fig 2 clearly shows the relationship between PAR and GEP is not straightforward. I can see all parameters (quantum yield, GEPsat, Pc, and LUE) showed large variability around the mean values. The uncertainties in each parameters might explain little correlation between EVI and photosynthetic potential in TBR site, and might help better interpret Fig 6.

R2C07: Uncertainty in estimates of photosynthetic potential and RS products were incorporated by use of Type II linear regressions that account for uncertainty in both variables. We propose to add the following text in Section 2.5 (in italics) to address the Reviewer's comments

“We fitted Type II (orthogonal) linear regressions *that account for uncertainty in both variables (satellite and EC)*. We obtained an array of very simple models of productivity and photosynthetic potential....”

Please note we present confidence intervals (CI) for all coefficients used on the regressions (Table 3) and other measures of statistical significance (e.g. AIC) to determine if the RS greenness indices represent the absolute value, the amplitude and timing of the seasonal cycle, rather than assuming non uncertainty. on the parameterization of the light response curve or the satellite product.

MODIS LST suddenly appeared in Fig 7 and 8. I understand the authors used LST which could constrain GEP reported by Sims et al.; however, it is out of context. See the title again: “MODIS vegetation products as proxies of photosynthetic potential.”

R2C08: We understand the concerns of the reviewer, thus as incorporating LST_{day} versus Pc may be distract the reader from one of the key objectives of the study -to .demonstrate RS greening indices to be measurements of photosynthetic potential. We propose to modify Fig. 8 by removing the corresponding panel LST_{day} versus *GEP.*

Specific comments:

P2 L2: measured -> estimated

R2C09: Done

P2 L10-12: I do not think the authors provided results on this argument. I expected comparison between in situ LAI with satellite greenness index, and between in situ Vcmax or Amax with satellite greenness index.

R2C10: *LAI* measurements at a temporal resolution longer than a year (i.e., seasonal) are difficult to obtain due to missing periods and restricted access to some of our remote sites. We wish to emphasize that is not merely the “quantity” of leaves, but rather, jointly “quality” (e.g. leaf-level photosynthetic capacity) and “quantity” (e.g. *LAI*) that drives the potential of the ecosystem to do photosynthesis.

We understand the parameterization of the net CO_2 assimilation rate (*A*) *versus* leaf internal CO_2 concentrations (Ci) represents the mechanistic basis behind many plant physiology models, and their parameterization (e.g. via maximum Rubisco activity or Vc_{max}) is key in determining the effects of elevated atmospheric CO_2 concentration on growth (Harley et al., 1992; Medlyn et al., 1999). However, scaling from leaf to ecosystem introduces additional uncertainty and assumes sufficient sampling from leaves from different species, age cohorts, and canopy levels (shaded versus full light). Moreover, at woodland and savannas C3/C4/base soil percentage cover changes over the year increasing the difficulties of scaling up leaf-base measures. Some of the site locations are remote and difficult to access, thus leaf-measurements may be only available for a few periods of the year. Our study takes advantage of available eddy covariance data, as it offers ***continuous ecosystem level*** data.

P3 L25: x -> multiplication symbol

R2C11: We used *x* as multiplication symbol throughout the document

P11 L25: GEP to PAR -> GEP to APAR?

R2C12: *LUE* = *GEP/PAR*

Please see response to Reviewer's comments R1C07 for an extended discussion.

P13 L16: Eq 3 was not related to filtering.

R2C13: Manuscript needs to be corrected, should have stated Eq 8.

P14 L6-16: I am curious why the authors used coarse resolution satellite estimates of SW and precipitation instead of tower based observations.

R2C14: Our intent is to construct relationships that can be scaled to regional and continental scale; therefore, we used satellite derived meteorological variables: SW_{down}, precipitation and LST_{day}. We propose the inclusion of text to the Section 2.3.2. (in italics) to address the Reviewer's concern:

"...No quality control was performed on the rain ($Precip_{TRMM}$) or short wave (SW_{CERES}) satellite derived time series. *We used satellite derived meteorological variables instead of in situ measurements as the independent variable in GEP models (see Section 2.5), thus, our findings (e.g. regressions) can be extrapolated to regional and continental scales.*"

P19 L27: remove a comma

R2C15: Done.

P28 L20-22: This conclusion is not true in TBR site which showed EVI did not correlate with LUE and Pc.

R2C16: Please refer to R2C03 of this response.

P43 Figure 2 caption: define Pc. Also, remove the equation of Pc in the figure which disrupts readership. The colors of dots look different. If this is true, then define; otherwise, use one colour.

R2C17: Please see uploaded figure

P44 L5: There was no “grey dashed line” in the figure

R2C18: Please see uploaded figure

Reviewer 1.

The authors investigate the potential of MODIS vegetation indices (VIs) to predict gross primary production in semi-arid ecosystems of Australia. This is an important topic since GPP of such ecosystem types are indeed difficult to capture by VIs and this deserves an in depth analysis. Overall, the paper contains several interesting aspects that are worth being published. But I agree with referee #2 that the manuscript requires substantial sharpening and streamlining.

The first objective was 'to gain understanding of ecosystem behaviour' but it is not clear what is meant by that. In that regard I had expected more insights on the role of **water limitation** (VPD and soil moisture) on GPP and to what extent VIs can capture that or not. Water limitation is in my view perhaps the most critical point on why VIs may not 'see' the productivity response properly.

R1C01: We appreciate the reviewer's comments as they introduce the issue of water availability (soil moisture and *VPD*) to the discussion. We observed the greater discrepancies between VIs and *GEP* at Tumbarumba (AU_Tum), a site that does not show signs of water limitation (Figure 1). In this sclerophyll forest, only 3% of the 10-year time series corresponds to *VPD* values greater than 3 kPa, a threshold identified for a 50% reduction in *LUE* (Ogutu and Dash, 2013). Mean seasonal evapotranspiration (*ET)* at AU_Tum was 2.4 mm/day (standard deviation of 1.23 mm/day), which is substantially less than the 2001-2012 average of 6.4 mm/day $Precip_{TRMM}$ ($Precip_{EC}$ = 6.4 mm/day)

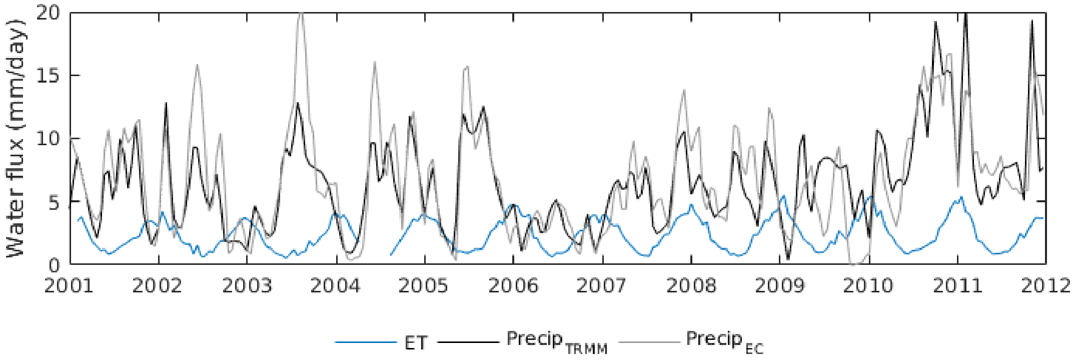

Figure 1. Water fluxes at Tumbarumba (AU_Tum) sclerophyll forest: Evapotranspiration (*ET*, blue lines), satellite derived ($Precip_{TRMM}$, black lines) and flux-tower ($Precip_{EC}$, grey lines) precipitation (mm/day).

We acknowledge the difficulties in separating the meteorological from the biophysical contributions (photosynthetic potential) to *GEP* based on radiation and *VPD* (e.g. derivation of Pc), particularly in woodlands as these ecosystems can be highly controlled by access to soil moisture (Cleverly et al., 2013). For example, at Alice Springs Mulga site (AU-ASM), Eamus et al. (2013) reported an increase in transpiration at moderate values of *VPD*, whereas the rate of photosynthesis remained unaffected, signalling the complexity of the controls on carbon exchange. However, we argue that VIs represent the “ecosystem potential” seasonality that can later be translated to photosynthetic activity if driven by water, temperature, light, and CO_2 availability. At seasonal time scales (e.g. 16-days, monthly), our analysis looks at the biotic drivers of productivity (parameterization of the light response curve); by contrast, at shorter time scales (e.g. hourly, daily) ecosystem photosynthetic potential should be scaled to reflect resource limitation (i.e. access to soil moisture), availability (e.g. incoming radiation) and the correspondent ecosystem responses (e.g. stomatal closure, CO_2 fertilization) that determine *GEP*.

We propose to add the following text (in yellow) at section *4.1. Derivation of measures of photosynthetic potential at tropical savannas, sclerophyll forests and semi-arid ecosystems*, as follows :

“In this study we were able to separate the biological (vegetation phenological signal) from the climatic drivers of productivity using eddy-covariance carbon exchange data. *Using the parameterization of the* *light response curve* we derived different measures of vegetation photosynthetic potential (α, *LUE*, GEP_{sat} and *Pc*). *At seasonal time scales (e.g. 16-days, monthly), our analysis looks at the biotic drivers of productivity, whereas at shorter time scales (e.g. hourly, daily), photosynthetic potential can be limited or enhanced by meteorological controls, thus GEP was linked to resource limitation (i.e. high VPD), availability (e.g. access to soil water) and corresponding ecosystem responses (e.g. stomatal closure, photoinhibition, and CO_2 fertilization).”*

Additional text is also proposed to be inserted into Section 4.2. Seasonality and comparisons between satellite products and flux tower based measurements of carbon flux: photosynthetic activity (productivity) and potential (phenology):

“Similar to Mediterranean ecosystems (AU-Cpr), in wet sclerophyll forests (AU-Tum) *without signs of water limitation*, the VIs were unable to replicate seasonality in *GEP*....”

Using precipitation from a coarse scale product does not seem appropriate to capture water availability. I’m wondering why not observed soil moisture or simple ecohydrological metrics like cumulative water deficit (from measured precip and ET) has been used here.

R1C02: It is our intent to obtain continental-wide relationships independent from biome classification or EC drivers (e.g. *ET*). Thus, as we want to offer an understanding and relationships that are able to capture spatial (e.g. ecotone) and temporal changes in land cover type (e.g. drought impact). The reviewer is correct about other measures of water availability (e.g. soil moisture) being more robust as the timing and intensity of precipitation will have an important effect on whether water is available to plants. However, issues related to the identification of threshold values (e.g. not all soil moisture increases translate in a phenological response at AU_ASM (Cleverly et al., 2016b)), time scales and other issues beyond the scope of this study may have an equal effect upon whether photosynthetic potential translates into activity (*GEP*). We believe that robust *GEP* models will incorporate: 1) satellite derived VIs as proxies for photosynthetic potential, 2) meteorological drivers, and 3) a mechanistic response from the vegetation to the short term variations in weather and climate, but we found the present MODIS *GPP* and other models to perform poorly across Australia. Future work should aim to look into different satellite products as, for example the Gravity Recovery and Climate Experiment GRACE-total water storage (*TWS*), and the Soil Moisture Active Passive, SMAP-soil moisture values, among others as *GEP* drivers and to refine the derivation of measures of photosynthetic potential.

It has been argued that during water stressed conditions the yellowing of the herbaceous understory may act as a ‘drought indicator’ which might drive the VI in the ‘right’ direction (Sims et al 2014, GCB; Jung et al 2008, GCB). If so, the capacity of VIs to reflect GPP response would depend on the presence and density of herbaceous vegetation and the openness of the forest canopy. The colour of the leaves is influencing the VIs and this could also indicate changes of LUE.

R1C03: We agree with the reviewer that the presence and density of herbaceous vegetation and the openness of the forest canopy can drive the VI signal at savannas and open woodlands at certain times of the year (e.g. AU_How and AU_ASM, see Chen et al. (2003); Cleverly et al. (2016b, Submitted); and Hutley et al. (2000). Moreover, we agree that VIs constitute a signal dominated by chlorophyll (red reflectance) and cellulose content (NIR), thus will indicate changes in *LUE*. However, we argue that satellite derived biophysical measures and other greenness indexes are not a measure of *GEP*. Instead, VIs and other biophysical products are proxies for ecosystem structure (e.g. leaf area index - quantity of leaves) and for function (e.g. leaf level photosynthetic assimilation capacity - quality of leaves). Our results should extend to other remote sensing sources, including phenocams and in situ spectroradiometers.

The authors mention repeatedly that ‘understanding’ is more important than ‘well-fitting models’ but the authors present a systematic analysis on which regression models work best (which I like!). Investigating the coefficients of these regression models shows often unexpected signs, e.g. GPP decreasing with VI, or the presence of intercept terms, which conceptually makes little sense. Discussing and explaining these things may be a chance to make the point why ‘understanding’ is important.

R1C04: We propose to incorporate the reviewer's suggestion into to section 4.3. Considerations for the selection of RS data to be used on *GEP* models and phenology validation studies, here in italics:

….”The fact that a brighter soil background results in lower *NDVI* values than with a dark soil background for the same quantity of partial vegetation cover (Huete, 1988; Huete and Tucker, 1991) may have a positive effect in the all-site Pc *versus* $NDVI_{SZA30}$ regressions (increase R^2). *Thus as darkened soils following precipitation generally result in higher NDVI values for incomplete canopies (Gao et al., 2000) and may similarly suggest higher vegetation or soil biological crust activity. On the other hand, soil brightness and moisture may have a negative effect on the confidence interval of the x-*

intercept for the proposed relationships (e.g. Pc versus $NDVI_{SZA30}$, for $NDVI_{SZA30}$~0). Moreover, at certain times the AU-ASM and AU-Cpr sites were at the low end of the vegetation activity range, and the observed RS signal may have been dominated by soil water content rather than by photosynthetic potential."

The second objective was to disentangle the seasonality of 'vegetation structure and function from climatic drivers of productivity'. The authors derive 4 metrics here (alpha, Pc, LUE, GEP_sat). I agree with referee #2 regarding the (non-optimal) nomenclature of 'photosynthetic potential' vs 'activity'. I also see a conceptual problem here because all 4 metrics are actually confounded by changes in light harvesting (reflected by VIs) such that vegetation structure and functioning cannot be disentangled from eco-physiological effects.

R1C05: See R2C02

In my opinion the authors should have used PAR*VI in the light response cure fitting to account for that. I'm also wondering about the usefulness of Pc – first it seems redundant given alpha and GEP_sat, and second it requires somewhat arbitrary thresholds and site specific knowledge to compute it.

R1C06: While other more refined biophysical measures of photosynthetic potential would be ideal (e.g. chlorophyll fraction of absorbed *PAR*), the parameterization of the light response curve offers an insight of seasonal ecosystem form, function and phenology (Hutyra et al., 2007; Restrepo-Coupe et al., 2013; Wu et al., 2016). *Pc* was calculated to remove the effect of day length, changes in radiation environment, cold/warm periods, among other non optimal meteorological conditions from *GEP* –thus, *Pc* represents the canopy's ability to do photosynthesis. We assumed optimal radiation to be equivalent to the site annual mean daytime *PAR* ± 100 μmol m^{-2} s^{-1} and *VPD* ± 1 standard deviation. By contrast, α and GEP_{sat}, would be characteristic of the vegetation response under conditions dominated radiation (diffuse and direct) and *VPD*, respectively (see Section 2.2.3).

I'm wondering why the
authors did not employ the 'classical' approach (GPP=APAR*LUE) here to disentangle 'biophysical' (APAR=VI*PAR) from 'ecophysiological' (LUE) components, which seem more straightforward and would do the job (?).
For example, given GPP=VI*RAD*LUE
it derives that GPP scales with VI if a) the product of RAD and LUE is nearly constant (compared to the variability of VI), or b) product of RAD and LUE is in phase with VI. I guess I'm lacking a more clear presentation and justification of a clear framework and motivation of the analysis strategy.

R1C07: For context:

$GEP = APAR \times \varepsilon$ as in Yuan et al., (2007) (Equation 1)

or

$NPP = APAR \times \varepsilon$ as in Gamon et al. (1995) (Equation 2) where ε *is the e*fficiency with which absorbed radiation is converted to fixed carbon (also refereed as *LUE* by some authors), *NPP* is net primary productivity, where *NPP* = *GEP* - autotrophic respiration, and *APAR* is the absorbed fraction of *PAR*.

$APAR = PAR \times fPAR.$

where *fPAR* is defined as the fraction of *PAR* absorbed by the canopy (leaves and woody tissue) and has been correlated to *NDVI* (Gamon et al., 2013; Myneni and Williams, 1994).

We consider *fPAR* and ε to be similarly representative of the canopy structure and function; therefore, separating ε and *fPAR* would be problematic as both variables would be considered similar measures of photosynthetic potential. In general, models that use Eq1 assume ε to be constant and biome-dependent (Yuan et al., 2007). Moreover, the determination of ε continues to be a major challenge in ecological research (Field et al., 1998; Running et al., 2004). Our analysis offers a ground-based measure of vegetation photosynthetic potential and constitutes an attempt to derive all-site regressions between the satellite products and ecosystem form and function independently of biome type. Thus, so that ecotones and sudden land use changes such as flooding or fire may not be misrepresented when extrapolated to regional and continental scales.

Minor points: -

Why were coarse scale products of radiation d precip being used?

R1C08: We used satellite derived vegetation indices and meteorological variables rather than in situ measurements; therefore, our findings (e.g. regressions) can be extrapolated to regional and continental scales.

We propose to add text to section 2.3.2. Satellite measures of precipitation (TRMM) and incoming solar radiation (CERES), to address the Reviewer's concerns:

…No quality control was performed on the rain ($Precip_{TRMM}$) or short wave (SW_{CERES}) satellite derived time series. We used satellite derived meteorological variables rather than in situ measurements as the independent variable in *GEP* models (see Section 2.5), thus, our findings (e.g. regressions) can be extrapolated to regional and continental scales.

Why monthly if those are available daily? -

R1C09: We are interested on the seasonal response of the ecosystem (e.g. monthly or 16-day), away from short term responses (e.g. hourly or daily). The 16-day window is a time scale representative of important ecological processes; in particular, leaf appearance to full expansion (Jurik, 1986; Restrepo-Coupe et al., 2013).

Page 19234, line 6: R2=0.16 does not suggest a 'strong' relationship to me -

R1C10: We observed a clear improvement in the ability of the model to predict *Pc* and *LUE* rather than *GEP*. At the evergreen wet sclerophyll forest of AU_Tum, there were no relationships between *GEP* and satellite derived measures of greenness (e.g. *GEP* and EVI_{SZA30} or $NDVI_{SZA30}$ $R^2<0.01$ and p=0.93, Figure 5b). In contrast the regression between *Pc* and VIs were statistically significant, meaning the regression was significantly higher than zero (R^2= 0.16, p<0.01; Figure 6 and Supplement Table 4), low R^2 values can be explained by the small dynamic range of both seasonal measures of photosynthetic potential and VIs (cf. Figure 4 and Figure 6). Thus, we would change strongly to significant on the text as we showed how at this site incoming solar radiation explained 60% and a multi-linear model driven by SW_{down} and EVI_{SZA30} was able to explain 70% of *GEP* indicating a meteorological driven ecosystem.

At Section 3.3. Relationship between EVI_{SZA30} and measures of photosynthetic potential (α, *LUE*, GEP_{sat}, and *Pc*):

"At the sclerophyll forest site (AU-Tum) the EVI_{SZA30} was able to predict vegetation phenology rather than productivity. For example we observed that *Pc* (but not α) was significantly related..."

Page 19240 line 23: I'm not sure but I thought a brighter soil (or snow) increases ndvi (?). In any case, this is an interesting section of **discussion** which might be expanded ('understanding' why things work or not)

R1C10: We quote Huete (1988) who found "Soil brightness influences have been noted in numerous studies where, for a given amount of vegetation, darker soil substrates resulted in higher vegetation index values when the ratio vegetation index (RVI= NIR/red) or the normalized difference vegetation index[NDVI--(NIR- red)/(NIR+ red)= (RVI-1)/(RVI+I)] were used as vegetation measures (Colwell, 1974; Elvidge and Lyon, 1985; Huete et al., 1985)".

We added text to the discussion to address the Reviewer’s suggestion see R1C04

Please note we were requested by Fluxnet and OzFlux to change the site abbreviations.

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Obs.

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Abstract

A direct relationship between gross ecosystem productivity (*GEP*) estimated by the eddy covariance (EC) method and Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation indices (VIs) has been observed in many temperate and tropical ecosystems. However, in Australian evergreen forests, and particularly sclerophyll and temperate woodlands, MODIS VIs do not capture seasonality of *GEP*. In this study, we re-evaluate the connection between satellite and flux tower data at four contrasting Australian ecosystems, through comparisons of *GEP* and four measures of photosynthetic potential, derived via parameterization of the light response curve: ecosystem light use efficiency (*LUE*), photosynthetic capacity (*Pc*), *GEP* at saturation (GEP_{sat}), and quantum yield (α), with MODIS vegetation satellite products, including VIs, gross primary productivity (GPP_{MOD}), leaf area index (LAI_{MOD}), and fraction of photosynthetic active radiation ($fPAR_{MOD}$). We found that satellite derived biophysical products constitute a measurement of ecosystem structure (e.g. leaf area index - quantity of leaves) and function (e.g. leaf level photosynthetic assimilation capacity - quality of leaves), rather than *GEP*. Our results show that in primarily meteorological-driven (e.g. photosynthetic active radiation, air temperature and/or precipitation) and relatively aseasonal ecosystems (e.g. evergreen wet sclerophyll forests), there were no statistically significant relationships between *GEP* and satellite derived measures of greenness. In contrast, for phenology-driven ecosystems (e.g. tropical savannas), changes in the vegetation status drove *GEP*, and tower-based measurements of photosynthetic activity were best represented by VIs. We observed the highest correlations between MODIS products and *GEP* in locations where key meteorological variables and vegetation phenology were synchronous (e.g. semi-arid *Acacia* woodlands) and low correlation at locations where they were asynchronous (e.g. Mediterranean ecosystems). Although, we found a statistical significant relationship between the seasonal measures of photosynthetic potential (*Pc* and *LUE*) and VIs, where each ecosystem aligns

along a continuum, we emphasize here that knowledge of the conditions in which flux tower measurements and VIs or other remote sensing products converge greatly advances our understanding of the mechanisms driving the carbon cycle (phenology and climate drivers) and provides an ecological basis for interpretation of satellite derived measures of greenness.

5. Conclusions

Satellite vegetation products have been widely used to scale carbon fluxes from eddy covariance (EC) towers to regions and continents. However, at some key Australian ecosystems MODIS GPP and VIs do not track seasonality of gross ecosystem productivity (*GEP*). In particular, we found $\mathrm{EVI}_{\mathrm{SZA30}}$ was unable to represent *GEP* at the temperate evergreen sclerophyll forest of Tumbarumba (AU-Tum) and at the Mediterranean ecosystem (Mallee) of Calperum-Chowilla (AU-Cpr). This result extends across satellite products overall: MODIS GPP_{MOD}, LAI_{MOD}, $fPAR_{MOD}$, and other VIs.

We aimed for a greater understanding of the mechanistic controls on seasonal *GEP* and proposed the parameterization of the light response curve from EC fluxes, as a novel tool to obtain ground-based seasonal estimates of ecosystem photosynthetic potential (light use efficiency (*LUE*), photosynthetic capacity (*Pc*), *GEP* at saturation (GEP_{sat}), and quantum yield (α)). Photosynthetic potential refers to the presence of photosynthetic infrastructure in the form of ecosystem structure (e.g. leaf area index-quantity of leaves) and function (e.g. leaf level photosynthetic assimilation capacity - quality of leaves) independent of the meteorological and environmental conditions that drive *GEP*. Based on basic linear regressions, we demonstrated that MODIS derived biophysical products (e.g. VIs) were a proxy for ecosystem photosynthetic potential rather than *GEP*. We reported statistically significant regressions between VIs (e.g. $NDVI_{SZA30}$ and EVI_{SZA30}) to long term measures of phenology (e.g. *LUE* and *Pc*), in contrast to ecosystem descriptors subject to short term responses to environmental conditions (e.g.

GEP_{sat} and α). Our results should extend to other methods and measures of greenness, including VIs and chromatic indices from phenocams and in situ spectrometers.

We found that the linear regressions between MODIS biophysical products and photosynthetic potential converged on a single function across very diverse biome types, which implies that these relationships may persist over very large areas, thus improving our ability to extrapolate in situ phenology and seasonality to continental scales, across longer temporal scales and to identify rapid changes due to extreme events or spatial variations at ecotones. We further found that saturation of $fPAR_{MOD}$ and $NDVI_{SZA30}$, restricted their usefulness, except in comparatively low biomass ecosystems (savannas and arid and semi-arid savannas and woodlands).

We quantified how much of *GEP* seasonality could be explained by different variables: radiation (SW_{down}), temperature (T_{air}), precipitation (*Precip*), or phenology (*VIs* as proxy). Our analysis showed the relationship between RS products and *GEP* was only clear when productivity was driven by either: (1) ecosystem phenology and climate, synchronously driving *GEP*, as was observed at Alice Springs Mulga woodland (AU-ASM), and similar to many temperate deciduous locations, or (2) solely by the vegetation photosynthetic potential, as observed at the tropical savanna site of Howard Springs (AU-How). At AU-How, radiation and temperature were constant across the year, although ecosystem photosynthetic activity (*GEP*) and potential (e.g. *Pc* and *LUE*) fluctuated with the highly seasonal understory. However, RS products do not follow *GEP* when: (3) phenology is asynchronous with key meteorological drivers such that *GEP* is driven by one or the other at different times of the year, as we observed at AU-Cpr; or when (4) *GEP* is driven by meteorology (SW_{down}, T_{air}, soil water availability, *VPD*, or different combinations) and photosynthetic potential is aseasonal, as observed at AU-Tum. At AU-Tum, changes in productivity were driven by SW_{down},, while the ecosystem biophysical properties remained relatively constant across the year, represented by the small amplitude of the annual cycles in *Pc* and *LUE* (true evergreen forest). An understanding of why satellite versus flux tower estimates of *GEP* relationships hold, or do not hold, greatly contribute to our comprehension of carbon cycle mechanisms and scaling factors at play (e.g. climate and phenology, among others).