#### **Response to Associate Editor**

#### Dear Dr. Schöngart,

5 We thank you and the reviewers for your responses and valuable suggestions. We have made small modifications to the manuscript throughout, in order to clarify issues, and further discussions. In particular, we have included more technical details on the model output, and have included discussions on other factors that may affect the results we have found (particularly the decrease in NDVI).

#### 10

With increasing CO2, we found a decrease in ET and an increase in canopy nitrogen, both consistent with theory, suggesting more water and nutrient use efficient canopies. However, we also observed a decrease in NDVI with increasing CO2, which may be consistent with increased efficiency of fewer leaves.

#### 15

Thank you for your continued consideration.

### Best,

Kerry Cawse-Nicholson

20

I have read the three reviews as well as your responses and how you will address those in the revised version of bg-2018-73. All reviewers acknowledge the importance of this study and its novelty filling an important gap in understanding how plants and ecosystems will

25 respond to continually rising CO2 coming up with different results as experiments, such as FACE, limited in space and time. I will ask you to address the valuable comments made by the reviewers and decided to accept bg-2018-73 for publication after a minor revision.

Dr. A. P. Ballantyne notes the importance of this study in testing different remote-sensing

- 30 techniques to test vegetation responses to elevated CO2 concentrations at the long-term. He focuses in his review much on the rather unexpected negative relationship between NDVI and soil CO2 flux which is an important observation. Possible factors, e.g., nutrient limitation, extreme climate events, oxygen deprivation of roots, soil acidification and plant vigor (see also comments of both anonymous referees) should be discussed indicating the
- 35 need for further studies in this complex system.

We thank the reviewers for raising all of these potential factors, and we have included a paragraph summarising these at the end of the Discussions section, as well as a more detailed analysis of several factors that have been repeatedly raised (such as soil acidification) discussed earlier in the section. Of particular interest is the nutrient limitation

5 – it is a plausible scenario that NDVI decreases because the leaves are more nutritionally efficient; thus there are fewer leaves needed. This is discussed in more detail in the manuscript.

The author's should also address the influence of elevation reducing the CO2 effect.

- 10 We have discussed both partial pressures and cold air drainage. The partial pressures at Mammoth are about 60% of sea level. The fact that we see systematic ecosystem effects suggests that elevation is not on the flat part of the A-Ci curve. In other words, even if elevation were to reduce the CO<sub>2</sub> effect, we still are seeing strong CO<sub>2</sub> effects regardless, highlighting just how important and strong of a response we are able to detect. We will add
- 15 this discussion to the revised manuscript.

Please also indicate some additional statistics and the order of magnitude of change in NDVI per change in Soil CO2 flux in the abstract.

Additional statistics have been provided throughout the manuscript, and we have included 20 the change in NDVI per change in soil CO2 flux in the abstract. I have used the 200 – 800

g/m2/day range in the abstract, since population sizes decrease beyond that level.

I encourage the authors also to indicate the limitations of the FACE experiments around the world in contrast to the long-term emissions of volcanic CO2 emissions especially focusing

- 25 on the warming trend. The FACE studies have been invaluable to our understanding of the CO2 effect, which contributes to among the largest uncertainties in projections of Earth's climate. While it is true that they primarily assess CO2, we argue that the actual biggest limitation of FACE is the short durations—there has been no way to assess long-term changes in ecosystems.
- 30 This is where the long term emissions of volcanic CO2 can play a game changing role in how to assess the long term CO2 effect on ecosystems.

Even if 99% of the emitted gas volume is CO2, the author should mention what other gases are emitted with the respective numbers. Even if CO2 is a trace gas in the atmosphere it has

35 a tremendous impact on the Earth system!

There is no significant H2S nor any SO2 present at soil levels at this site; see, for example, data in Sorey et al 1998, Werner et al, 2014, and a number of papers on volcanic degassing at Mammoth Mountain by our USGS co-author Lewicki (2006, 2007, 2008, 2012, 2014). The other contributing gases by volume are N2 and O2.

5

Please do also consider the minor concerns indicated my Dr. Ballantyne. We have clarified many points throughout the manuscript in response to Dr. Ballantyne's suggestions.

- 10 Anonymous Referee #1 notes the novelty of this study filling an important gap in understanding how plants and ecosystems will respond to continually rising CO2 by overcoming limitations of previous studies in spatial and temporal scales. As he indicated, the authors should indicate some explanation to why looking at several different vegetation indices and comparing each individually to enhanced CO2 may be beneficial for
- 15 understanding how plant physiology and growth is impacted and what methodologies may be selected in investigating other ecosystems. While all vegetation indices are indeed related, they differ enough to be considered independent variables. E.g. some account for soil moisture, others weight plant greenness more heavily. This was an exploratory effort in investigating the effects of CO2 on any
- 20 measure of plant function, composition, and structure, and so we attempted to cover all avenues of investigation. This discussion has been included in the newest revision of the manuscript.

As Dr. Ballantyne, anonymous reviewer #1 also focuses a lot on possible negative impacts (oxygen deprivation of roots, soil acidification, plant vigor) on elevated CO2 (contrasting results obtained by the FACE experiment) indicating the need for further studies especially on soil pH and O2 and citing important literature which should be considered by the authors.

We note for clarification that the "kill-zone" is the exact location where  $CO_2$  is emitted from

- 30 the soil—a property of the soil being altered by the emission; but, we focus on the "fertilization zone", which is away from those emission points, with unaffected soils, where tree canopies are exposed to the CO<sub>2</sub>, which has diffused in the atmosphere away from the emission points. We have also included a discussion on other negative impacts, as above.
- 35 The strength of the paper is the long-term monitoring vs. short-term observations as in FACE, and this should be evidenced in the discussion (as pointed out by the other reviews).

#### A more detailed discussion of the long-term monitoring aspect has been included.

Please consider also the minor concerns and technical corrections indicated by reviewer #1. We have addressed the minor concerns raised by this reviewer.

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Anonymous referee #2 acknowledges the long-term character of this monitoring, but also criticizes the empirical model used for the analysis of many covariates (which are closely related to each other as pointed out by referee #1) to discern the effects of eCO2 on structure and dynamic.

10

This reviewer has two major concerns. The first focuses on the variability of eCO2 over time and the authors give an interesting response indicating the history of measurements of CO2 emissions at Mammouth Mountain and I would find in interesting to include this in the Material and Method section. The second one was addresses soil conditions as important

- 15 factor on structure and dynamics of vegetation which was already indicated by the other two reviewers and should be sufficiently addressed in the revised version of bg-2018-73. We have included the review response in the revised manuscript, and have addressed soil conditions as indicated previously.
- 20 Please also consider the minor concerns indicated by referee #2. We have addressed the minor concerns raised by this reviewer.

I am looking forward to the revised version of bg-2018-73. Thank you for choosing Biogeosciences to publish this fascinating study.

25 Thank you!

#### Anonymous Referee #1

Received and published: 2 June 2018

Overview and significance

In this analysis Cawse-Nicholson et al. describe ecological attributes measured through 5 several remote sensing platforms in relation to ground-measured and modeled elevated CO2 originating from volcanic degassing. The primary objective and novelty of this study is to estimate the impact of elevated CO2 on plant growth and whole ecosystems by utilization naturally occurring gradients of elevated CO2 from volcanic degassing. Previous experiments and studies in estimating the impact of elevated CO2 on plants and ecosystems approach

- 10 scaling limitations; whether through limited species diversity, space or time of exposure to elevated CO2, and/or cost of artificially elevating CO2. Therefore conclusions of experimental CO2 enhancements are limited to relatively few species and over short periods of time without leveraging natural gradients of elevated CO2. Methodologies to use natural CO2 gradients in determining plant and ecosystem responses to elevated CO2 described herein, in
- 15 conjunction with elevated CO2 experiments, will fill important gaps in understand how individual plants to whole ecosystems will respond to continually increasing levels of CO2. The hope for the methodology described herein is for it to be applied where gradients of CO2 exists in order to understand the impact of elevated CO2 across multiple biomes.

We thank the reviewer for noting the novelty of our study in overcoming scaling limitations of previous studies, and the important gap that we aim to fill in understanding how plants and ecosystems will respond to continually rising CO2.

General comments:

The authors outline their objectives as

Evaluate the viability of using a passively degassing volcano system to study the properties
 of ecosystems; 2. assess the detectability of ecological responses to elevated soil CO2 emissions via airborne data alone; 3. Present key lessons enabling future studies to extend our framework to other biomes.

Objective 1 is approached using soil CO2 flux measurements at a spatial resolution of 1 meter. This was made possible through the records of soil CO2 flux measurements at Mammoth Mountain. The authors acknowledge that measurements from soil CO2 fluxes will be much different and more stable than atmospheric fluxes of CO2 (page 5 line 10 and page 15 line

5 35). This approach makes estimating actual atmospheric CO2 measurements intractable under known methodologies but is strong enough to infer that atmospheric CO2 was greater than background where soil CO2 flux was greater.

Mammoth Mountain included a tree-kill zone for which the authors selected the trees around this zone. The presence of a tree-kill zone naturally leads to hypotheses that elevated CO2

- 10 will have a negative effects on vegetation at some point up the CO2 gradient. Previous studies pointing this out are cited in the manuscript and detected by NDVI (Rouse et al. 2010 and Cholathat et al. 2011) and through tree ring anal- and biomass measurements derived from Lidar as proposed in Objective 2. Soil CO2 flux was shown to be a significant predictor for these indices and remotely sensed attributes. While the vegetation indices are all slightly
- 15 different they are largely related to one another vs. the other measurements of biomass, plant foliar traits, and canopy evapotranspiration. Some explanation as to why looking at several different vegetation indices and comparing each individually to enhanced CO2 may be beneficial for understanding how plant physiology is impacted and what methodologies may be selected in investigating other biomes (Objective 3).
- 20 While all vegetation indices are indeed related, they differ enough to be considered independent variables. E.g. some account for soil moisture, others weight plant greenness more heavily. This was an exploratory effort in investigating the effects of CO2 on any measure of plant function, composition, and structure, and so we attempted to cover all avenues of investigation. A note to this effect will be included in the next revision of the manuscript.
- 25 We note for clarification that the "kill-zone" is the exact location where CO<sub>2</sub> is emitted from the soil—a property of the soil being altered by the emission; but, we focus on the "fertilization zone", which is away from those emission points, with unaffected soils, where tree canopies are exposed to the CO<sub>2</sub>, which has diffused in the atmosphere away from the emission points.

The hypothesis and observations that elevated CO2 has negative effects on vegetation is 30 contrary to many greenhouse and FACE experiments of artificially enhancing CO2, but is likely related to the intensity of elevated CO2 at the volcanic site. The authors also speculate that elevated soil CO2 may lead to oxygen deprivation of roots and soil acidification (page 15 line 34 and cited in Farrar et al., 1995; Qi et al., 1994; McGee and Gerlach, 1998). This has major confounding effects on being able to use volcanic degassing to detect the impact of elevated atmospheric CO2 on photosynthesis and carbon sequestration if suitable soil chemistry for plant growth becomes a limiting factor. Rouse et al. (2010) did observe that in multispectral analysis of vegetation revealed that plant vigor degraded under high CO2 but slightly

- 5 increased under low CO2. Along the same lines that Cawse-Nicholson et al. have speculated, slight increase in plant vigor may exist in zones where soil O2 is still above a certain threshold and/or soils are adequately buffered. I suggest that in order for the methodology put forth by Cawse-Nicholson et al. to effectively capture the impact of elevated atmospheric CO2 on ecosystem traits that measurements be made of soil O2, soil pH, and atmospheric CO2 be
- 10 made in future studies. As is, the study of Cawse-Nicholson et al. provides a valuable step forward in being able to scale-up the impact of elevated CO2 on plants to whole ecosystems and across differing biomes.

We thank the reviewer for complimenting our study as a valuable step forward, as well as the suggestion for measurements in future studies. As one of our objectives was to provide guidance for future studies, these suggestions fit well with our objectives.

As in our previous response above, we will clarify that any vegetation impacts are due not to soil changes from direct CO<sub>2</sub> emissions, as we excluded the emission zones from our study. We will also clarify that the effects should not necessarily be given a subjective description of 'negative'; rather, it is important to note that the CO<sub>2</sub> fertilization effect is unlikely to continue indefinitely, particularly at the same rates that FACE studies have shown only in the short-term. All other experiments have been unable to show long-term effects. Our study suggests that over the scale of decades, some of these hypothesized greening or biomass increases may not be sustainable. Other results, such as an increase in canopy nitrogen with increasing 25 CO<sub>2</sub>, do seem to remain consistent with our study, however.

Specific comments: - Table 2. As the primary subject of this paper is elevated  $CO_2$ , a complete ranking of the explanatory variables against CO2 would be informative even for dependent variables in which eCO2 was not the most influential variable.

This is a good suggestion, and the complete ranking will be included.

Technical corrections: Page 11 line 15 slope and aspect seem mixed up as slopes of 350 are not feasible.

Thank you. This has been corrected.

#### Review response to SC1

5

The authors thank Prof. Ballantyne for the positive review and useful feedback on this manuscript. This paper aimed to demonstrate the capability of both the natural elevated CO<sub>2</sub> experiment and the collection of airborne instruments to provide innovative ecology results.

We have responded to specific comments in red below:

Review: Ecosystem responses to elevated CO2 using airborne remote sensing at Mammoth 10 Mountain, California

In this analysis Cawse-Nicholson use a volcanically active site where elevated CO2 fluxes have been monitored as a natural experiment to test vegetation response using remote sensing approaches. Given the contradictory results from previous studies at this site, it seems logical

- 15 to revisit using new approaches. The rationale and methods for this study seemed logical and it provides a nice testing ground for testing a range of remote sensing techniques. I was quite surprised by the results showing the apparent suppression of growth (i.e. negative relationship between NDVI and soil CO2 flux), especially because this main conclusion was not clearly stated in the title or the abstract. It seems that the forests in this volcanic setting are
- 20 responding adversely to something, but it is not clear why it would be elevated CO2 concentrations. I think that most folks reading the title, perhaps the abstract and looking at the figures will be a bit perplexed as I was. This is a really fascinating study system that is fairly complex in terms of terrain and gases emitted.

We thank you for noting the innovativeness on using volcanically-derived elevated CO<sub>2</sub> as a

- 25 means to assess long term ecosystem responses through remote sensing approaches. Some of the results were indeed unexpected—but, this is exactly why such a study is needed. It may be possible that the NDVI decrease is due to a progressive nutrient limitation, as has been suggested throughout the literature, but has never been tested empirically. However, much more in depth investigation is required to determine the underlying mechanisms explaining
- 30 the results. As such, we frame this paper as more suggestive than conclusive, ideally leading to further work on this topic.

General Comments: The authors go to great lengths to control for distance from these hotspots of CO2 to derive a gradient over which to investigate vegetation responses, which is

35 no easy task, especially using remotely derived metrics over complex terrain. In particular, I wonder how cold air drainage at night affects CO2 concentrations at these sights (Pypker et al. 2007). It is conceivable that much higher CO2 concentrations are found downslope than upslope or adjacent to these CO2 efflux hotspots (Fig. 2a). In fact, biomass hotspots appear to

be adjacent or downslope from the CO2 hotspots (Fig. 2b); although it is difficult to discern without elevation contours.

We agree that a more thorough assessment of  $CO_2$  flow through the landscape is needed. It is remarkable that we were able to detect clear signals from soil fluxes alone; we expect that the

5 results would be improved with above- and within-canopy CO<sub>2</sub> measurements, and better tracking over time. Given the available measurements from USGS, the best we could do was shift the ground CO<sub>2</sub> dataset in all cardinal directions, to see if this resulted in an improved fit. The best model fit was found at the original ground CO<sub>2</sub> location. We will include elevation contours in the revised manuscript.

10

Where on the A-Ci curve are we operating? The vegetation at these sites is responding to the partial pressure of CO2 in the atmosphere, among other gases at this site. Figure 1 suggests that the CO2 flux was maybe 2 orders of magnitude greater than typical estimates at non-volcanic sites (Jensen et al. 1996), but what is the partial pressure of CO2 in the atmosphere

15 at these sites. I suspect that we are operating well above the asymptote on the A-Ci curve(Tissue, Griffin, and Ball 1999), such that we would see very little vegetation response to even large changes in the partial pressure of CO2. The partial pressures at Mammoth are about 60% of sea level. The fact that we see systematic

ecosystem effects suggests that elevation is not on the flat part of the A-Ci curve. In other

20 words, even if elevation were to reduce the CO<sub>2</sub> effect, we still are seeing strong CO<sub>2</sub> effects regardless, highlighting just how important and strong of a response we are able to detect. We will add this discussion to the revised manuscript.

What are the other gases are being emitted from this volcanic field? The negative relationship

- 25 between CO2 soil flux and NDVI is perplexing and needs explaining. Are these particularly sulfur rich volcanic fields? Has anyone developed a 'rotten egg' remote sensing index? No but seriously, if there are significant sulfur emissions this could be leading to sulfuric acid deposition and cation loss from the soils, such that the negative response to soil fluxes could actually be the result of another gas that is detrimental to plant growth other than CO2.
- 30 There is no significant H2S nor any SO2 present at soil levels at this site; see, for example, data in Sorey et al 1998, Werner et al, 2014, and a number of papers on volcanic degassing at Mammoth Mountain by our USGS co-author Lewicki (2006, 2007, 2008, 2012, 2014). Furthermore, we excluded the direct areas of CO2 emissions, which impacts the local soil conditions, not representative of the larger ecosystem. We will add and clarify this detail in 25 the revised measurement.
- 35 the revised manuscript.

Specific Comments: The abstract is a bit vague reporting statistical relationships but not the apparent negative response to increased soil CO2 flux and without any response numbers (change in NDVI per change in Soil CO2 flux).

We will add more statistics to the revised manuscript.

5

P2 L14 to 26 Perhaps the most fundamental flaw of FACE studies is very few have concomitant warming, which greatly limits ourinsight for the real world. The FACE studies have been invaluable to our understanding of the CO<sub>2</sub> effect, which contributes to among the largest uncertainties in projections of Earth's climate. While it is

10 true that they primarily assess  $CO_2$ , we argue that the actual biggest limitation of FACE is the short durations—there has been no way to assess long-term changes in ecosystems. This is where the long term emissions of volcanic  $CO_2$  can play a game changing role in how to assess the long term  $CO_2$  effect on ecosystems.

P3 What other gases are being emitted from these volcanic fields.

15 As discussed above, CO2 dominates by up to 99% of gas volume.P3 L37 'can be applied' This will be corrected.

P4 L20 is this g C or g CO2 per day...you might want to make this absolutely clear in the units

- These are g.m-2.d-1 of CO<sub>2</sub>, and will be clarified.
   P4 L27 why were these data not just aggregated to a coarser resolution. Further smoothing of already smooth data may lead to loss of meaningful variance.
   The original raw field CO2 flux measurement data were not available anymore. We worked from the 1m data that were provided to us by the USGS, which are aggregates of data
- 25 collected by several different surveys in the 2011-2012 time frame, with the Horseshoe Lake area visited multiple times to characterize any very subtle temporal variation (Fig. 1 in Werner et al, 2014).

P5 L20 some discussion of cold air drainage important in this mountainous terrain (see Pypker below).

- 30 Thank you, we will include this discussion and reference.
  P7 L 12 as demonstrated by the authors- where?
  As demonstrated by Ma et al (2018). This will be made clearer in the next version.
  P11 L 18 Why not use a random forest model to identify variables of greatest importance.
  We considered random forest models and obtained similar result. We presented the results of
  the linear regression since the model itself is more assily interpretable by the reader.
- the linear regression since the model itself is more easily interpretable by the reader.
   P12 L3 'well modeled' be more descriptive precisely or accurately?
   Canopy height and biomass were accurately modelled with high R2. Will edit in the revision.
   Fig. 1 could benefit from a log y-scale or even better some estimate of pCO2

This will be modified in the revised manuscript. Fig. 3 the caption seems to be incomplete in describing all the panels. This will be modified in the revised manuscript.

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  - Geothermal Research, 284, pp.1-15.

#### Anonymous Referee #3

This is an interesting study using a purported natural CO2 enhancement gradient to understand ecosystem scale responses to elevated CO2. The authors use a linear regression model to control for a couple of covariates to discern the effect of eCO2 on structure and 5 process.

We thank the reviewer for noting the interest of our study using a well-documented natural  $CO_2$  enhancement to understand ecosystem scale responses to elevated  $CO_2$ .

Overall, the empirical model results in confusing results, which the authors try to explain by referring to similar studies in other naturally enhanced CO2 systems.

- 10 Some of the results may seem confusing because they go against shorter-term experiments. But, this is exactly why we did the study—if we knew what the results were going to be, there would be no reason for the study. Moreover, the results highlight numerous points made throughout the literature with respect to the FACE experiments—their short-term nature has been unable to uncover long-term results, which is exactly a primary purpose of our study.
- 15 We edited the manuscript to make these points more clear (and to make understanding the results less confusing).

I find the discussion quite speculative and have two concerns on the study and the usefulness of volcanic-CO2 seepage as an experimental setting.

We agree that the Discussion is structured more as a Discussion, less as Results. We tried to 20 make clear that this study was exploratory, rather than definitive, and that this study was meant to identify both potential signals as well as design elements for further study.

1) The authors argue that the Mammoth Mt region is very well studied and that variability in CO2 over time and space is minimal, and that the ecosystems in the area are in some equilibrium with the seepage. But even ignoring variability before measurements began, the

25 Figure 1 shows very high variability since measurements first started. I don't think we can say with any confidence what the CO2 exposure has been over time and space, and whether the current study reflects the equilibrium conditions to eCO2.

It is a fundamental principal of volcanology that all active volcanoes emit  $CO_2$  continuously during their entire life cycle. The  $CO_2$  emissions at Mammoth Mountain have been well

known since at least 1989, and their variability well documented by repeated CO<sub>2</sub> efflux mapping between at least 1995 (ongoing), by the USGS (Werner et al. 2014). The CO<sub>2</sub> seeps at the site have been known for even longer (Varekamp & Buseck 1984, and geothermal assessment reports from the 1970s at least). All these studies show that the active Mammoth

5 Mountain volcanic system has experienced a replenishment of the magmatic CO<sub>2</sub> source in the deep subsurface in about 1989, possibly already an earlier one in 1978, though no systematic CO<sub>2</sub> measurements were conducted in that earlier time period (Hill, 1996). Werner et al show remarkable spatial consistency for 9 years of systematic measurements at the CO<sub>2</sub> gas seeps on Mammoth Mountain.

10

2) The authors focus only on eCO2 as a driver of variability in structure and processes. Soil conditions (physical and chemical) are overlooked and it is quite possible that some sort of chemical toxicity is interacting with plant growth and causing the unusual 'eCO2 responses' that the team finds.

- 15 The reviewer is correct in that soil chemistry is altered at the points of CO<sub>2</sub> emission. However, we excluded those areas, instead focusing on the fertilization zone, which is away from those emission points, with unaffected soils, where tree canopies are exposed to the CO<sub>2</sub>, which has diffused in the atmosphere away from the emission points.
- 20 Minor comments: Define MASTER and ASO when first used Effect of canopy height model (selecting tallest pixel in each 1 m2 grid cell) will likely bias the biomass estimate to outliers, why not use percentiles, i.e. 90th, to avoid this artefact? Please discuss a bit more the sample size used to develop the plant traits models with AVIRIS.

We will define MASTER and ASO at first use. Outliers have already been removed as part of the preprocessing of the biomass estimate. We will clarify this point.

We will include information on the foliar trait model development in the next version of the manuscript.

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# Ecosystem responses to elevated CO<sub>2</sub> using airborne remote sensing at Mammoth Mountain, California

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- 15 **Abstract.** We present an exploratory study examining the use of airborne remote sensing observations to detect ecological responses to elevated CO<sub>2</sub> emissions from active volcanic systems. To evaluate these ecosystem responses, existing spectroscopic, thermal, and lidar data acquired over forest ecosystems on Mammoth Mountain volcano, California, were exploited, along with *in situ* measurements of <u>persistent</u> volcanic soil CO<sub>2</sub> fluxes. The
- 20 elevated CO<sub>2</sub> response was used to statistically model ecosystem structure, composition and function, evaluated via data products including biomass, plant foliar traits and vegetation indices, and evapotranspiration (ET). Using regression ensemble models, we found that soil CO<sub>2</sub> flux was a significant predictor for ecological variables, including <u>canopy greenness</u> (Normalized Vegetation Difference Index, -(NDVI<sub>7</sub>), canopy nitrogen, ET, and biomass. With
- 25 increasing CO<sub>2</sub>, we found a decrease in ET and an increase in canopy nitrogen, both consistent with theory, suggesting more water and nutrient use efficient canopies. However, we also observed a decrease in NDVI with increasing CO<sub>2</sub> (a mean NDVI of 0.27 at 200 g m<sup>2</sup> day<sup>1</sup> CO<sub>2</sub> reduced to a mean NDVI of 0.10 at 800 g m<sup>2</sup> day<sup>1</sup> CO<sub>2</sub>). This is inconsistent with theory; though consistent with increased efficiency of fewer leaves<del>nonetheless, with</del>
- 30 more efficient leaves, it may be that the trees needed fewer leaves. We found no changea decrease in aboveground biomass with increasing CO<sub>2</sub>, also inconsistent with theory; but, we did findalso found a decrease in biomass variance, pointing to a long-term homogenization of structure with elevated CO<sub>2</sub>, saw decreasing NDVI, increasing ET, increasing canopy nitrogen, and a decrease in biomass variance, pointing to trees with fewer, but more efficient
- 35 <u>leaves.</u> Additionally, the relationships between ecological variables changed with increasingly elevated (volcanically influenced) over non-volcanic "background" soil CO<sub>2</sub>

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fluxes, suggesting a shift in coupling/decoupling among ecosystem structure, composition, and function synergies. For example, ET and biomass were significantly correlated for areas without elevated  $CO_2$  flux, but decoupled with elevated  $CO_2$  flux. This study demonstrates that a) volcanic systems show great potential as a means to study the properties of ecosystems

5 and their responses to elevated CO<sub>2</sub> emissions and b) these ecosystem responses are measureablemeasurable using a suite of airborne remotely sensed data.

#### **1** Introduction

Terrestrial ecosystems have consistently taken up carbon over the past century, in excess or balancing losses due to deforestation and land use change, and this sink has grown with time (Le Quéré et al., 2016; Schimel et al., 2015). Much debate, however, has centred on the

- 5 drivers of this uptake. Suggested mechanisms include nitrogen deposition (Peterson & and Melillo, 1985), land use (Schimel, 1995), and the direct effects of carbon dioxide on plant growth (Norby et al., 2016). The last, which proposes that increased atmospheric CO<sub>2</sub> yields increased photosynthetic rates, is both the most probable and the most controversial. Although a multitude of experiments have shown positive photosynthetic responses to
- 10 increased CO<sub>2</sub> consistent with the observed growth in the terrestrial sink (Drake et al., 1997), many ecologists have argued that plant growth in intact ecosystems is limited by water, light or nutrients, rather than CO<sub>2</sub> (Körner, 2006; McGuire et al., 1995).

The Free-Air Carbon Enrichment (FACE) experiments, introduced in the 1990s, allow for

- 15 CO<sub>2</sub> fertilization of intact ecosystems by creating controlled fumigation conditions without the use of a growth chamber (Lewin et al., 1994). The FACE studies have been invaluable to our understanding of the CO<sub>2</sub> effect, which contributes to among the largest uncertainties in projections of Earth's climate. These studies have shown some consistent responses indicative of enhanced growth (Norby et al., 2016), as well as other physiological,
- 20 morphological and ecosystem consequences, but also suffer from several structural deficiencieslimitations. Perhaps most notably, only short-term study periods are feasible; the longest-running experiment spanned only a decade, while atmospheric CO<sub>2</sub> has been steadily rising for more than an order of magnitude longer than that duration. FACE can thus elucidate physiological responses to elevated CO<sub>2</sub>, but cannot unshroudand it is difficult to
- 25 <u>measure</u> slower processes like plant acclimation, shifts in species dominance induced by CO<sub>2</sub>, or other long-term mechanisms mediated by changes to soil organic matter and nutrients. Additionally, because FACE experiments are vastly expensive to construct and operate, they tend to be small in scale, limited in replicability, and homogeneous in species, soils and landscapes.
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The FACE studies have been invaluable to our understanding of the CO<sub>2</sub>-effect, which contributes to among the largest uncertainties in projections of Earth's climate. While it is true that they primarily assess CO<sub>2</sub>, we argue that the actual biggest limitation of FACE is the short durations — there has been no way to assess long term changes in ecosystems. This is

35 where the long-term localized emissions of volcanic CO<sub>2</sub> can play a game changing role in how to assess the long-term CO<sub>2</sub> effect on ecosystems.

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As a result of limited empirical evidence for the strength of CO<sub>2</sub> fertilization effects, global carbon cycle models disagree about the significance of their associated impacts. Some models show very large CO<sub>2</sub> effects, while others indicate a smaller or saturating effect (Kolby Smith et al., 2015). Because future predicted fossil carbon uptake is highly dependent

- 5 on the strength of the simulated CO<sub>2</sub> fertilization, any constraints on the long-term effect of elevated CO<sub>2</sub> on ecosystems would be valuable in reducing uncertainty in coupled carbonclimate models (Friedlingstein et al., 2014).
- Diffuse Persistent diffuse volcanic CO<sub>2</sub> emissions through soils result from the degassing of
   magma beneath volcanoes and offer a continuous natural experiment to study vegetation
   responses to elevated CO<sub>2</sub> that is expansive in both space and time. These surface discharges yield broad atmospheric enhancements that transport CO<sub>2</sub> downwind (Kerrick, 2001),
   resulting in swaths of variably affected plants whose periods of exposure can be over hundreds of years (Cook et al., 2001). Because volcanic CO<sub>2</sub> emissions are a vital part of the
- 15 global carbon cycle (Mason et al., 2017; Schwandner et al., 2017) and have been monitored worldwide for decades (Boudoire et al. 2017; Camarda et al., 2012; Perez et al., 2011; Gerlach, 1991), the rate and spatial distribution of these fluxes are well-understood due to an abundance of field surveys in many volcanic systems (e.g. Hernández et al., 1998; Cardellini et al., 2003; Werner & and Brantley, 2003; Giammanco et al., 2007; Lewicki et al., 2014a).
- 20 The "kill-zone" is the exact location where CO<sub>2</sub> is emitted from the soil—a property of the soil being altered by the emission. Although the spatial distributions of CO<sub>2</sub> emissions within tree kill areas have been well mapped (Pickles, et al., 2001; Werner & and Brantley, 2003; List, et al., 2005, and others), linking CO<sub>2</sub> measurements to vegetation responses along a spatially diffuse CO<sub>2</sub> degassing continuum (outside of the tree-kill zone) is a natural yet
- 25 underutilized opportunity for studying the effects of elevated CO<sub>2</sub> on plants (Schwandner et al., 2004). Furthermore, many CO<sub>2</sub> emissions in volcanic systems have been ongoing for decades or centuries, thus allowing for the observation of equilibrium, long-term ecosystem responses after transient and acclimational responses have passed.
- 30 While FACE experiments may demonstrate ecological responses to increased CO<sub>2</sub> at the outset of elevation, studies in volcanic basins can do the same on super-century scales. However, because volcanic emissions can affect entire landscapes differentially depending on the flow <u>dynamics</u> of the gas, they require new and innovative techniques for analysis. Remote sensing observations allow for detailed measurements across a wide spatial extent
- 35 that can be used to analyse ecological indicators of  $CO_2$  effects.

Here, we present an exploratory study examining the use of airborne remote sensing data to detect ecological responses to elevated volcanic CO<sub>2</sub> emissions. It is a fundamental principal

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of volcanology that all active volcanoes emit  $CO_2$  continuously during their entire life cycle. We We leveraged existing data over Mammoth Mountain, California – a much-studied volcano that has been passively emitting  $CO_2$  at high concentrations through faults and fissures on its flanks, measured systematically since a large earthquake swarm in 1989. and

- 5 their variability well documented by repeated CO<sub>2</sub> efflux mapping (Farrar et al., 1995; Lewicki et al., 2014b, b; Werner et al., 2014). Figure 1 shows that the elevated soil CO<sub>2</sub> fluxes, measured by the USGS over a span of two decades, far exceed the atmospheric CO<sub>2</sub> measured by a flux tower at the same site.
- 10 We developed a statistical framework for examining the relationships between field measurements of soil CO<sub>2</sub> emissions into the air below the forest canopy and a suite of remotely sensed ecological variables. In this investigation, we aim to: (i) evaluate the viability of using a passively degassing volcanic system to study the properties of ecosystems; (ii) assess the detectability of ecological responses to elevated soil CO<sub>2</sub>

15 emissions via airborne data alone; and (iii) present key lessons enabling future studies to extend our framework to other biomes. <u>This methodology can be applied to any site that is exposed to elevated CO<sub>2</sub></u>.

#### 2 Methods

## 2.1 Data

20 Airborne remote sensing data from multiple sources have been acquired over Mammoth Mountain, California, USA, providing a substantial means to assess ecosystem structure (products derived from lidar, such as canopy height and biomass), composition (products derived from spectral data, such as vegetation indices and plant foliar traits), and function (data products derived from thermal data, such as evapotranspiration). Figure 42 illustrates

25 several of the different products used in this study, highlighting the diversity of data sources and spatial resolutions.

Mammoth Mmountain is an upper montane forest ecosystem, characterised by abundant *Pinus contorta* (lodgepole pine<sub>7</sub>), and also by mature stands of *Abies magnifica* (red fir<sub>7</sub>).
30 *Pinus jeffreyi* (Jeffrey pine<sub>7</sub>), *Pinus albicaulis* (whitebark pine<sub>7</sub>), and *Juniperus occidentalis* (western juniper) (Potter, 1998). The elevation of our study areas ranged from 2700 to 2950 m. Tree-kill soils are immature High Sierra soils formed from granite, pumice, rhyolite, and obsidian parent materials (McGee & and Gerlach, 1998).

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#### 2.1.1 Ground measurements

We investigated soil CO<sub>2</sub> fluxes within five actively degassing areas on Mammoth Mountain documented by Werner et al. (2014) in 2011 and 2012, which represents a period of relatively high emissions. (up to 2000 g m<sup>-2</sup> day<sup>-1</sup> of CO<sub>2</sub>). As described by Werner et al. (2014), fluxes

- 5 were measured along fixed grid points using the accumulation chamber method (Rahn et al., 1996). In situ measurements were obtained using a West Systems® (Florence, Italy) portable fluxmeter equipped with a LI-COR820 infrared gas analyzeranalyser. Based on statistical analysis, Werner et al. (2014) found soil CO<sub>2</sub> fluxes measured within areas of volcanic CO<sub>2</sub> emissions to be significantly elevated over background areas that were dominated by soil
- 10 respiration of CO<sub>2</sub>. Maps of soil CO<sub>2</sub> flux were simulated from in-situ measurements at 1 m resolution using a sequential Gaussian simulation algorithm by these authors and we resampled their data to <u>the Airborne Visible/Infrared Imaging Spectrometer (AVIRIS)</u> resolution (13 m) using nearest <u>neighbourneighbour</u> resampling. Conventionally, studies of diffuse soil degassing of CO<sub>2</sub> on volcanoes have emphasized understanding of the modes,
- 15 locations, geometries, and changes in volcanic flank degassing for purposes of volcanologicalyulcanological research, hazard assessment, and monitoring. In many cases, volcanologists have focussed on areas associated with sufficient emissions of heat and CO<sub>2</sub> that vegetation has been killed off. In this study however, we focussed on vegetated areas where somewhat more mildly enhanced levels of volcanic CO<sub>2</sub> emissions into the forest
- 20 ecosystems might be beneficial for plant growth, rather than adverse. As such, we investigated zones and gradients *around* tree-kill areas, excluding areas that were barren or contained dead trees by filtering by fractional vegetation cover, where appropriate. <u>The tree-kill areas have local soil conditions that are not representative of the larger ecosystem.</u> In addition, because tree-kill areas on Mammoth Mountain are largely associated with "cold"
- CO<sub>2</sub> emissions, we completely avoided confounding influences of hydrothermal heat or acidic vapour emission on ecosystem response. Indeed, t<u>There is no significant H<sub>2</sub>S nor any SO<sub>2</sub> present at soil levels at this site, and CO<sub>2</sub> makes up ~99% of the gas by volume; see, for example, data in (Sorey et al 1998, Werner et al, 2014), and a number of papers on volcanic degassing at Mammoth Mountain (Lewicki 2006, 2007, 2008, 2012, 2014). The remaining
   1% is made up of N<sub>2</sub> and O<sub>2</sub>.
  </u>

The use of a high-spatial-resolution time-averaged (to limit the influence of varying meteorological conditions) map of canopy-level atmospheric CO<sub>2</sub> concentration would be most applicable to assess ecosystem response to elevated atmospheric CO<sub>2</sub> concentrations.

35 However, such maps are unavailable. We therefore took advantage of the extensive record of soil CO<sub>2</sub> fluxes available for Mammoth Mountain. Although the effects of elevated CO<sub>2</sub> in the soil may be difficult to de-convolve from elevated CO<sub>2</sub> in the atmosphere, we treat their effects uniformly. Implications of this are discussed below.

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SO<sub>2</sub> present at soil -99% of the gas by volume; see, for example, data in (Sorey et al 1998, Werner et al, 2014). and a number of papers on volcanic decassing at Mammoth Mountain (Lewicki 2006 2008, 2012, 2014). Nitrogen is measured in small quantities (-1%).

Although the AVIRIS, MASTER, and ASO lidarairborne datasets cover a wider region, only points with associated soil CO<sub>2</sub> flux measurements were used to derive our models. The CO<sub>2</sub> flux measurements were spatially resampled to match the resolution of the other datasets. which resulted in small estimations with low confidence along the edges. To avoid spurious

model fits, edge points with  $CO_2 < 5 \text{ gr} \text{m}^{-2} \text{-} d^{-1}$  were excluded, where the  $CO_2$  range is [0,2000] g-m<sup>-2</sup>-d<sup>-1</sup>. In the remainder of this manuscript, analysed points with elevated CO<sub>2</sub> flux will be referred to as eCO<sub>2</sub>.

## 2.1.2 AVIRIS

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- The Airborne Visible/Infrared Imaging Spectrometer (AVIRIS) Classic instrument acquires 15 data from 400 to 2500 nm in 224 contiguous spectral channels. AVIRIS imagery was acquired over Mammoth in October 2014; this flight was chosen from a number of possible surveys of the area to minimize snow cover, and also because of its temporal proximity to the eCO<sub>2</sub> ground measurements. The standard level 2 (L2) atmospherically corrected reflectance
- data (Thompson et al., 2015) was used (available from https://aviris.jpl.nasa.gov/), and the 20 data had a spatial resolution of 13 m. This data was collected as part of the NASA HyspIRI Preparatory Airborne Campaign.

## Vegetation indices

- 25 Vegetation indices are commonly used as an indicator of vegetation health and/or greenness. While many vegetation indices are related, they differ enough to be considered independent variables. E.g. some account for soil moisture, others weight plant greenness more heavily. This was an exploratory effort in investigating the effects of CO<sub>2</sub> on any measure of plant function, composition, and structure, and so we attempted to cover all avenues of 30
  - investigation. The following indices were derived from the AVIRIS spectral data:
    - The Normalized Difference Vegetation Index (NDVI)
    - Simple Ratio Index
    - Enhanced Vegetation Index
    - Red Edge Normalized Difference Vegetation Index ٠
    - Modified Red Edge Simple Ratio Index
      - Modified Red Edge Normalized Difference Vegetation Index

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• Vogelmann Red Edge Index 1

Each uses a ratio between narrow bands to represent vegetation health as a single index, and all are described more fully in (Thenkabail et  $al_{7a}$  2016).

## 5 Foliar traits

The chemical composition of plants affects light interactions, especially in the short-wave infrared (Singh et al., 2015). Therefore, imaging spectroscopy can be used to map key vegetation properties, especially those affecting carbon and nutrient interactions. Spectral features, derived from data such as AVIRIS, have been shown to correlate significantly with

10 certain chemicals and plant properties, such as carbon, nitrogen, nitrogen isotope 15, Leaf Mass per Area (LMA), cellulose, and acid digestible lignin (Singh et al<sub>7.1</sub> 2015). These properties are associated with photosynthesis, light-harvesting ability, nutrient fluxes, and can be used to characterise vegetation responses to disturbances or climate trends (Townsend et al., 2008).

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The data were first corrected for its bi-directional reflectance distribution function (BRDF), using the Ross-Thick BRDF model with a quadratic volumetric scattering term (Roujean et alr., 1992; Lucht et alr., 2000). In situ vegetation chemical measurements, along with propagated uncertainties, were used to derive partial least squares regression models for each

20 trait. Since these equations were derived in the nearby area of the Sierra Nevada Mountains (\*\*more info here), these equations were applied to the BRDF-corrected AVIRIS data used in this study.

Infeasible negative numbers were removed for the modelling.

## 25 2.1.3 MASTER

The MODIS/ASTER (MASTER) airborne simulator acquires data in 50 channels between  $0.4 - 13 \mu m$ . We utilized the <u>5five</u> thermal channels ( $10 - 13 \mu m$ ), which had been processed to Level 2 (available from https://master.jpl.nasa.gov/). MASTER data were acquired in November 2013, with a <u>50m50 m</u> spatial resolution.

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## Land Surface Temperature

The five thermal bands from MASTER were used to calculate Land Surface Temperature (LST) in a standard Level 2 product. The acquired data were processed to radiance using MODTRAN 5.2 for the atmospheric correction, along with a water vapour scaling method

35 (Tonooka, 2005). The Temperature Emissivity Separation (TES) algorithm was then used to derive LST and spectral emissivity (Gillespie et al., 1998).

The MASTER data are at coarser spatial resolution (50 m) compared to the other datasets (e.g., the working resolution for reprojection is the AVIRIS resolution of 13 m). An ideal dataset would have MASTER acquired at <u>13m13 m</u>, or similar (~10 m; i.e., the scale of an individual tree canopy), but in order to build a comparable dataset for this analysis, we used

- 5 two resampling methods: the standard nearest neighbour resampling; and a statistically principled method proposed in Ma et al. (2018). The statistical model proposed by Ma et al. (2018) represented LST as a combination of low-dimensional random effects linked with basis functions and a Gaussian graphical model (also called Gaussian Markov random field). As demonstrated by the authorsMa et al. (2018), this model provides a flexible and
- 10 computationally efficient way to characterize potentially complex and nonstationary spatial variability. The parameters of the underlying statistical model were fitted to MASTER LST and ET data at 50 m resolution, using maximum likelihood estimation via an Expectation-Maximization (EM) algorithm. The resampled data at 13 m spatial resolution were then generated via conditional statistical simulation in which we required that when aggregated
- 15 back to the original coarse resolution, the resampled data matched the original MASTER data exactly.

#### *Evapotranspiration*

Evapotranspiration (ET) is the key water variable in ecosystem functioning, indicating plant water use and loss (Fisher et al., 2017). In this study, ET was calculated using the PT-JPL retrieval (Fisher et al., 2008), which partitions ET into canopy transpiration, soil evaporation, and interception evaporation by transforming potential ET (Priestley & and Taylor, 1972) into actual ET using ecophysiological constraints. The ECOSTRESS ET retrieval system was used to incorporate MASTER LST as the thermal input (Fisher et al., 2015); additional

25 ancillary data were incorporated from MODIS and Landsat to constrain meteorological and phenological controls on ET (Verma et al., 2016; Famiglietti et al., 2018; Ryu et al., 2011; Kobayashi et al., 2008). The final ET product used here was only the canopy transpiration component (referred to as ET throughout), as our analytical interest lies only in the vegetation response to eCO<sub>2</sub>.

## 30 2.1.4 ASO

The Airborne Snow Observatory (ASO, http://aso.jpl.nasa.gov) is a coupled lidar (Riegl Q1560) and spectrometer (CASI-1500) mounted on a King Air A90 aircraft, and was originally developed to monitor snow in the mountains for water resource management (Painter et al., 2016). The Riegl Q1560 is a dual scanning lidar with two 1064 nm laser

35 sources; each scanner is tilted in the along-track direction by ±8° and the cross-track direction by ±14° for enhanced retrieval of vertical surfaces. On June 27, 2017 ASO surveyed Mammoth Mountain, retrieving comprehensive lidar point cloud data at a mean of 7.8 pt. m<sup>-2</sup>

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(max. value ~60 pt- m-2). Riegl RiPROCESS software was then used to a) extract point cloud data from raw waveforms (RiANALYZE) using the RiMTA Multiple Time Around algorithm and the RLMS Simple Classification Procedure for classification (SCP1), b) georeference the point cloud (RiWORLD), and c) export the point cloud to LAS 1.2 in UTM

5 projection (RiWORLD).

#### Digital Terrain Model

The ASO lidar point cloud data were filtered to remove outliers by applying an elevation filter to eliminate points that exceed  $\pm 100$  m from a baseline digital terrain model (DTM) that

was obtained from the USGS (United States Geological Survey). The ASO data processing 10 chain includes the identification of ground and off-ground points using the Multiscale Curvature Classification algorithm (Evans & and Hudak, 2007) and the calculation of a DTM  $(3m3 m \times 3m3 m)$  that corresponds to the bare soil surface as interpolated from the lidar points classified as ground. Any data voids were then in-filled using search windows that

15 were centred on each void pixel.

#### Slope and Aspect

The slope (steepness) and aspect (direction) were derived directly from the DTM with the terrain analysis processing tool provided by QGIS. These geo-algorithms use a first-order

20 derivative estimation to calculate the slope angle for each pixel in degrees relative to the horizontal plane and the slope exposition in degrees counter-clockwise from north. Aspect was processed to account for circular angles, by considering:

$$K1 = \sin(\alpha + (90 - d)) + 1$$
(1)  

$$K2 = \cos(d - \alpha) + 1$$
(2)

$$K2 = \cos(d - \alpha) + 1$$

25 where  $\alpha$  is the aspect derived from the DTM as described above, and d is the prevailing wind direction. In the absence of local data, we assumed the prevailing wind direction to be  $270^{\circ}$ (e.g. Anderson & and Farrar, 2001; Lewicki et al., 2008; Lewicki & and Hilley, 2014). (Note, the results presented below were not sensitive to this assumption.)

30 Canopy Height and Biomass

The aboveground biomass (AGB) map (30 m x 30 m) was calculated by integrating ASO lidar measurements on forest structure and field inventory data into an allometric equation developed by (Garcia et al., (2017):

$$AGB = 11.50 \times MCH^{1.20} \times FC^{0.83}$$

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(3)

35 where MCH and FC are lidar-derived maps of mean canopy height and fractional cover, respectively. Eq. 3 was calibrated using AGB reference values derived from 69 field

inventory plots located in the Stanislaus National Forest and Yosemite National Park, Sierra Nevada, California, To compute the lidar-derived maps, we first normalized the ASO lidar point cloud to calculate the effective height of vegetation by removing the effect of topography using the DTM described here above. Then, we used the normalized point cloud

- 5 to calculate a canopy height model (CHM, 1m x 1m) by selecting the highest lidar point within each grid cell. -Finally, the MCH was calculated by averaging the CHM within each 30 m cell, whereas the FCC was computed as the ratio of grid cells covered by vegetation (i.e. MCH>2 m) to the total number of cells. Note that we defined both MCH and FC with a grid cell size of 30 m in order to agree with the size of the field samples (Garcia et al., 2017).
- 10 We assumed that Eq. 3 was transferable to our study site because the calibration plots are located only 80 km apart and they are both populated by vegetation of the upper montane and subalpine biotic zones.

#### 2.1.5 Compiling the Dataset

- 15 The data were first processed to create derived products, and then geolocated to the AVIRIS native resolution of 13 m. That is, for each AVIRIS pixel, the other datasets were resampled and reprojected so that every pixel is associated with a vector of remotely sensed and derived values. Datasets with finer resolution (soil CO<sub>2</sub> flux and lidar) were averaged using the nearest neighbour principle. Derived products with coarser resolution (fractional cover,
- 20 biomass, and evapotranspiration) were resampled using nearest neighbour resampling (e.g. the same biomass value may cover multiple AVIRIS pixels). Because its pixels were the largest, ET was also resampled using a statistically based method, described above in Section 2.1.3. We note that although the downscaling approach is robust and statistically sound, we acknowledge that our statistical estimates involving ET will include some uncertainty due to 25
- spatial resolution.

Once all pixels had been resampled, we had a total of 5520 data points. For certain experiments we found it necessary to threshold by fractional vegetation cover (FC>0.7; n=55), although the full dataset was used wherever possible.

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The dates of acquisition also differed across datasets. The soil CO<sub>2</sub> flux datasets used in this study were measured during a peak in  $CO_2$  emissions (Werner et al., 2014), and this peak in emissions which is thought to affect future plant growth after the fact. However, we are observing a snap shot of vegetation function within a zone small enough to be influenced by

35 the same meteorological inputs, and our models have accounted for confounding factors such as slope, elevation, and aspect. Therefore, we considered measurements to be relative on a spatial scale, by comparing neighbouring pixels. The topographic confounders and the

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fractional cover are derived from the lidar data acquired 4<u>four</u> years after the MASTER data; however, we do not expect changes in the terrain during that time period, and tree presence is unlikely to have changed significantly.

#### 2.2 Statistical Modelling

- 5 The variables assessed included: vegetation indices; plant foliar traits; evapotranspiration; canopy height; and, biomass. Given this combination of variables, we tested whether changes in eCO<sub>2</sub> were associated with significant changes in vegetation. We performed a series of multiple linear regressions using eCO<sub>2</sub> as a predictor of various vegetation variables; in particular, regression ensembles build <u>ensemblescollections</u> of linear regression models,
- 10 utilizing different predictor combinations, including multiplication of predictor variables. To control for confounding variables including elevation, slope, and aspect<sub>7</sub> (which are topographic proxies for temperature, moisture, and light<u>, respectively</u>), we included them as predictors in the model. Then, the regression coefficient estimate for eCO<sub>2</sub> is an estimate of the change in the response variable due to a change in eCO<sub>2</sub>, holding all other variables in the
- 15 model (the confounders) constant. Random forests were investigated, and found to produce similar results. For ease of interpretation, we present here the results of the linear regression ensembles.

Fractional vegetation cover (FC; derived from the lidar) was considered a proxy for

- 20 vegetation presence. The geometric variables elevation, slope, and aspect were also derived from the lidar point cloud, as described above. Figure 23 illustrates the stratified behaviour of NDVI as coloured by the four confounding variables. There is a particularly clear separation for fractional cover, which reinforces an expected result: eCO<sub>2</sub> had negligible effect on vegetation indices and other variables over bare ground, but showed higher impacts on fully
- 25 vegetated pixels. Therefore, we model each vegetation variable, V, as

$$V = b_1 C + b_2 F + b_3 S + b_4 A + b_5 E + f(C, F, S, A, E) + \varepsilon$$
(4)

where *C* is the elevated soil CO<sub>2</sub> flux, *F* is the fractional vegetation cover, *S* is the slope, *A* is 30 the aspect, *E* is the elevation, and  $\varepsilon \sim N(0, \sigma^2)$  is random error. The function  $f(\cdot)$  describes relationships between the predictor variables, which for this model is limited to the first order interactions:

$$f(C, F, S, A, E) = b_6 C \cdot F + b_7 C \cdot S + b_8 C \cdot A + b_9 C \cdot E + b_{10} F \cdot S + \cdots$$
(5)

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Our hypothesis is  $H_A: b_1 \neq 0$ , that is, that the effect of eCO<sub>2</sub> on vegetation variable V

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is different from zero. Our null hypothesis is then  $H_{0:} b_1 = 0$ .

Certain other confounding variables may affect the modelled relationships. The following scenarios and/or variables were also tested as confounders, but did not affect the model

5 outcome: pixel position; site number; and species (plant species were estimated by performing an unsupervised classification on the AVIRIS data). The eCO<sub>2</sub> dataset was also shifted to simulate winds and atmospheric pressure (Ogretim et al., 2013). This did not have an impact on the results.

- 10 Additionally, diurnal patterns of mountain slope air flows may dilute and enrich the bulk air mass the trees are exposed to with respect to CO<sub>2</sub> concentrations (Pypker et al., 2007). If these air flow patterns are strong, they may drain the local CO<sub>2</sub> enhancement during morning and evening hours, when these flow events are usually strongest. However, due to the constant nature of these localized enhanced emissions, the gradient, if it was diluted by such
- 15 effects, re-establishes itself during calmer daytime and night-time hours, as is evident by the <u>"volcanic diffuse CO<sub>2</sub> emission" signal being detectable from airborne in-situ measurements</u> above the investigated sites as well (Gerlach et al. 1999).

The eCO<sub>2</sub> dataset was also shifted to simulate winds and atmospheric pressure (Ogretim, et al., 2013). This did not have an impact on the results.

When evaluating the dynamics between different variables, it is assumed that the study from which our ground measurements were derived (Werner et al., 2014), covered most of the known  $CO_2$  diffuse emission areas, and so the remainder of the scene exists as a control. The

25 control pixels were also thresholded according to the range of the confounding variables found for the eCO<sub>2</sub> points. Therefore, we considered only control points with elevation, slope, and aspect values, respectively, between 2700 and 2950 m, less than  $350^{\circ}$ , and less than  $350^{\circ}$ .

### **3** Statistical Estimation

- 30 Although the models were run for 42 explanatory variables (including additional vegetation indices, foliar traits, and other vegetation descriptors), for the sake of brevity we only present the best performing variables (traits with significant p-values are shown, and for all other variables, those with significant p-values and R<sup>2</sup>>0.5). For the variables shown in Table 2, the p-value of the eCO<sub>2</sub> term,  $b_1$ , was for each model <0.05, and in most cases <<0.05. The most
- 35 significant predictor was determined by ordering terms by p-values.

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As the confounding variables are expected to drive the behaviour of ecosystem properties, a reduced  $eCO_2$  "rank" (in terms of p-value significance) does not negate the impact of  $eCO_2$  in the models; in fact, each ecosystem variable was strongly influenced by increasing  $eCO_2$ , given the low p-values for the  $eCO_2$  coefficient in each model. The rank of each predictor

5 variable is given in Table 3. Since multiplicative terms are allowed, two terms in a single ranking column (say, slope and fractional cover) means that the multiplication between the two terms is the term with the lowest p-value. To reduce the complexity of the table, each variable is listed only once, in order of first appearance, whether singly or as a product.

## 4 Results

#### 10 4.1 Structure: Canopy Height and Biomass

Canopy height and biomass were <u>well-accurately</u> modelled <u>with high R<sup>2</sup></u>, as seen in Table 2 and Figure <u>34</u>, although eCO<sub>2</sub> was the least significant predictor. In each case, eCO<sub>2</sub> was still regarded as statistically significant, but had lower predictive power than the topographic variables.

15

Figure 45 shows the predictor variable eCO<sub>2</sub> against the predicted biomass. There is variability at low eCO<sub>2</sub> levels, but overall a small decrease in biomass with increasing eCO<sub>2</sub>. This decrease appears to saturate, and is better fit by a logarithmic function, however, given that interactions between terms in the model is allowed, we do not necessarily expect a linear

20 fit, since the eCO<sub>2</sub> contribution to the model may be multiplied by other confounding variables. There is also a decrease in biomass variance. In other words, trees exposed to higher eCO<sub>2</sub> are more similar.

#### 4.2 Composition: Vegetation Indices and Foliar traits

The performance of different vegetation indices and foliar traits varied. NDVI was best
 modelled, with an (R<sup>2</sup> of = 0.68), and with eCO<sub>2</sub> as the most significant predictor (p-value of 1e-12). In general, the indices were better modelled than the traits.

Figure  $\frac{56}{50}$  shows the predicted model for NDVI (a) and the canopy nitrogen concentration trait (b) against the eCO<sub>2</sub> predictor variable. Modelled NDVI decreases with increasing eCO<sub>2</sub>, and there is a decrease in variance with increasing eCO<sub>2</sub>. The modelled canopy nitrogen

30 concentration trait increases with increasing eCO<sub>2</sub>.

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#### 4.3 Function: Evapotranspiration

Canopy transpiration was relatively well represented by the eCO<sub>2</sub> model with an  $R^2 = 0.55$ . For comparison, total ET was not well represented by the eCO<sub>2</sub> model ( $R^2 = 0.23$ ), which is sensible, as eCO<sub>2</sub> is expected to affect only plant transpiration and not soil evaporation. eCO<sub>2</sub>

- 5 was the second most significant predictor, with fractional vegetation cover the most significant. Given that MASTER data were originally acquired at a much coarser resolution (50 m) than the eCO<sub>2</sub> ground data (1 m), and that both were resampled to 13 m resolution for the overall consistent analysis, there may have been error introduced due to the resampling. This effect is seen by the much lower model fit with the statistical resampling, although the
- 10 predicted models follow the same trend. In the remainder of the manuscript, references to ET refer to the data resampled using nearest neighbour resampling. Figure 67 shows the ET predicted by the model for the predictor variable eCO<sub>2</sub>. There is a decrease in ET for increasing eCO<sub>2</sub>, along with a decrease in variance.

#### 4.4 Ecosystem synergies

- 15 Given that many of the vegetation indices and traits are only appropriate in the presence of vegetation, a fractional cover threshold of 0.7 was used for the eCO<sub>2</sub> sample, for the sake of evaluating the dynamics between modelled variables. With this threshold, only 55 data points remained, and so the sample size is too small to make claims of statistical significance. Therefore, we present the following results as interesting observations that may inform future
- 20 data acquisition.
  - Figure 78 shows the dynamics between variables in the entire scene (i.e., non-elevated, background soil CO<sub>2</sub>) versus the points with eCO<sub>2</sub> measurements. It is important to note that in each sub-figure, independent data sources are used to avoid showing intrinsically
- 25 correlated datasets. Fractional cover and biomass are derived from the ASO lidar data; the vegetation trait data and foliar traits are derived from AVIRIS imagery; and ET is derived from MASTER data. In this case, the variables shown are directly as observed (or derived directly from the data source).
- 30 We observed interesting dynamics between ecosystem variables, suggesting great potential for future research. In the eCO<sub>2</sub> subset, NDVI was, on average, lower than that observed for the same fractional cover in the control dataset (Figure 8 a). This is consistent with the model illustration of decreased greenness for increasing eCO<sub>2</sub>. Similarly, ET was lower in the eCO<sub>2</sub> subset for pixels with the same NDVI observed in the control, showing a greater degree of
- 35 stress even when plants have the same greenness (Figure 8 b). In addition, the strong linear relationship between ET and NDVI appears to break down for the points affected by eCO<sub>2</sub>.

Canopy nitrogen in the eCO<sub>2</sub> subset increased with fractional cover, unlike the control which remained flat, which again mimics the modelled data findings (Figure 8 c). ET was lower in the eCO<sub>2</sub> subset for the same biomass, which implies that plants are doubly affected by the

5 enhanced  $CO_2$  – the biomass decreases with increasing eCO<sub>2</sub>, and the ET decreases further with decreasing biomass (Figure 8 d). Again, the strong linear relationship between ET and biomass breaks down for those points affected by eCO<sub>2</sub>. These findings suggest complex relationships between ecosystem parameters in their response to increasing eCO<sub>2</sub>.

#### 5. Discussion

- 10 Using airborne remotely sensed ecosystem properties against a ground measured database of eCO<sub>2</sub> (volcanic excess CO<sub>2</sub> emanating into the forest canopy through the soil), we evaluated the effects of increasing eCO<sub>2</sub> on plant structure, function, and composition. Our aims were to: (i) evaluate whether a passively degassing volcanic system is a viable means to study properties of ecosystems; (ii) determine if ecosystem variables are adequately detected using
- 15 airborne data; and (iii) present key lessons learnt that can enable similar studies over different biomes.

This study has provided initial observations of ecological responses to eCO<sub>2</sub> that are measurable from airborne data. We found that: a) eCO<sub>2</sub> was a significant predictor in
regression ensemble models of ecosystem variables, and b) there were visual differences between the sites of increased eCO<sub>2</sub> and the background image. This work also demonstrates that an active volcanic system is a viable way in which to study the CO<sub>2</sub> effect on ecosystems.

- 25 The regression ensemble model showed that eCO<sub>2</sub> was a significant predictor for two structural variables (canopy height and biomass), nine composition variables (6 vegetation indices, 3 foliar traits), and a function variable (ET). Therefore, as hypothesised hypothesized, eCO<sub>2</sub> affects ecosystems in structure, composition, and function, all of which are detectable both with airborne observations as well as within a volcanically-derived eCO<sub>2</sub> system.
- 30 Further evaluation of the model showed that both canopy height and biomass decreased with increasing eCO<sub>2</sub>; the vegetation indices decrease with increasing eCO<sub>2</sub>; canopy nitrogen concentration increases; LMA decreases; Carbon decreases; and ET decreases.

Some of these observations contrasted with results found in other published studies, while
 others agreed. For instance, our study found a decrease in NDVI with increasing eCO<sub>2</sub>, which correlates to the multispectral satellite findings of Rouse et al., (2010) and Cholathat et al.,

(2011). In some cases, the decrease <u>others have found</u> can be explained by the tree-kill effect, where vegetation is removed. However, by accounting for fractional cover in our models, we have shown that NDVI decreases independently from fractional cover (see in Figure 78). This shows that, regardless of whether the number of trees changes, the greenness of individual

5 trees is reduced. This finding is in direct contrast with the CO<sub>2</sub> fertilization hypothesis which states that rising CO<sub>2</sub> has a positive effect on plant growth and productivity due to increased availability of carbon, and which has been shown using field data (Huang et al., 2007; Zhu et al., 2016). However, this decrease in NDVI could also be explained by a reduction in leaves, rather than a reduction in leaf health, due to more efficient leaves (e.g., higher nutrient

10 concentration, more water use efficient in water use).

The decrease in canopy height and biomass agrees with the tree-ring study done by (Biondi &and Fessenden, (1999), which also found slower Lodgepole Pine growth rates in high  $CO_2$ emission areas on Mammoth Mountain. However, a study by (Smith et al., (2013) found an

15 increase in biomass in the mixed-species temperate forest FACE experiment. In that experiment, there was large variation between and within species, and the experiment was limited to 4<u>four</u> years. Perhaps a long-term species composition shift due to eCO<sub>2</sub> was the cause of the change in biomass in our study, but we do not have individual tree species-level data to support this hypothesis.

20

Our model showed an increase in canopy nitrogen, which could indicate species selection or individual plant optimization, given the decrease in NDVI, biomass, and ET. Canopy nitrogen is associated with plant's investment in photosynthesis (Singh et al., 2015). We also found an increase in canopy nitrogen relative to fractional cover, showing that the change in

- 25 nitrogen was not impacted by an increase in overall vegetation for those sites (Figure 78). Tercek et al. (2008) noted that <u>Dichanthelium lanuginosum (hot springs Paniegrasspanic grass)</u> in Yellowstone had made physiological adjustments to photosynthetic enzymes in response to long-term exposure to CO<sub>2</sub>, and a study of ice cores showed a 40% decrease in stomatal density over the last 200 years, which paralleled an increase in global CO<sub>2</sub>
- 30 (Woodward, 1987). However, Sharma & Milliams (2009) evaluated vegetation naturally exposed to CO<sub>2</sub> in Yellowstone National Park, and found reduced nitrogen at a leaf level in <u>Pinus contortus</u> (Lodgepole <u>Pines,Pine</u>), and increased nitrogen at a leaf level for <u>Linaria dalmatica</u> (Dalmation Toadflax<del>, ; an invasive, non-native herb).</del> Once again, the species-level differences highlight the need for remote sensing analysis over areas that encompass wide
- 35 species variation, in order to understand overall trends.

Kimball<sub>7</sub> et al. (1998) found a slight increase in ET in a FACE experiment over cotton fields, but that increase was within the error of the ET estimation, and so was not deemed

statistically significant. In contrast, (Nendel<sub>7</sub> et al., (2009) found a decrease in ET, and an increase in dry above-ground biomass over a FACE crop rotation experiment. In this study, we found a decrease in ET. In addition, we found a decrease in ET relative to both NDVI and biomass, when comparing the points affected by  $eCO_2$  to those unaffected points in the

5 surrounding area. The unaffected sites showed a positive linear relationship between ET and both NDVI and biomass, which appeared to break down for points affected by  $eCO_2$  in both relationships.

The combination of lower NDVI, higher canopy nitrogen, and higher ET suggests a canopy
 that uses less water with rising CO<sub>2</sub>CO<sub>2</sub>, resulting in higher water use efficiency, with a nutrient rich canopy. Since leaves are stronger and more efficient, fewer are required for photosynthesis. While biomass increased slightly, the more obvious change was the decrease in the variance of biomass, which points to alignment to more similar trees with elevated CO<sub>2</sub>.

15

High fluxes of CO<sub>2</sub> through soils <u>in "kill zones"</u> on Mammoth Mountain have likely impacted forest ecosystems through oxygen deprivation in soil pore space, inhibition of root respiration and soil acidification (Farrar et al., 1995; Qi et al., 1994; McGee <u>& and</u> Gerlach, 1998). Since we used soil CO<sub>2</sub> flux as the predictor variable in the model, some of the observed ecosystem

- 20 responses may therefore be due to the effects of high concentrations of CO<sub>2</sub> on the soil environment or some combination of soil and atmospheric effects. <u>However, by using fractional cover as an input to the model, and excluding the "kill zones" altogether to derive Figure 8, we are focusing on the CO<sub>2</sub> gradient over vegetated areas around these zones, that are less-unlikely to be due to affected by soil acidification. The Mammoth Mountain soil CO<sub>2</sub></u>
- 25 flux dataset does, however, provide a record of CO<sub>2</sub> emissions that is more stable in space and time than measurements of atmospheric CO<sub>2</sub> concentrations. In particular, forest canopies will through time be exposed to eCO<sub>2</sub> at highly variable levels, because <u>the</u> <u>originally mostly invariant</u> eCO<sub>2</sub> once emitted through the soil into the sub-canopy atmosphere, is subject to highly variable dispersion from thermal and wind disturbances at
- 30 minutes, diurnal, and seasonal scales (Staebler <u>& and</u> Fitzjarrald, 2004). In-canopy concentration measurements of eCO<sub>2</sub> will therefore be highly variable, and especially if conducted instantaneously, may not be representative of the long-term relative exposure strength in the canopy.
- 35 Vegetation at this site is also responding to the partial pressure of CO<sub>2</sub> in the atmosphere, among other gases. A response above the asymptote of the <u>Nnet photosynthetic rate versus</u> internal CO<sub>2</sub> partial pressure (A-Ci curve) would result in very little vegetation response to the partial pressures (Tissue, Griffin, and Ball 1999). However, the partial pressure even at

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elevated molar concentration at Mammoth are about 60% of those at sea level. The fact that we see systematic ecosystem effects suggests that elevation is not on the flat part of the A-Ci curve. In other words, even if elevation were to reduce the CO<sub>2</sub> effect, we still are seeing strong CO<sub>2</sub> effects regardless, highlighting just how important and strong of a response we

5 are able to detect.

We will clarify that the effects should not necessarily be given a subjective description of 'negative'; rather, it is important to note that the CO<sub>2</sub> fertilization effect is unlikely to continue indefinitely, particularly at the same rates that FACE studies have shown only in the

- 10 <u>short-term. All other experiments have been unable to show long-term effects. Our study</u> <u>suggests that over the scale of decades, some of these hypothesized greening or biomass</u> increases may not be sustainable. Other results, such as an increase in canopy nitrogen with increasing CO<sub>2</sub>, do seem to remain consistent with our study, however.
- 15 This exploratory study leveraged existing data acquired over Mammoth Mountain. We used ASO lidar, AVIRIS, and MASTER data to derive products that describe ecosystem structure, composition, and function, and used field eCO<sub>2</sub> measurements to show that elevated CO<sub>2</sub> was a significant predictor of ecosystem variables, including vegetation indices, plant foliar traits, biomass, and evapotranspiration. While our study has shown the promise of airborne remote
- 20 sensing in detecting measurable ecosystem changes in forest ecosystems on and around a CO<sub>2</sub>-emitting volcanic system, it was also completed using an existing ad-hoc collection of data. The nature of the collection of data sources enabled us to understand the details of the data characteristics necessary for future studies.

## 25 Key lessons learnt from this study include:

- 1. Future campaigns should acquire all data at the same or similar resolution, at individual tree-scale
- 2.<u>1.More than 55 vegetated tree points are necessary in order to draw meaningful conclusions regarding the dynamics between variables</u>
- 30 <u>3.1.Combining lidar and spectral data across a range of wavelengths yielded a more complete view than using any one data source alone.</u>

While this study is useful for showing the benefit of both a passively emitting volcanic system and airborne data for evaluating the ecosystem response to eCO<sub>2</sub>, we anticipate that

35 more meaningful results would be obtained with all datasets acquired simultaneously, at the same resolution. ET in particular varies over short time periods due to the influence of meteorological inputs, and so multi-temporal acquisitions would provide a better overview of the ecosystem function. Other possible factors could affect this very complex system, some

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of which have been discussed previously, including pH, oxidative stress, water/nutrient availability, extreme climate events, and plant vigour. More fieldwork and test sites would be needed to rule out many of these factors. Other data, such as photosynthesis, may also add to future analysis. We note that this study was exploratory, rather than definitive, and that this

5 study was intended to identify both potential signals as well as design elements for further study.

## 6. Conclusions

This exploratory study used airborne remote sensing data, coupled with ground measurements of soil  $CO_2$  flux on a forested volcano, to derive relationships between rising

- 10 CO<sub>2</sub> emissions and ecosystem structure, function, and composition metrics. We have shown that passively emitting volcanic systems are viable environments in which to study CO<sub>2</sub> impacts on ecosystems, with eCO<sub>2</sub> the most significant predictor in regression ensemble models of several ecological variables, including NDVI, canopy nitrogen concentration, ET, and biomass. When comparing differences between vegetation parameters affected by eCO<sub>2</sub>
- 15 and those estimated over the background scene, we found contrasting patterns and dynamics between ecological variables, showing that a combination of different remote sensing platforms is capable of providing a comprehensive view of ecosystem responses to <u>long-term</u> <u>elevated</u> volcanic CO<sub>2</sub>.

20 Key lessons learnt from this study include:

- 1. Future campaigns should acquire all data at the same or similar resolution, at individual tree-scale
- 2. <u>MWell more than 55 vegetated tree points are necessary in order to draw meaningful conclusions regarding the dynamics between variables in Mammoth Mountain (which has one dominant tree species). The number of required points in other environments</u>
- has one dominant tree species). The number of required points in other environments will vary according to ecosystem complexity, and will likely far exceed this number.
- 3. Combining lidar and spectral data across a range of wavelengths yielded a more complete view than using any one data source alone.

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0 CO<sub>2</sub> Flux (g m<sup>-2</sup> day<sup>-1</sup>) 2000 0

Biomass (Mg ha<sup>-1</sup>) 200 0 Transpiration (W m<sup>-2</sup>) 120 0

NDVI (unitless)

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**Figure 2:** A wealth of remotely sensed imagery has been acquired over Mammoth <u>Mmountain.</u> Some data products used in this study include (a) maps of soil CO<sub>2</sub> flux simulated based on accumulation chamber measurements, shown overlain on aerial

5 RGB image; (b) above-ground biomass derived from Airborne Snow Observatory (ASO) lidar; (c) evapotranspiration derived from the MODIS/ASTER (MASTER) airborne simulator; and (d) Normalized Difference Vegetation Index (NDVI) derived from Airborne Visible/Infrared Imaging Spectrometer (AVIRIS image).

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Data source	Year	Original	Resampling method		Formatted: Font: Bold, No underline
	acquired	resolution			
Soil CO <sub>2</sub> flux	2011-2012	1 m	Nearest neighbour		
Canopy height	2017	1 m	Nearest neighbour		
Vegetation indices	2014	13 m	Original resolution		
Foliar traits	2014	13 m	Original resolution		
Fractional cover	2017	30 m	Nearest neighbour		
Biomass	2017	30 m	Nearest neighbour		
Evapotranspiration	2013	50 m	Nearest neighbour;		
			Ma et al. (2018)		
			resampling		

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Table 2: The best performing vegetation indices $(VI)$ and traits are shown with the predictive significance of $eCO_2$ in
the model, and with their correlation with a regression ensemble that included elevation, slope, aspect, and fractional
cover as confounding variables (n=5520). The most significant predictor was determined by ordering terms by p-
values.

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Variable	Most	Estimate	Standard	p-	Model R <sup>2</sup>
	significant predictor term	for eCO <sub>2</sub> coefficie nt	error for eCO <sub>2</sub> coefficient	valu e for the eCO 2 term	
Structure:					
Canopy height	Slope, FC	6e-3	1e-3	4e-6	0.92
Biomass	FC	1e-1	2e-2	5e-6	0.83
Composition (Vegetation indices):					
Normalized Difference Vegetation Index (NDVI)	eCO <sub>2</sub>	-6e-5	8e-6	1e- 12	0.68
Red Edge Normalized Difference VI	eCO <sub>2</sub>	-3e-5	6e-6	1e-9	0.67
Modified Red Edge Normalized Difference VI	eCO <sub>2</sub>	-7e-5	6e-6	2e- 27	0.65
Vogelmann Red Edge Index 1	eCO <sub>2</sub>	-3e-5	1e-5	2e-3	0.64
Enhanced Vegetation Index	eCO <sub>2</sub>	-1e-4	1e-5	2e- 22	0.62
Modified Red Edge Simple Ratio Index	FC	-1e-4	2e-5	5e- 10	0.61
<i>Composition (Plant foliar traits):</i>					
Trait: Canopy nitrogen concentration	Intercept	-8e-3	1e-3	2e-7	0.45
Trait: Carbon	FC	3e-2	5e-3	5e-9	0.45
Trait: Leaf Mass per Area (LMA)	Aspect	3e-1	1e-1	6e-2	0.40

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Function:

Evapotranspiration	FC	-8e-3	1e-3	5e-	0.55
(nearest neighbour)				16	
Evapotranspiration	FC	-3e-4	2e-3	8e-1	0.38
(statistical resampling)					

Variable	Ordered predictor terms (from most to least significant)						
<u>Structure:</u>							
<u>Canopy height</u>	<u>Slope,</u> FC	Intercept	Elevation	<u>eCO<sub>2</sub></u>	Aspect		
<b>Biomass</b>	<u>FC</u>	Elevation	<u>Slope</u>	Intercept	<u>eCO<sub>2</sub></u>	Aspect	
<u>Composition</u> (Vegetation indices):							
<u>Normalized</u> <u>Difference</u> <u>Vegetation Index</u> <u>(NDVI)</u>	<u>eCO2</u>	<u>FC</u>	<u>Slope</u>	<u>Aspect</u>	<u>Elevation</u>	Intercept	
<u>Red Edge</u> <u>Normalized</u> Difference VI	<u>eCO<sub>2</sub>, FC</u>	<u>Aspect</u>	<u>Slope</u>	Intercept	Elevation		
<u>Modified Red</u> <u>Edge</u> <u>Normalized</u> Difference VI	<u>eCO<sub>2</sub></u>	<u>FC,</u> <u>Elevation</u>	Intercept	Aspect	<u>Slope</u>		

<u>Vogelmann Red</u> Edge Index 1	<u>eCO<sub>2</sub>, FC</u>	Intercept	<u>Aspect</u>	Elevation	<u>Slope</u>	
<u>Enhanced</u> Vegetation Index	<u>eCO</u> 2	Intercept	<u>Slope</u>	<u>Elevation,</u> <u>FC</u>	<u>Aspect</u>	
<u>Modified Red</u> <u>Edge Simple</u> <u>Ratio Index</u>	<u>FC</u>	<u>eCO<sub>2</sub></u>	Intercept	<u>Slope</u>	<u>Aspect</u>	<u>Elevatio</u> <u>n</u>
<u>Composition</u> (Plant foliar traits):						
<u>Trait: Canopy</u> <u>nitrogen</u> <u>concentration</u>	Intercept	<u>eCO2,</u> <u>Elevation</u>	<u>FC</u>	<u>Slope,</u> <u>Aspect</u>		
<u>Trait: Carbon</u>	<u>FC</u>	Elevation	<u>eCO<sub>2</sub></u>	Intercept	Slope	Aspect
<u>Trait: Leaf Mass</u> per Area (LMA)	Elevation	<u>FC</u>	Intercept	eCO <sub>2</sub> , Slope	<u>Aspect</u>	

**Function:** 

<u>Evapotranspirati</u> <u>on (nearest</u> neighbour)	<u>FC</u>	<u>eCO</u> 2	Elevation	<u>Slope</u>	<u>Aspect</u>	Intercept
<u>Evapotranspirati</u> <u>on (statistical</u> <u>resampling)</u>	<u>FC</u>	Elevation	<u>Slope</u>	eCO <sub>2</sub>	<u>Aspect</u>	Intercept



Figure 3: Relationships between many ecological variables, including NDVI, and eCO<sub>2</sub> depend highly on confounding factors. The NDVI data is partitioned into quartiles and coloured such that, if z is the confounding variable (fractional cover, slope, aspect or elevation), then  $z_{Q1}$  is the first quartile of the confounding data;  $z_{med}$  is the median of the confounding data; and  $z_{Q3}$  is the third quartile. Partitioning by fractional cover yields clear separations in the response variable

(a) fractional cover, as expected, since rising eCO<sub>2</sub> will have a less measureablemeasurable

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effect on sparse vegetation within the pixel. <u>The impact of (b) slope, (c) elevation, and (d) aspect</u> is less clear visually, but their contribution to the model is statistically significant.



Figure 4: Canopy height is well modelled by the eCO<sub>2</sub> model, with an R<sup>2</sup>=0.92, and the 5 1-1 line shown in black. However, the very tallest trees are not well captured.

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Figure 5: The biomass model prediction is shown for increasing eCO<sub>2</sub>. There is high variability at low eCO<sub>2</sub> values, but overall there is a small, but apparent, decrease in biomass with increasing eCO<sub>2</sub>.

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Figure 6: (a) The modelled NDVI prediction is shown for predictor variable eCO<sub>2</sub>. There is a decrease in NDVI for increasing eCO<sub>2</sub>, despite larger variance at low eCO<sub>2</sub> values. (b) The modelled canopy nitrogen concentration trait prediction is shown for predictor variable eCO<sub>2</sub>. There is a clear increase in canopy nitrogen concentration

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with increasing eCO<sub>2</sub>.

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Figure 7: The normalized canopy transpiration prediction is shown against predictor variable eCO<sub>2</sub>, for training data with nearest neighbour resampling. There is a clear decrease in ET for increasing eCO<sub>2</sub>, with larger variance at low eCO<sub>2</sub> values.

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Figure 8: Ecosystem dynamics inside (blue data points) and outside (orange data points) of the eCO<sub>2</sub> measurement boundaries contrast. (a) In the entire image, NDVI increases slightly with increasing fractional cover. In the small eCO<sub>2</sub> subset, NDVI appears to decrease with increasing fractional cover. (b) In the entire image, evapotranspiration increases with increasing NDVI, whereas the small eCO<sub>2</sub> subset seems to cover points with lower ET. (c) Across the entire image, the nitrogen trait remains constant with increasing fractional cover. (d) In the entire scene, evapotranspiration increases with increasing biomass. In the small eCO<sub>2</sub> subset, the evapotranspiration seems to be lower, on average, for the same range of biomass values.