BG Reviewer Comments:
RC1: 'Comment on bg-2021-95', Anonymous Referee #1, 04 May 2021
Summary of the research and my overall impression

Merrick and coauthors present a novel dataset of remotely sensed vegetation indices (VIs) (NDVI, EVI, NIRv, NIRvrad, FCVI) from an UAS in a tropical forest canopy in Panama. They explore both spatial and temporal variability between indices and highlight potential uses for these indices at those varying scales. Specifically, the authors explore temporal correlations between GPP and VIs over the course of a day, diurnal changes in the spatial variation between Vis, and dominant spatial scales for variability in VI signals.

The paper is generally well written and structured and provides exciting insights on how VIs relate to each other. Both the dataset and the comparison are novel and within the scope of BG. Additionally, such direct comparisons between VIs are highly valuable because they provide insight in a field saturated with different VIs as to which VIs are most applicable for certain questions and specific strengths and limitations of each. The data collection approach is largely appropriate for the study, however, the temporal resolution of measurements is a major limitation. Additionally, the authors make claims about their findings in relation to SIF measurements that are not sufficiently substantiated. These major concerns are outlined with more specifics below.

Overall, this an interesting study that will be of interest to the scientific community but needs some revisions to clarify what their findings are vs. what their findings imply. Therefore, I recommend this paper be accepted with major revisions.

Major Concerns

- The methods section is quite dense and difficult to follow. This makes it challenging for the reader to connect measurement approach to the presented results. I recommend the authors present some sort of conceptual figure showing their measurement approach and processing. I think this will be highly beneficial, particularly for a study that explores spatial variability.

    Thank you for this suggestion. We have included a methods and materials summary diagram in Section 2 as a new Figure 1 (Lines 512-521).

- Only one day of GPP data is available. This has led to two specific issues:
    - I am concerned about the validity of a single day's worth of GPP data. I feel as though the statistics used to partition GPP from NEE may be insufficient with only one day available. It's worth some discussion about the limitations of this approach at a minimum. I believe Matteo uses more data to estimate GPP but we only present one day. Ask him to explain and fill in this response?
        - Thank you for pointing out the ambiguity in our description of the GPP from eddy covariance. The GPP estimates were derived from eddy covariance system data continuing several months, from which we extracted the one day of data. Unfortunately, due to a power issue,

these data were not available for the first day corresponding with the hyperspectral and lidar data collection.

- In section 3.1, the authors explore the diurnal trend in VI, PAR, and GPP data. They use this trend to draw conclusions over the utility of NIRvrad as a proxy for GPP. However, I do not believe one day of data is sufficient to draw such strong conclusions. Additionally, there is insufficient discussion over how potential physical (illumination, viewing direction, etc.) or environmental effects (drought, seasonality, etc.) may impact these conclusions and the limitations posed by one day of data. Finally, Figure 1 appears to show a higher correlation between GPP and PAR than between GPP and NIRvrad – therefore significantly undercutting the authors main claim in this section – that NIRvrad is an appropriate proxy for GPP over short temporal scales. To me, this section would be better off as a discussion of how NIRvrad in fact does **not** sufficiently capture diurnal variability in GPP – and moreso reflects changes in PAR. I also recommend the authors provide a bit of additional commentary on why the other VIs show low correlations with GPP data.
  - Thank you for the suggestion for added clarity and purpose. We address the limitations of using one day of data throughout the manuscript, specifically in lines 488; 490-492, 534-538, 704-706, 735-737. Throughout the manuscript we have made changes to carefully state that there is greater potential for NIRvrad as a proxy for GPP compared to the reflectance-based vegetation indicators (indices). The reflectance-based indicators, NDVI, EVI, NIRv, and FCVI, have been shown to trend seasonally with GPP in most biomes, but by virtue of calculating reflectances, these omit short timescale changes in incoming, scattered, and reflected radiation. NIRvrad, in contrast to reflectance-based indicators, includes the incoming, scattered, and reflected radiation in the NIR region. For this reason, recent studies (e.g. Wu et al 2020) and our study are pointing to the potential of NIRvrad to trend with GPP on short timescales through a joint relationship between NIRvrad, PAR and GPP. We have added more text in the introduction, results, discussion and conclusion, to address of this for clarity, lines 192-195, 506-509, 532-540, 866-869, and 954-955.

- The authors repeatedly draw the conclusion that presented VI data is suitable for separating out the physiological from the structural component of the SIF signal when SIF measurements are available. However, the authors are not presenting SIF data and therefore not substantiating this claim with sufficient results or appropriate citations. Specific comments are included in specific examples. I feel that much of the SIF discussion in fact takes away from the authors main conclusions and novelty of their other results as it focuses the discussion on what they aren't doing (normalizing SIF with VI data). In particular, the majority of the introduction focuses on SIF. I recommend the authors cut down on this discussion significantly and make it more clear what conclusions they are drawing from their results vs. potential directions for future work.
  - The authors appreciate these suggestions regarding the overemphasis on SIF in the discussion and introduction. Based on this thoughtful review, we

have modified the manuscript extensively to focus the introduction on the quantities measured in the study and minimize the text and references to SIF and how the quantities may relate to SIF. Specifically, we removed almost all of Lines 52-101 from the original submission. We maintained mentioning SIF in the Introduction only as the studies presented compared NIRv, FCVI, or NIRvrad specifically to GPP and SIF (Lines 193-201), and in the Results and Discussion (Lines 729-731) and Conclusion (Lines 865-869 to make comparisons between measurement techniques for reflectance-based indices and SIF as well as emphasizing how this study might be relevant to SIF, which is an emerging, important potential measurement of GPP.

Specifics:

- Lines 16-18: The statement ‘presented here for the first time’ is a bit misleading since you are not presenting these VI’s for the first time, you’re presenting them at this specific field site for the first time. Additionally, this opening does not make it clear the scientific question or problem you are trying to address or appropriate background information.
    - Thank you for assisting with clearer wording for this part of the abstract. We have removed the phrase “presented here for the first time” and modified the text (lines 16-23, 593-596) to clarify the purpose of the study. We see that the previous phrasing suggested the vegetation indicators were presented for the first time, when we only intended to point out these indicators specifically from UAV data are novel.
- Line 38: Unoccupied might be a more appropriate term, as presumably the UAS was piloted (just not with someone on board).
    - We have updated to use the term ‘unoccupied’, as it is more appropriate (Lines 24 and 59).
- Line 57: ‘SIF is mechanistically linked to photosynthesis of plants, and thereby, has also been shown to be more sensitive to changes in forest canopy function and structure than RIs’ – this deserves a citation. I also don’t think you can say it’s more sensitive to changes in forest canopy structure (although function yes). See the following for comparisons between SIF and VI’s (among others):
    - Cheng, R., Magney, T. S., Dutta, D., Bowling, D. R., Logan, B. A., Burns, S. P., Blanken, P. D., Grossmann, K., Lopez, S., Richardson, A. D., Stutz, J., & Frankenberg, C. (2020). Decomposing reflectance spectra to track gross primary production in a subalpine evergreen forest. Biogeosciences, 17(18), 4523–4544. https://doi.org/10.5194/bg-17-4523-2020
    - Magney, T. S., Bowling, D. R., Logan, B. A., Grossmann, K., Stutz, J., Blanken, P. D., Burns, S. P., Cheng, R., Garcia, M. A., KÓ§hler, P., Lopez, S., Parazoo, N. C., Raczka, B., Schimel, D., & Frankenberg, C. (2019). Mechanistic evidence for tracking the seasonality of photosynthesis with solar-induced fluorescence. Proceedings of the National Academy of Sciences of the United States of America, 116(24), 11640–11645. https://doi.org/10.1073/pnas.1900278116

- Pierrat, Z., Nehemy, M. F., Roy, A., Magney, T., Parazoo, C., Laroque, C., Pappas, C., Sonnentag, O., Bowling, D. R., Seibt, U., Ramirez, A., Helgason, W., Barr, A., & Stutz, J. (2021). Tower-based remote sensing reveals mechanisms behind a two-phased spring transition in a mixed-species boreal forest. Journal of Geophysical Research: Biogeosciences. https://doi.org/10.1029/2020JG006191.
    - Thank you for this comment. Based on this and the earlier suggestions, this portion of the manuscript was removed and portions of the manuscript referring to SIF significantly more focused on how the vegetation indicators measured related specifically to SIF. These references, however are valuable for our future work and are greatly appreciated.

- Line 87-89: It's worth mentioning which ecosystem types because this is not true across all ecosystems/some types show much better performance than others. The citations you have all have ecosystem type information.
    - We have updated this text to include the ecosystem or coverage of data, i.e., global, from the literature. This portion now appears in lines 82-84, but portions of the paragraph after these lines has also been updated to include more specifics (Line 85, Lines 88-92, Lines 94-98),
- Lines 99-101: Again it's worth mentioning ecosystem type here (ie: specifically tropical in your case) – this doesn't necessarily apply for all ecosystems/we don't have enough studies testing this across varied vegetation cover.
    - Thank you for pointing out this omission. We have now included text to clarify the data used in previous studies, which helps us highlight the tropical forest on which we focused (lines 94-98).
- Lines 111-113: This deserves a citation (or several).
    - Thank you for pointing out this ambiguous statement. We have removed references to using the emerging indices to potentially separate the SIF signal into physiological and physical components, as we did not test this. As a part of this process, this particular phrase was removed.
- Line 124: The introduction deserves some final statement about the broader aims of this work. What ultimate goal this information provides.
    - Thank you for this suggestion. We added a sentence at the beginning of the last paragraph of the introduction (Lines 99-104) to state the broader aims.
- Line 146: there's a period . typo after 12 ms.
    - Thank you, this error has been corrected (Line 129).
- Line 160: As mentioned above there should be additional discussion on the limitations of only one day of data.
    - Thank you for reminder here. We have addressed this in lines 488; 490-492, 534-538, 704-706, 735-737.
- Line 173: I believe the original citation for NDVI is:

- Tucker, C. J. (1979). Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, *8*(2), 127–150. https://doi.org/10.1016/0034-4257(79)90013-0.
    - Thank you for pointing out this oversight, we have inserted this citation (Line 158).

- Figure 1: There appears to be some sort of accidental grid to the side of panel d?

Thank you for catching our oversight. The figure has been corrected (Now Fig. 2, Line 218).

- Lines 236-238: 'Our results demonstrate that UAS-based data are suitable for normalizing SIF at high spatial resolution in addition to recording structural heterogeneity of a tropical forest' – your results don't really demonstrate this because you don't have SIF data. Maybe if you say they have 'the potential' however I still think this distracts here from the other findings.
    - Thank you, we agree and we have removed this reference to normalizing SIF and focused this portion of the manuscript on NIRv, FCVI, and NIRvrad instead (Lines 229-234).
- Line 239: 'Because NIRv and NIRvrad use NDVI, these results also indicate that including NIR reflectance or NIR radiance is the largest contributing factor to this variability' – This is built into the definitions of NIRv and NIRvrad so I would rephrase this to reflect that.
    - Thank you. Lines 233-234 have been updated to clarify this point.
- Lines 250-251: rephrase for clarity to 'The low variability and high means at midday of NIRv, FCVI, and NIRVrad indicate that…' T
    - These lines, now Lines 247-250 have been revised to make this point more clearly. Thank you for suggesting a change in wording here.
- Line 266: 'strong peak' is a bit of an overstatement, it seems much more rounded to me.
    - Thank you, we have rephrased to "distinct" to avoid overstating the shape of the peak (Line 262).
- Line 277: remove 'note how'.
    - We have removed this part of the sentence (Line 272).
- Lines 286-297: This discussion of SIF is much better because it acknowledges the potential, but also notes that SIF measurements are not available. This however also deserves some citations.
    - Thank you. We have included the appropriate citations for this statement in the revised version (Lines 290-298).
- Line 313: Remove 'for the first time' – it's confusing as you're not presenting new indices, you're presenting new data at this particular location.

    - Thank you, we removed this from that line (now Line 315), and created a new sentence (Lines 315-316) to clarify that we think we are the first to use such high spatial resolution data of NIRv, FCVI, and NIRvrad (from UAS). Based on this helpful suggestion, we think this more correctly asserts the claim.
- Line 317: I do not believe you can draw this conclusion with one day of data (see my major concern above).
    - We appreciate this suggestion and we re-worded this sentence (now Lines 317-318) to discuss the potential, as well as throughout the manuscript.
- Lines 334-337: SIF discussion here is distracting from your main points.
    - We see this now and agree. We have removed references to SIF and SIF disaggregation from the conclusions.
- Lines 345-346: You do not show that these measurements can be used to separate the components of a SIF signal and you're also not really showing how to use it as an estimate of fPAR, APAR, or GPP. Also worth noting this is for a tropical ecosystem.
    - We have also removed these and updated this portion of the manuscript to reflect this helpful advice. Instead, we discuss the importance of future work using these vegetation indicators in tropical ecosystems and beyond to explore vegetation structure and function (Lines 337-344).

RC2: ['Comment on bg-2021-95'](), Anonymous Referee #2, 13 May 2021 [reply]()

- **General Comments**
  - The authors present a very interesting and novel dataset of high-resolution vegetation indices (VI) in a tropical forest. They present correlations of the VIs to the gross primary productivity (GPP) of this forest and show how the VIs compare in capturing GPP for a given day. The authors also present a comparison of the VIs in their ability to capture structural heterogeneity of the forest. I found the study to be relevant and current given the emerging VIs used in this study. The spatial component of this study is very interesting as well. Here the authors show that NIRv and FCVI can capture more spatial heterogeneity in this forest in the reflection and absorption of radiation. My comments mostly focus on encouraging enhancement of the discussion that could provide more context for the analysis that was done and reducing the discussion of distracting concepts that were not tested. To tie the introduction and discussion to the analysis and results, the discussion and the introduction could better explain why NIRv_rad would be correlated to GPP with a clearer explanation of the GPP and NIRv (reflectance or radiance based) relationship and a reduced discussion of the role of the VIs in the SIF-GPP relationship. The paper could benefit from discussing the connections between canopy structure (height, size of tree clusters) and function (GPP) rather than the links between VIs and SIF. Below are some specific comments.

- **Specific comments**
  - The Light-Use Efficiency (LUE) model is the most widely used model to explain the relationship between GPP and vegetation indices such as NDVI as mentioned by the authors in line 42. I find the description of the LUE model to be inadequate in this paper considering it plays such a key role in understanding why vegetation indices correlate with GPP. Thinking of NIRv as an indicator of fPAR x f_esc could serve an analysis which includes observed SIF, but for the current analysis, it would be better to discuss NIRv_rad as an indicator for APAR. I would encourage the authors to present either: the equation for the LUE model with an explanation of the terms or a written description of the LUE logic and a description of its terms. Medlyn (1998) and Yuan et al. (2014) provide overviews of the LUE model and its terms. Presenting the LUE model can help readers understand exactly where vegetation indices fit in estimating GPP when one does not have SIF observations and would help clarify vague sentences like "thus a joint relationship between a remote sensing vegetation quantity, PAR, and GPP." (lines 206 – 207)
      - This insight is particularly helpful to clarify our message for the readers. We have updated the manuscript to remove the emphasis on fPAR x fesc and to include information about the links to LUE (Lines 58-62). Additionally, based on this comment, others by this reviewer, and those made by other reviewers, we have significantly cut the introductory material related to the SIF~GPP~vegetation indicator descriptions and links because we did not measure SIF. We feel as if this provided a clearer background for our study focusing on traditional RS vegetation indicators and emerging indicators.

- Since the study focuses solely on vegetation indices, can the authors expand more on why near-infrared reflectance or reflected near-infrared radiation and the vegetation indices that are built from it have shown good correlations with GPP?
    - We fine-tuned the introduction to the vegetation indicators and GPP to provide links, especially based on previous studies in Lines 62-70. We follow this portion of the manuscript with a careful description of the traditional and emerging vegetation indicators without pulling in tertiary information not related to what we are testing, such as SIF. We feel this now provides a better basis for our study.
- Making a clearer link between spatial canopy heterogeneity and GPP in the discussion can also help tie both the correlation and the power spectrum analysis together.
    - Thank you for this suggestion. We have updated the introduction, results and discussion to include better links between canopy spatial heterogeneity and GPP Lines 38-44, 49-55, 228-234, 289-297.
- I find the discussion of SIF here to be a bit too extensive given that SIF was not actually tested. The authors have covered an important point in mentioning the use of NIRv to capture the structural component of observed SIF and it is worth mentioning in a sentence or two, but I think an analysis which is not focused on a comparison between SIF and VIs does not need to explain how VIs are related to SIF as extensively as has been done. Instead, a focus on how near-infrared reflectance of vegetation, canopy structure, and light capture/absorption is related to GPP could help address the actual comparison being made. If the authors want to focus on how NIRv can be used in the GPP-SIF relationship, then the links between NIRv, SIF, and GPP need to be discussed further to allow a reader to understand what role NIRv plays in estimating GPP through the GPP-SIF relationship. Expanding the fPAR x f_esc equation to show the full GPP equation could help in this area. However, again, since the NIRv-GPP relationship was tested, the LUE model without SIF is a better conceptual glue for this analysis.
    - Thank you for these helpful and very detailed suggestions. Based on this reviewer's perspective, we updated the manuscript, especially the introduction, to increase the focus on NIRv, FCVI, and NIRvrad and reduce the focus on SIF. Specifically, we removed paragraph 2 from the introduction, as well as extraneous references to SIF in Paragraph 3 (Lines 52-101). We only retained a reference to SIF in regard to comparing techniques for measurement (Lines 78-81), measurements of FCVI in our study related to SIF (Lines 88-90), studies specifically comparing the vegetation indices to GPP and SIF (Line 96), and in the discussion regarding uses for emerging vegetation indices (Lines 295-296 and 316-319).
- Line 113: Can the authors expand on why NIRv needs to serve as a proxy for SIF if it can serve as a proxy for GPP and a radiance based NIRv can serve as a proxy for APAR? Using NIRv for addressing the structural component of the SIF-GPP relationship makes sense, but the utility of using NIRv as a proxy for SIF is not as clear.

        - We agree that stressing the connection between NIRv, NIRvrad, and SIF takes away from the central message that these metrics from UAS provide fine-scale structural information that may help address gaps in understanding GPP. Based on this helpful suggestion, we have scaled back references to SIF, and specifically removed the references in Line 113.
    - R in equation 3 and equation 4 is not explained until after equation 5. It can be clearer to explain what R represents after equation 3 and 4.
        - Apologies for this oversight. We have now corrected this omission (Lines 158-161).
    - It is unclear how this analysis supports the claim at line 236 since normalizing SIF with the UAS data was not done in this study.
        - Thank you, we have removed this reference to normalizing SIF as a part of focusing the manuscript more clearly on NIRv, FCVI, and NIRvrad (Lines 230).
    - Claims made at the following lines need citations: line 32 – 33, lines 56 – 57, lines 75 – 76, lines 78 – 80, lines 91 – 94
        - We added appropriate citations for lines 32-33 (now Lines 41-42). Due to modifications related to decreasing the discussions of SIF in the introduction, Lines 52-101 were removed from the manuscript. Thank you for pointing out these omissions.

- **Technical Corrections**
    - Line 49 – 50: consider changing “and questions linger about their ability to track green-up with RIs in tropical regions” to “and questions linger about the ability to track green-up with RIs in tropical regions” or “and questions linger about their ability to track green-up in tropical regions”
        - Thank you for this helpful suggestion, we have reworded according to your advice (lines 49-53.
    - Line 84: consider changing “SIF signal or used to independently as” to “SIF signal or used independently as”.
        - This is a helpful suggestion, but this sentence has been removed in this revision.

References

Medlyn, B. E.: Physiological basis of the light use efficiency model, Tree Physiology, 18, 167–176, https://doi.org/10.1093/treephys/18.3.167, 1998.

Yuan, W., Cai, W., Xia, J., Chen, J., Liu, S., Dong, W., Merbold, L., Law, B., Arain, A., Beringer, J., Bernhofer, C., Black, A., Blanken, P. D., Cescatti, A., Chen, Y., Francois, L., Gianelle, D., Janssens, I. A., Jung, M., Kato, T., Kiely, G., Liu, D., Marcolla, B., Montagnani, L., Raschi, A., Roupsard, O., Varlagin, A., and Wohlfahrt, G.: Global comparison of light use

efficiency models for simulating terrestrial vegetation gross primary production based on the LaThuile database, Agricultural and Forest Meteorology, 192–193, 108–120, https://doi.org/10.1016/j.agrformet.2014.03.007, 2014.

Thank you for bringing these references to our attention. We have corrected this omission and included the information and appropriate references (Lines 59, 61, 68, 556-557, 671-676.

Unveiling spatial and temporal heterogeneity of a tropical forest canopy using high-resolution NIRv, FCVI, and NIRvrad from UAS observations

Trina Merrick[1,4,8*], Stephanie Pau[1], Matteo Detto[2,3], Eben N. Broadbent[4], Stephanie. A. Bohlman[2,5], Christopher J. Still[6], Angelica M. Almeyda Zambrano[7]

[1] Department of Geography, Florida State University, 113 Collegiate Loop, Tallahassee, Florida 32306, USA
[2] Smithsonian Tropical Research Institute, Apartado 0843–03092, Balboa, Ancon, Panama
[3] Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544 USA
[4] Spatial Ecology and Conservation Lab, School of Forest, Fisheries and Geomatics Sciences, University of Florida, Gainesville, FL, 32608 USA
[5] School of Forest, Fisheries and Geomatics Sciences, University of Florida, Gainesville, FL, 32608 USA
[6] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon 97331 USA
[7] Spatial Ecology and Conservation Lab, Center for Latin American Studies, University of Florida, Gainesville, Florida 32608 USA
[8] Naval Research Laboratory, Remote Sensing Division, 4555 Overlook Ave. SW, Washington, DC, 20375, USA

**Author's current location*

Correspondence to: Trina Merrick (trina.merrick@nrl.navy.mil)

Abstract. Recently, remotely-sensed measurements of the near-infrared reflectance (NIRv) of vegetation, the fluorescence correction vegetation index (FCVI), and radiance (NIRvrad) of vegetation, have emerged as indicators of vegetation structure and function with potential to enhance or improve upon commonly used indicators, such as the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI). The applicability of these remotely sensed indices to tropical forests, key ecosystems for global carbon and biodiversity, have been limited. In particular, fine-scale spatial and temporal heterogeneity of structure and physiology may contribute to variation in these indices and the properties, such as gross primary productivity (GPP) and absorbed photosynthetically active radiation (APAR), that are presumed to be measured by these indices. In this study, fine-scale (15cm and greater) tropical forest heterogeneity represented by NIRv, FCVI, and NIRvrad, is investigated using unoccupied aerial systems (UAS) data, and compared to NDVI, EVI, and Lidar. By exploiting near-infrared signals, emerging vegetation indicators captured the greatest spatiotemporal variability, followed by the enhanced vegetation index (EVI), then the normalized difference vegetation index (NDVI). Wavelet analyses showed the dominant spatial scale of variability of all indicators is driven by tree clusters and larger-than-tree-crown size gaps rather than individual tree crowns. Emerging indices and EVI captured variability at smaller spatial scales (~50 m) than NDVI (~90 m) and lidar (~70 m). We show that spatial and temporal patterns of NIRv and FCVI are virtually identical for a dense green canopy, confirming predictions in earlier studies. Furthermore, we show that NIRvrad, which does not require separate irradiance measurements, correlated more strongly with GPP and PAR than did other indicators. These emerging indicators, which are related to canopy structure and the radiation regime of vegetation canopies, are promising tools to improve understanding of tropical forest canopy structure and function.

1 Introduction

Important spatial and temporal heterogeneity in structurally complex and species-rich tropical forests are not well characterized. Many factors, including varying microclimate, light conditions, topography, crown structure, and patterns of tree mortality and regeneration, contribute to high heterogeneity that underlies coarse scale gross primary production (GPP) measurements in tropical forest (e.g., Xu et al., 2015; Guan et al., 2015; Morton et al., 2014; Bohlman and Pacala, 2012; Laurance et al., 2012; Clark et al., 2008; Huete et al., 2008). Improving knowledge of tropical forest dynamics at multiple scales is crucial to monitoring and predicting resilience of tropical ecosystems and productivity under climate change (Liu et al., 2021; Clark et al., 2017; Laurance et al., 2012; Malhi, 2012; Wright, 2010; Saatchi et al., 2010; Lewis et al., 2009). Remote sensing (RS) measurements have been employed to uncover vegetation patterns of structure and productivity from local to global scales, often with a focus on filling gaps in knowledge regarding variation and uncertainties in GPP estimates (e.g., Jung et al., 2011; Glenn et al., 2008; Huete et al., 2002; Ryu et al., 2018; Yang et al., 2017; Jiang et al., 2008; Zhao et al., 2010; Heinsch et al., 2006; Running et al., 2004; Turner et al., 2003). Yet, there is a spatial mismatch between satellite data (e.g., 30 m to 1 km pixel resolution), which provides observations across large extents at repeat intervals, and site-specific plot level data (e.g., 0.1 – 1 hectare) that contributes to uncertainties in GPP estimates (Gelybó et al., 2013; Zhang et al., 2020). There is a lack of high spatial and temporal resolution data that can capture fine-grained heterogeneity of tropical forests (Clark et al., 2017; Mitchard, 2018; Saatchi et al., 2011; Lewis et al., 2009). Unoccupied aerial systems (UAS) with hyperspectral imaging sensors present an opportunity to collect tropical forest canopy data at high spatial resolution, which could address unknowns related to the high heterogeneity of tropical forests.

Traditional reflectance-based indices (RI) using RS data, such as the normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI), are known to capture structural changes that are coincident with changes in GPP. RIs have provided optical methods using RS to track GPP via the light use efficiency (LUE) model (J.L.Monteith, 1977; Yuan et al., 2014; B. E. Medlyn, 1998). In the most commonly used formulation of the LUE model for RS, GPP is the product of the absorbed photosynthetically active radiation (APAR) and the efficiency (ε) with which the target vegetation converts the radiation to carbon (Gamon, 2015;Yuan et al., 2014; Running et al., 2004). APAR is derived from the incoming photosynthetically active radiation (PAR) times the fraction of PAR (fPAR). RIs commonly used in the LUE model of GPP as well as direct proxies for GPP are NDVI and EVI, because of a strong relationship to fPAR (Springer et al., 2017; Morton et al., 2015; Gamon et al., 2015; Porcar-Castell et al., 2014; Glenn et al., 2008; Gao et al., 2007; Huete et al., 2002; Zarco-Tejada et al., 2013). NDVI and EVI are typically used as proxies on seasonal timescales, or, when used to examine changes on shorter timescales, they have been multiplied by photosynthetically active radiation (PAR) to account for changes in radiation (incoming, absorbed, and scattered) which better align with GPP changes (Springer et al., 2017; Yuan et al., 2014). However, RIs alone have often not shown enough sensitivity to capture more fine-scale or rapid changes in vegetation, such as those in tropical forests, and questions linger about the ability to track green-up with RIs in tropical regions (Liu et al., 2021; Yang et al., 2018a; Lee et al., 2013; Xu et al., 2015; Morton et al., 2014; Samanta et al., 2010; Sims et al., 2008).

Recently, three emerging vegetation indicators have been shown to track with GPP more closely than traditional RIs. These indicators are the near-infrared reflectance of vegetation (NIRv) (Badgley et al., 2017), the fluorescence correction vegetation index (FCVI) (Yang et al., 2020) and the near-infrared radiance of vegetation (NIRvrad) (Wu et al., 2020). Because they exploit additional information from the NIR region of the spectrum, NIRv, FCVI, and NIRvrad do not saturate in dense canopies or suffer the same level of contamination from senesced vegetation and soils as traditional RIs (Baldocchi et al., 2020; Badgley et al., 2017). Additionally, these emerging indicators require only moderate spectral resolution data and are similarly straightforward to measure and calculate as RIs, making them accessible in a broad range of studies. In contrast, SIF measurements require very high spectral resolution and multiple instruments. Therefore, NIRv, FCVI, and NIRvrad could be employed as valuable indicators of canopy structure and function (Badgley et al., 2019; Badgley et al., 2017; Dechant et al., 2020) and have practical advantages over making SIF measurements.

NIRv, the product of NDVI and the near-infrared reflectance (NIR), from moderate spectral resolution satellite imagery and field spectrometers has been shown to empirically track measured and modelled GPP globally (with highest uncertainties in the tropics) at monthly to seasonal timescales presumably because changes in canopy phenology influence light capture and these changes coincide with changes in GPP (Badgley et al., 2019; Badgley et al., 2017; Dechant et al., 2020). FCVI, derived from radiative transfer theory rather than an empirical relationship, is calculated from RS data by subtracting the reflectance in the NIR from the reflectance in the visible range (Yang et al., 2020). Yang et al. (2020) demonstrated that FCVI, by capturing structure and radiation information from a vegetated canopy, tracked GPP and solar-induced fluorescence (SIF; a radiance-based indicator of GPP) in field experiments with crops and in numerical experiments. Yet FCVI showed differences from NIRv due to exposed soil within the vegetated study areas. In previous studies, FCVI and NIRv were similar for dense green canopies where soils have less of an impact, but this has not yet been tested in the tropics (Wang et al., 2020; Badgley et al., 2019; Dechant et al., 2020). NIRvrad was proposed as a proxy for GPP on half-hourly and daily timescales, in contrast to NIRv and FCVI which track changes on longer timescales (Wu et al., 2020; Dechant et al., 2020; Baldocchi et al., 2020; Zeng et al., 2019). NIRvrad is calculated by multiplying NDVI by the NIR radiance, and because the radiance of NIR accounts for incoming radiation at short timescales, has tracked GPP and SIF on half-hourly and diurnal scales as well as seasonally in crops and, to a limited extent, natural grass and savanna ecosystems (Dechant et al., 2020; Baldocchi et al., 2020; Zeng et al., 2019; Wu et al., 2020).

Readily available UAS-based hyperspectral sensors are capable of robust measurements of NIRv, FCVI, and NIRvrad at ultra-high spatial scales, i.e. in tens of centimeters. In this regard, UAS-based data have the potential to improve our understanding of tropical forest structure and function over a range of scales that are poorly resolved by other RS platforms. Here, we use high spatial resolution UAS measurements to characterize spatial and temporal variation in a semi-deciduous tropical forest canopy during the dry season, and compare commonly used spectral indices (NDVI and EVI) to newer vegetation indicators (NIRv, NIRvrad, and FCVI) by (i) examining correlations between GPP and vegetation indicators using mean values across the canopy throughout the day, (ii) evaluating the distribution of fine spatial resolution values (~15 cm) across the canopy and examining changes in this spatial variation throughout the course of two days, and finally (iii) identifying the dominant spatial scale driving variation across our 10 ha study region.

2 Materials and Methods

2.1 Study Area

Barro Colorado Island (BCI), Panama, is a 1560 ha island (approximately 15 km^2) in Gatun Lake, which was formed by the construction of the Panama Canal. The Smithsonian Tropical Research Institute manages the preserved area specifically for research. This semi-deciduous moist tropical forest receives approximately 2640 mm mean annual precipitation and has a mean temperature of 26ºC with a dry season from approximately January through April (Detto et al., 2018). There is high species diversity, with approximately 500 tree species, approximately 60 species per ha, and about 6.3% of trees at >30cm diameter at breast height (dbh) (Bohlman and O'Brien, 2006; Condit et al., 2000). The UAS and ground measurements were focused on an area approximately 10 ha within the footprint of an eddy covariance tower near the center of the island (9.156440°, -79.848210°).

2.2 Data collection

The GatorEye Unmanned Flying Laboratory is a hardware and software system built for sensor fusion applications, and which includes hyperspectral, thermal, and visual cameras and a Lidar sensor, coupled with a differential GNSS, internal hard drives, computing systems, and an Inertial Motion Unit (IMU). Hardware and processing details, as well as data downloads, are available at www.gatoreye.org. The GatorEye flew 13 missions on January 30 and 31, 2019 over the forest canopy within the eddy covariance tower footprint at an average height of 120 m above ground level (AGL) and at 12 m/s (Fig. 1). In this study, we used radiometrically calibrated flight transects from the Nano VNIR 270 spectral band hyperspectral sensor (Headwall Photonics, Fitchburg, MA, USA) which covered approximately 1 ha per flight within the EC footprint in this study. The Nano spectrally samples at approximately 2.2 nm and 12-bit radiometric resolution from 400 to 1050 nm. The frame rate was set to 100 fps, with an integration time of 12 ms and provided a pixel resolution of approximately 15x15 cm. The Nano was calibrated to radiance by the manufacturer before the field campaign and pixel drift was removed by dark images collection, which was corrected for during the conversion from digital number to radiance. The hyperspectral transects were equally subset for each flight in ENVI + IDL (Harris Geospatial, Boulder, CO). Each flight resulted in 1920 transects of approximately 400 m length composing three blocks discretized in 2500 data points. Simultaneous lidar was collected using a VLP-32c ultra puck (Velodyne, San Jose, CA), which was processed to a 0.5x0.5 m resolution digital surface model (DSM).

Turbulent fluxes and meteorological variables were measured from a 40 m Eddy Covariance (EC) flux tower (Fig. 1). The eddy covariance system includes a sonic anemometer (CSAT3, Campbell Scientific, Logan, UT) and an open-path infrared CO2/H2O gas analyzer (LI7500, LiCOR. Lincoln, NE). High-frequency (10Hz) measurements were acquired by a datalogger (CR1000, Campbell Scientific) and stored on a local PC. Other measurements made at the tower include air temperature and relative humidity (HC2S3, Rotronic, Hauppauge New York), and photosynthetically active radiation (PAR; BF5, Delta-T Devices, UK). EC data were processed with a custom program using a standard routine described in Detto et al. (2010). GPP was derived from daytime values of NEE by adding the corresponding mean daily ecosystem respiration obtained as the intercept of the light response curve (Lasslop et al., 2010). Due to a power issue, data corresponding to the January 30 flights was not collected, so only January 30 GPP were available.

An HH2 Pro Spectroradiometer (HH2; ASD/Panalytical/Malvern, Boulder, CO) fitted with a diffuse cosine receptor was used on the ground in full sun at the forest edge to record incoming irradiance on January 30 and 31, 2019 (~ 3nm FWHM and spectral sampling at 1nm). HH2 irradiance was resampled to match the Nano hyperspectral sensor and used to calculate reflectance. A calibrated reference tarp was placed in full sun at the forest edge and the UAS flew over and recorded the tarp each UAS flight. Reflectance was calculated separately using the HH2 and tarp data and resulting reflectance values compared as a method to vicariously cross-calibrate reflectance from the hyperspectral data (<7.0% difference for all data in the study). In addition, PAR was calculated with the HH2 data and compared to the tower-mounted PAR measurement (approximately 1.5 km apart) to help understand any differences in the sky conditions during flight times. PAR differences across the site for each flight time for the duration of flights (approximately 10-15 minutes in length each) ranged between 4.0% and 10.3%. A summary of materials and methods is provided in Fig.1 at the end of Section 2.

2.3 Vegetation indicators

We calculated NDVI and EVI as (Tucker, 1979; Huete et al., 2002; Rouse JR et al., 1974):

$$NDVI = \frac{R_{770-800} - R_{630-670}}{R_{770-800} + R_{630-670}} \qquad (3)$$

and

$$EVI = \frac{2.5(R_{770-800} - R_{630-670})}{R_{770-800} + 6 \times R_{630-670} - 6 \times R_{460-475} + 1} \qquad (4)$$

where R is reflectance and the subscripts indicate wavelengths. Here, we used the averages of 770-800 nm for NIR, 630-670 nm for red reflectance, and 460-475 nm for blue bands reflectance and normalized to reduce noise. We further calculated the near-infrared vegetation index NIRv as:

$$NIRv = NDVI \times R_{770-800} \qquad (5)$$

where R770-800 is the NIR reflectance (Badgley et al., 2017). The fluorescence correction vegetation index (FCVI) was calculated from spectral data by subtracting the reflectance in the visible range (R400-700) from the NIR reflectance (Yang et al., 2020) as follows

$$FCVI = R_{770-800} - R_{400-700} \qquad (6).$$

The near-infrared radiance of vegetation (NIRvrad) was calculated similarly to the NIRv, except NDVI was multiplied by the radiance, rather than reflectance, from the NIR region (Rad770-800) (Wu et al., 2020) as follows:

$$NIRvrad = NDVI \times Rad_{770-800} \qquad (7).$$

2.4 Data Analysis

We examined mean values across the canopy over the course of one day by creating a diurnal time series of scatterplots of the tower-based PAR data, tower-based GPP data, and means of all spectral vegetation indicators, on

Jan 31, 2019, and ran comparisons using Pearson's correlation coefficients to examine correlations. At fine spatial scales, i.e. pixel level of ~15 cm, we created density plots, calculated the coefficient of variation (CV), and calculated the means of all vegetation indicators (NDVI, EVI, NIRv, FCVI, NIRvrad) for each flight to compare spatial and temporal variability (Fig. 1). To determine which spatial scales dominate the variability of each vegetation quantity, we ran power spectrum wavelet analysis using code created in the Matlab programming language (Mathworks, Natick, Massachusetts). For each vegetation quantity and each flight, and for the lidar elevation model representing canopy height, we computed the Morlet wavelet power spectrum of individual transects (Torrence and Compo, 1998). All power spectra from the wavelet analysis were normalized to unit variance. An ensemble power spectrum for each vegetation indicator was created by averaging across all the transects of each flight and then across flights. We then compared the power spectra for each vegetation indicator and lidar data to compare the spatial scales at which the quantities captured variability as well as the spatial scale at which the lidar-based elevation model captured variability. For illustration purposes, Fig. S3 is an example of two signals, a higher and lower noise signal created with fractals (Signal A and B, respectively, Fig. A1) and the corresponding power spectra which decay differently at smaller spatial scales (Power Spectra, Fig. A1). Initial UAS data processing was carried out in Interactive Data Language (IDL) and Environment for Visualizing Images (ENVI) (Harris Geospatial, Boulder, CO). Other analysis, including graphical illustrations, were carried out using the R open source environment with libraries dplyr, ggplot, and tidyverse (R Development Core Team, 2010; Wickham et al., 2018; Wickham, 2017, 2016) and Matlab (Mathworks, Natick, Massachusetts).

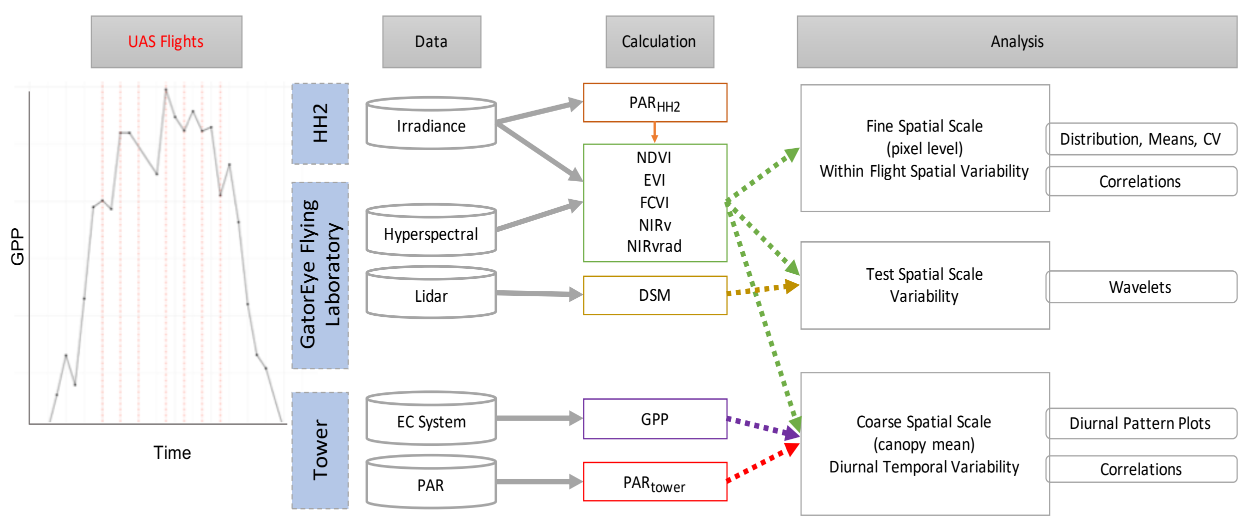

Figure 1. Summary of methods. Concept of diurnal GPP and UAS flights (far left). Platforms and instrumentation (blue) consisted of the Analytical Spectral Devices (ASD) Handheld Spectroradiometer Pro 2 (HH2), the GatorEye Flying Laboratory, and the Tower at Barro Colorado Island (BCI). Data collected included Irradiance, Hyperspectral, Lidar, Eddy Covariance System (EC), and Photosynthetically Active Radiation (PAR). Calculations made were PAR with the HH2 (PARHH2), the Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), Fluorescence Correction Vegetation Index (FCVI), the Near Infrared Vegetation Index (NIRv), the Near Infrared Radiance of Vegetation (NIRvrad), the Digital Surface Model (DSM), Gross Primary Productivity (GPP)and PAR from the PAR Sensor on the Tower (PARtower). An overview of the data analysis at each scale is provided in the right of the diagram.

3 Results and discussion

3.1 Diurnal trend in spectral vegetation indicators, PAR, and GPP

The degree to which remote sensing vegetation indicators represent changes in GPP depend largely on canopy structure-dependent light absorption and scattering processes, that is, a joint relationship between a remote sensing vegetation quantity, PAR or APAR, and GPP. Fig. 2 shows GPP, PAR, and the mean value of each vegetation quantity at each flight time over the course of January 31, the day on which we had overlapping data between the UAS and eddy covariance system (Fig. 2a-d). Additionally, Pearson correlation coefficients among mean NIRv, FCVI, NIRvrad, EVI, and NDVI for each flight time and the GPP and PAR values at the flight times are shown in Fig. 2d. NIRv is significantly and strongly positively correlated to both FCVI ($r=0.9$, $p<0.001$) and EVI ($r=0.9$, $p<0.01$). NIRvrad is the only vegetation quantity with a significant correlation to PAR and GPP, with a strong positive relationship (0.9 and 0.81, respectively, p-values <0.05; Fig. 2d). Mean NIRvrad values also have the greatest relative diurnal change among the vegetation indicators (Fig. 2c and d). These results demonstrate that a shared correlation of NIRvrad and GPP to PAR results in mean NIRvrad tracking diurnal changes in GPP to a greater degree than NIRv, FCVI, NDVI or EVI, because NIRvrad takes incoming radiation into account whereas the other vegetation indicators do not. This evidence – albeit based on only one day of data – supports the proposed use of NIRvrad as a proxy for changes in GPP on short timescales. NIRvrad is also a more efficient measurement of GPP in the sense that a separate instrument to measure PAR is not needed (Wu et al., 2020; Zeng et al., 2019). Given that the relationship between NIRvrad and GPP depends on PAR, it is unclear if the association between NIRvrad and GPP would weaken during the wet season when low light or diffuse light conditions are more common (Berry and Goldsmith, 2020).

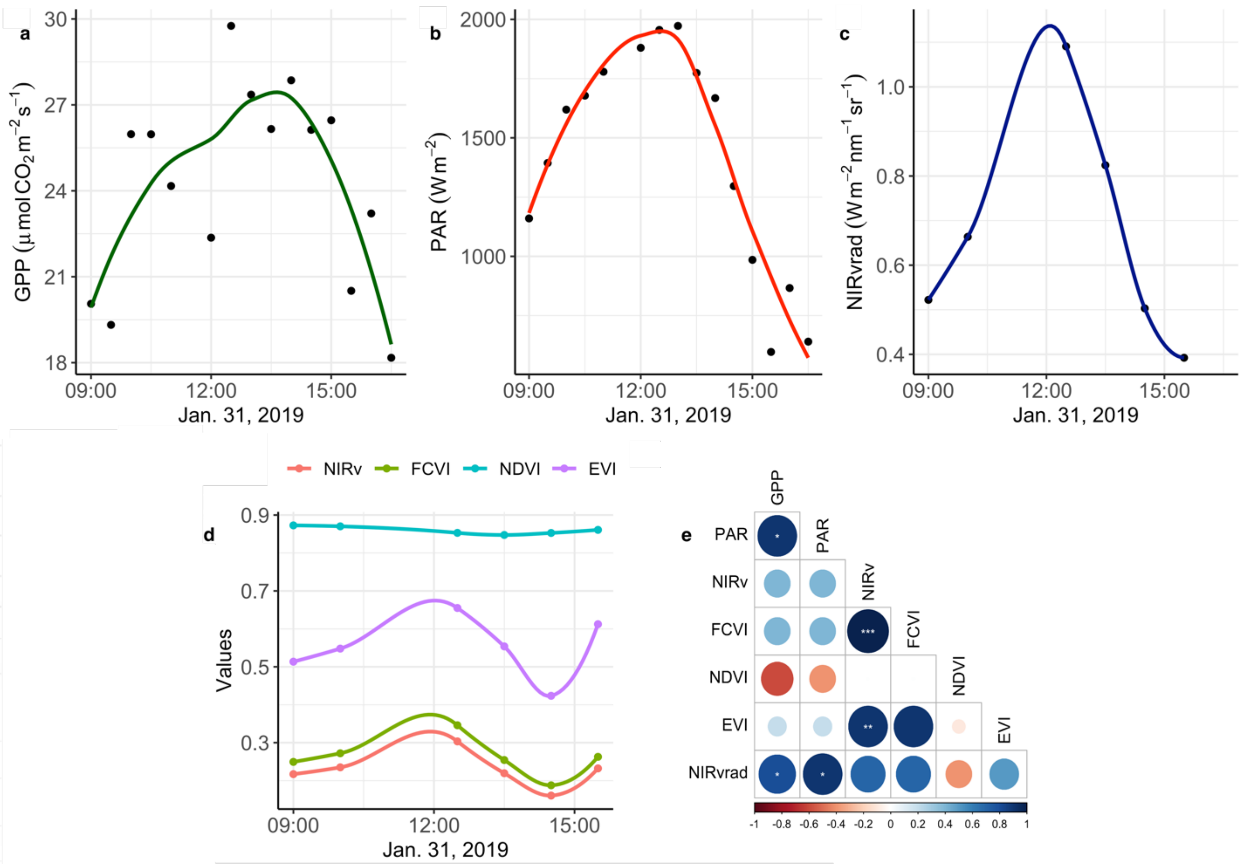

Fig. 2. Diurnal time series of a) GPP b) PAR c) NIRvrad d) NIRv, FCVI, NDVI, and EVI e) comparisons of quantities using Pearson correlations color indicates strength of relationship, * = p-value<0.05, ** = p-value <0.01, *** = p-value <0.001.

3.2 Tropical forest canopy variation

Spatial distributions and CV of all pixels of NIRv, FCVI, and NIRvrad are generally similar to one another and show considerable variation spatially across the canopy and temporally over the course of a day and across days (Fig. 3a-c, Table A2). NIRv, FCVI, and NIRvrad distributions are distinct from EVI and NDVI (Fig. 3a-e, Table A2, and Table A2). NIRv, FCVI, and NIRvrad have the highest CV at each flight time (between 39.78% and 91.54%, Table A1), followed by EVI (between 20.24% and 37.24%, Table A2) and NDVI varied the least at any flight time (between 9.83% and 12.82%, Table A2). For some indices, mean values across the canopy fail to capture extreme high (NIRv, NIRvrad, and FCVI) or low values (NDVI) during morning and afternoon hours. This pattern suggests "hot" and "cool" spots of activity related to heterogeneity in forest structure and low sun angles. In previous studies, the directional effects on NIRv have been examined on coarse spatial scales (i.e. satellites) and have been proposed as a means of improving understanding of NIRv agreement to GPP (Hao et al., 2021; Dechant et al., 2020; Baldocchi et al., 2020; Zhang et al., 2020). Our results demonstrate that NIRv, FCVI, and NIRvrad capture fine-grained heterogeneity of this tropical forest canopy, which was obscured by EVI and NDVI (Fig. 3a-e). NIRv and NIRvrad use NDVI, thus, by definition, NIR is the largest contributing factor to the heterogeneity captured (Fig. 3a, c, and e). While NIRv and NIRvrad distributions are generally similar, they diverge in the afternoons when PAR declines, which likely why NIRvrad is better correlated with GPP. EVI variability was higher than NDVI variability, but lower than that of NIRv, FCVI, and NIRvrad, indicating that EVI has a different level of sensitivity to viewing geometry and canopy components (potentially understory), light absorption and scattering regime of the canopy than the other indices (Table A1and Table A2). We also show empirically that NIRv and FCVI are virtually the same in a dense tropical forest presumably due to both indices similarly representing the radiation regime of the tropical forest canopy, i.e. light capture and scattering, in conditions with little background soil, supporting the predictions of earlier studies (Dechant et al., 2020; Zeng et al., 2019; Yang et al., 2018b; Wu et al., 2020).

Midday distributions of NIRv, FCVI, and NIRvrad on Jan. 30 at 12:00 and 1330 and Jan. 31 at 12:30 are less skewed than at other times of the day whereas morning and afternoon distributions are skewed toward lower values, except for Jan. 31 at 15:30 (Fig. 3a-c). On both days, when mean values peak at midday, the variation for all vegetation indicators is lowest (Jan 30, 1200 CV between 47.6 and 49.2 and Jan 31, 1230 CV between 45.6 and 47.2) (Fig. 3, Table A1). The highest variability occurred in the afternoon on both days (Jan 30, 1630 CV between 91.3% and 91.5 and Jan 31, 1430 CV between 83.3% and 83.8% for all quantities) (Fig. 3, Table A2). At midday, NIRv, FCVI, and NIRvrad variability was low and means were high, indicating that viewing and sun geometry drive the higher and lower values during morning and afternoon. This effect is greater in the afternoon than the morning (Fig. 3, Table A2). However, a different pattern is apparent on Jan. 31 during the 1530 flight time when mean values increased from the 1430 flight time means and the CV values were the lowest of any flight observations in the study and this influence appears to be greatest on EVI. It is possible that this was due to another type of effect on illumination geometry, such as wind influencing the UAS, diffuse radiation effects, or hotspot effects.

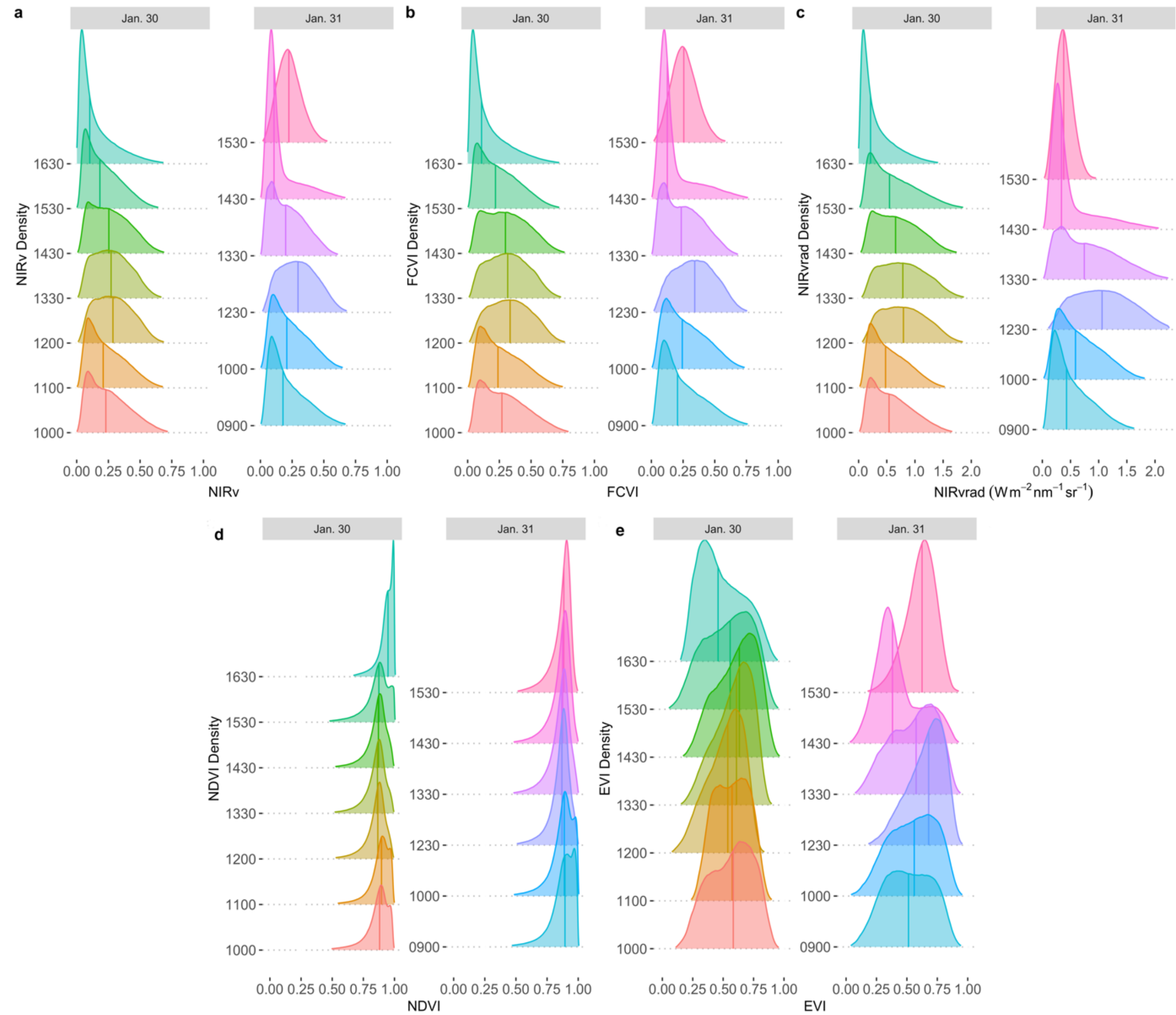

Fig. 3. NIRv (a), FCVI (b), and NIRvrad (c) density plots for each flight time on January 30, 2019 (column 1each panel) and January 31 (column 2 each panel). Colours of distributions indicate the flight time and day.

3.3 Power Spectrum Analysis

Power spectrum analysis was used to identify the dominant spatial scales driving variability across the canopy (Fig. 4). In Fig. 4, the area beneath the curve is proportional to the variance because it is the spectrum divided by the corresponding scale and then plotted as a function of the log of the scale (example signals and power spectra provided Fig. A1). Similar to their spatial distributions (Fig. 3), NIRvrad and FCVI are indistinguishable in their dominant scales of spatial variability (Fig. 3) (Dechant et al., 2020; Zeng et al., 2019). Power spectrum analysis shows a distinct peak around 50 m spatial scale for NIRv, NIRvrad, FCVI, and EVI, whereas NDVI peaks at approximately 90 m. The largest tree crown sizes on BCI are on the order of 20-30 m in diameter and the most common crown sizes are between 4-10 m (Fig. A2). Thus, the spatial variability of the vegetation indicators is strongly influenced by larger forest structures, such as forest gaps and tree clusters, rather than individual tree crowns.

This larger scale of variability is also confirmed by the power spectrum of the lidar-derived canopy surface model, which displays a peak at 70 m scale, indicating that larger than tree crown scales produce the most variability in canopy height. In other words, UAS-based lidar data also show that canopy heights within a 70 m spatial scale create strong spatial features on the landscape. Vegetation indicators and the lidar canopy surface model appear less effective at capturing smaller scale differences within a canopy (leaves or leaf clumps) or among the most frequent tree crown sizes on BCI (4-10 m sunlit tree crown sizes determined by stereophotos; Fig. A2). However, the peaks in the vegetation indicators are broader than the peak in the lidar data, showing that smaller features of the canopy are still contributing to the total spatial signal in the power spectra. These results suggest that satellite data with a spatial resolution greater than ~50 m may miss important variation in diverse tropical forest canopies. NDVI displays a different shape with a slower decay at small scales, indicating less distinguishable spatial structures from the canopy, and a peak shifted to the larger scales (Fig. 4), i.e. NDVI does not distinguish smaller spatial structures. At much larger scales (>100-200 m), the vegetation indicators decline smoothly, while NDVI and especially lidar show an increase in variance probably associated with topographic heterogeneity.

One reason why vegetation indicators and LiDAR captured variability at spatial scales larger than the most common tree crown sizes on BCI is that canopy heights tend to be more uniform on BCI compared to other tropical forests, possibly due to wind (Bohlman and O'Brien, 2006). For example, Dipterocarpus dominated South-East Asian forests have emergent trees, unlike BCI, which can reach up to 60 m in height. Additionally, tree crowns on BCI tend to be more flat-topped than conical or rounded, and trees can be found clumped in similar heights, which could explain why the most often detected unit is larger than the mean of a single crown. On the other end of the spectrum, forest gaps can be larger than a single crown because treefall often affects neighbouring trees.

Vegetation indicators and the Lidar-derived surface model represent the spectral and structural properties most broadly of the upper canopy, and thus it is conceivable that they display similar spatial variability. However, NIRv, FCVI, NIRvrad, and EVI discriminated details at a different spatial scale from NDVI and LiDAR. These results parallel the variability detected in their distributions (Fig. 3 and Table A1), where NDVI patterns were distinct from the other vegetation indicators. Taken together, these results show that NIRv, FCVI, and NIRvrad have a smoother spatial pattern and peak at finer scales than NDVI, which is known to saturate at high green biomass (Zhu and Liu, 2015; Huete et al., 2002), whereas the emerging vegetation indicators should better correlate with aspects of photosynthetic capacity. Thus, these emerging indicators should measure finer resolution spatial heterogeneity and should be more adept at monitoring changes in structure and function of the canopy than NDVI. Additionally, the emerging indicators can potentially disaggregate the physiological and structural component of SIF when SIF measurements are available since changes in structure of the forest coincide with changes in GPP (Wang et al., 2020; Wu et al., 2020; Yang et al., 2020; Dechant et al., 2020). Emerging indicators' heightened ability to differentiate the fine-scale spatial variability in the canopy is likely due to the influence of high upwelling of NIR from the canopy and understory, particularly in the dry season, which tend to blur the signal of the upper canopy for NDVI. Notably, EVI and NDVI, two common indicators of vegetation greenness, show differences in their power spectrum, in particular the slope of the curve for scales less than 20 m. EVI was designed to better capture vegetation changes by exploiting variability in the reflectance in the blue range, especially effective in dense green canopies. This may help explain the scale of variability in this canopy where variation in the blue may be expected to manifest, especially because deciduous crowns, which have high reflectance in blue wavelengths compared to fully leaved crowns, are present on BCI.

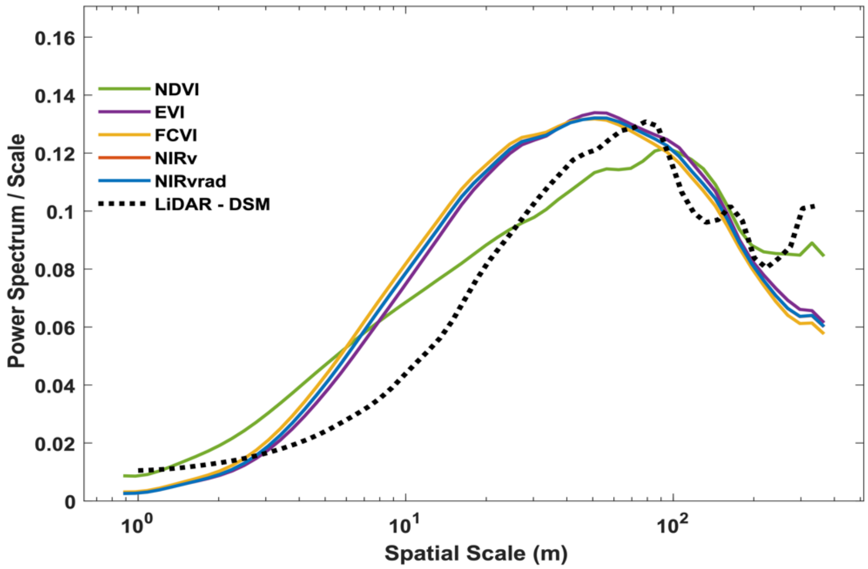

Fig. 4. Ensemble wavelet power spectra for all the quantities used in this study and a LiDAR-derived digital surface model (DSM). Note that FCVI and NIRv are similar, thus the NIRv curve is obscured by the FCVI. Ensembles were created by averaging the spectrum of individual transects, then averaging across flights. Note that in this representation, the spectrum divided by the corresponding scale as a function of the log of the scale, the area beneath the curve is proportional to the variance.

4 Conclusions

We examined NIRv, FCVI, and NIRvrad, emerging vegetation indicators related to fPAR and the scattering of SIF photons, of a semi-deciduous tropical forest canopy using UAS-based hyperspectral data. Our findings demonstrate that NIRvrad has greater potential to track GPP over the course of a day than the non-radiance-based indices as evidenced by a shared correlation among NIRvrad, PAR, and GPP. Thus NIRvrad is a potential proxy for tracking GPP on short timescales without the need for separate measurements of incoming irradiance, which SIF requires. Also, NIRv, FCVI, and NIRvrad at high spatial resolution (~15cm) unveil greater spatial and diurnal variability of BCI's tropical forest canopy versus EVI or NDVI, which may pave the way to improve our understanding of the relationship between GPP and remote sensing observations. The dominant scale driving spatial variability of spectral measurements and lidar data are larger forest structures occurring on BCI, such as groups of similar trees or forest gaps. Yet, smaller, broader peaks in the power spectra of NIRv, FCVI, NIRvrad, and EVI indicate these four indices incorporate smaller scale information compared to NDVI. Taken together, the demonstrated potential to track GPP, measure spatial heterogeneity and variability, and capture forest structural characteristics of BCI open greater possibilities to examine structure and function within and across this tropical forest.

Because remote sensing advancements are making it possible to capture physiological responses of vegetation, the importance of improved techniques to examine the radiation regime, for instance estimating fPAR or APAR, can be overlooked. However, recent studies have highlighted the importance and difficulties of measuring fPAR and APAR, the strong dependence of measurements on illumination and viewing geometry, as well as the need for increased understanding of structure-related radiation regime information more generally e.g. (Hao et al., 2021; Dechant et al., 2020; Baldocchi et al., 2020; Rocha et al., 2021; Zhang et al., 2020). For NIRv, FCVI, and NIRvrad, inclusion of the NIR spectral region makes the emerging indices more sensitive to incoming, absorbed, and scattered radiation, which can be influenced by illumination and viewing geometry, changes in canopy leaf angles or associated structure changes. In the case of NIRvrad, which was most strongly associated with GPP, changes in light regime and associated photosynthetic capacity can even be captured diurnally. This study highlights the importance of understanding the incoming solar radiation, absorbed and scattered radiation, and illumination and viewing geometry of any remote sensing data, but it also encourages exploiting RS observations to improve our ability to measure structure-related light capture and scattering patterns. It is in this role, we show these measurements should be further investigated as valuable tools to improve our understanding of complex tropical forest canopies and potentially as an improved estimate of fPAR, APAR, or GPP. While this study focuses on BCI, these techniques could be applied more broadly for the purposes of defining the dominant scale of spatial variability, tracking structural changes, monitoring coincident changes in GPP or light regime, or as inputs to vegetation models of tropical forest structure and function.

5 Appendix

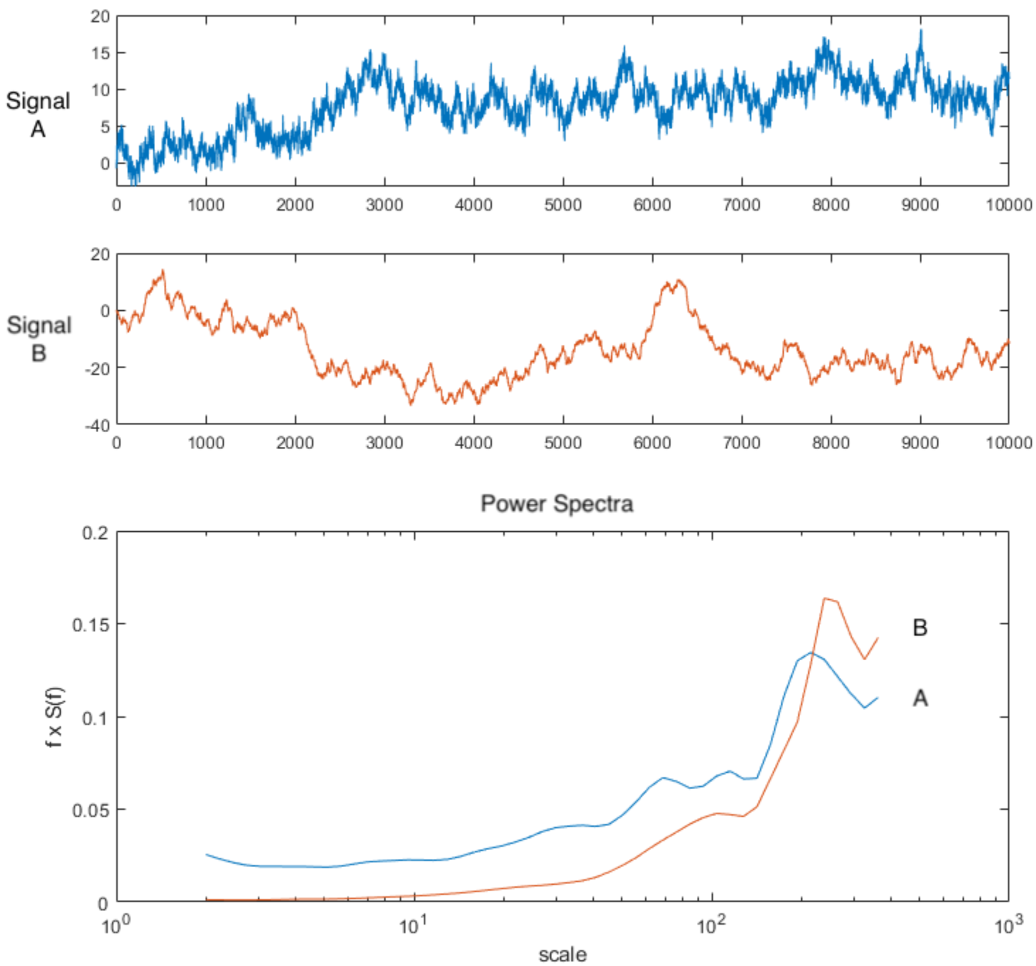

Figure A1. Sample signals with relatively higher noise (Signal A) and lower noise (Signal B) and their corresponding Power Spectra ensemble plotted as normalized on log scale. Note the representation of the variance by area under the curve is preserved by multiplying the Power (S(f)) by the frequency (f). In this way the area beneath the curve is still proportional to the variance.

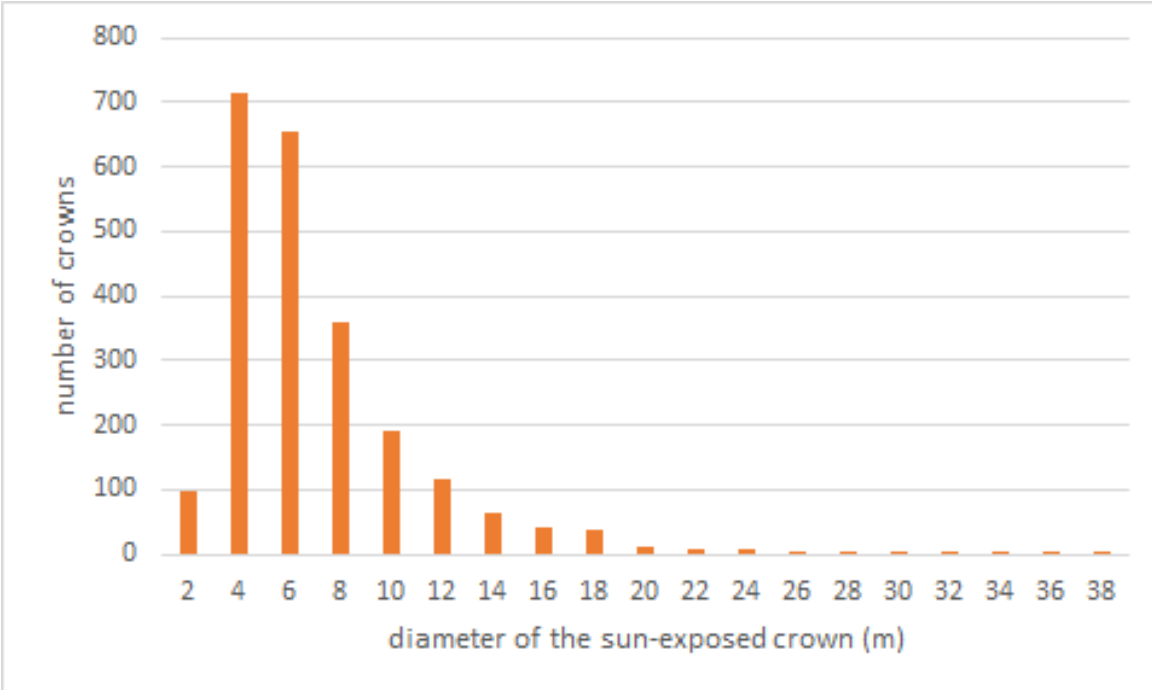

Figure A2. **Distribution of tree crown sizes on BCI in a sample ~10 ha plot taken from digitized high spatial resolution stereo photos that were linked to stems in the field (Bohlman and Pacala 2012). This ~10 ha plot does not coincide with the ~10 ha area sampled by the UAS near the eddy covariance tower in this study.**

Table A1. Mean, standard deviation (Sdev) and coefficient of variation (CV) of NIRv, NIRvrad, and FCVI measurements for the study.

Flight Time	Mean NIRv	SDev NIRv	CV NIRv (%)	Mean NIRvrad	SDev NIRvrad	CV NIRvrad (%)	Mean FCVI	SDev FCVI	CV FCVI (%)
Jan30_1000	0.26	0.16	61.36	0.60	0.36	60.54	0.29	0.18	59.69
Jan30_1100	0.24	0.15	61.48	0.54	0.33	60.56	0.27	0.16	60.89
Jan30_1200	0.29	0.15	49.20	0.82	0.39	47.59	0.34	0.16	47.88
Jan30_1330	0.28	0.14	50.46	0.81	0.40	49.24	0.32	0.16	49.16
Jan30_1430	0.27	0.15	55.46	0.70	0.38	54.38	0.31	0.17	54.22
Jan30_1530	0.21	0.14	65.10	0.63	0.41	64.71	0.25	0.16	64.01
Jan30_1630	0.16	0.14	91.54	0.32	0.30	91.54	0.17	0.15	91.39
Jan31_0900	0.22	0.14	66.31	0.52	0.34	65.25	0.25	0.16	66.01
Jan31_1000	0.24	0.14	59.43	0.66	0.39	58.29	0.27	0.16	59.04
Jan31_1230	0.30	0.14	47.17	1.09	0.50	45.63	0.35	0.16	45.91
Jan31_1330	0.22	0.14	61.91	0.82	0.51	61.47	0.25	0.15	60.53
Jan31_1430	0.16	0.14	85.32	0.50	0.42	83.81	0.19	0.16	83.83

Jan31_1530	0.86	0.08	9.83	0.61	0.12	20.24	0.53	0.04	8.15

Table A2. Mean, standard deviation (Sdev) and coefficient of variation (CV) of NDVI and EVI measurements for the study.

Flight Time	Mean NDVI	SDev NDVI	CV NDVI (%)	Mean EVI	SDev EVI	CV EVI (%)
Jan30_1000	0.86	0.10	11.64	0.57	0.18	31.54
Jan30_1100	0.88	0.09	10.15	0.57	0.14	24.40
Jan30_1200	0.85	0.09	10.38	0.52	0.15	28.48
Jan30_1330	0.85	0.09	10.60	0.59	0.15	25.24
Jan30_1430	0.85	0.09	10.35	0.61	0.16	26.84
Jan30_1530	0.85	0.11	12.52	0.54	0.19	35.21
Jan30_1630	0.93	0.06	6.69	0.49	0.18	36.90
Jan31_0900	0.87	0.10	11.54	0.51	0.19	37.24
Jan31_1000	0.87	0.10	11.08	0.55	0.19	34.66
Jan31_1230	0.85	0.08	9.82	0.66	0.15	22.72
Jan31_1330	0.85	0.09	10.70	0.55	0.19	33.80
Jan31_1430	0.85	0.09	10.58	0.42	0.18	43.07
Jan31_1530	0.86	0.08	9.83	0.61	0.12	20.24

Code availability

Data availability

GatorEye data related to this project can be downloaded from www.gatoreye.org. Code and other material with links provided upon request (repository forthcoming).

Author contributions

T.M. designed the study with the help of S.P. and S.A.B.. M.D. and T.M. outfitted the tower and collected tower-based data, T.M. and E.N.B. collected the UAS data. E.N.B., A.M.A.Z., and T.M. pre-processed the hyperspectral and lidar data. T.M. and M.D. further processed UAV, lidar, and GPP data and ran data analysis. M.D., S.P., S.A.B., C.S., contributed with the methodological framework, data processing analysis and write up T.M., M.D., S.P., S.A.B., C.S., E.N.B., and A.M.A.Z. contributed to the interpretation, quality control and revisions of the manuscript. All authors read and approved the final version of the manuscript.

Competing interests

The authors declare no conflict of interest.

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