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## ***Interactive comment on “Landscape-scale changes in forest structure and functional traits along an Andes-to-Amazon elevation gradient” by Asner et al.***

**Asner et al.**

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Many thanks for the excellent comments. We strived to address all of them fully, and many of them facilitated clarifications to the manuscript as well as a few corrections to the data reported.

Reviewer 1:

General comments: This study aims to assess forest canopy structural and functional properties along an altitudinal transect located in the Peruvian Amazon-Andes interface. The authors used data from LIDAR to overlap and significantly enlarge (from 1 ha to 25ha) the plot-based sampling employed in several publications that characterize

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and describe forest structure and function along this altitudinal gradient. The use of this Airborne technology opens new doors for improving our understanding about the role played by the environmental variability on determining forest functioning. I think that the work made by Asner and colleagues posits and reinforced the new roads built-up by many of the authors, which effectively link remote-sensed data to forest ecology and conservation. The work perfectly fits the BGD aims, and I think that it is almost ready for publication in its current stage. A couple of minor comments are included in the specific comments.

Specific comments.

**Methods.** Despite of the new technology employed significantly enlarged the field-based 1 ha plots, the sampling design still suffers of pseudo-replication. Indeed, plots located at an altitude below 400 masl (11) could be considered true replicates, but not the rest. The remaining plots over 400 masl are not real replicates, which may be taken into account by the authors throughout the text, but particularly in the discussion.

We agree that the study is pseudo-replicated, as is every elevation-gradient study we have found for the Andes. Our main intention in the study is to develop an understanding and sensitivity of a variety of ecological properties to changes in elevation, and this comes with some degree of pseudo-replication even using high-resolution remote sensing. We have made this more clear in the Methods, and we suggest the need for expansion of the study to larger geographies so that replicates can be selected at various elevations.

**Discussion.** Page 15430, second paragraph (lines 6 to 18). There are some issues related to the problem stated above that deserves clarification in line with the sampling limitations. When the authors conclude that: “western Amazon lowlands harbor variation in canopy functional traits often exceeding that produced by 3200 m of elevation change to Andean treeline”, they need to take caution. The variability assessed across each altitudinal sites in terms of soils and physiography varies significantly between

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lowland and highland plots.

We agree, and we have rephrased the interpretation to “highlight the strong degree to which canopy structural and functional variation is linked to regional patterns of geologic, hydrologic, and soil fertility variation in the lowlands.”

Likewise, they claimed that lowland canopies respond to geological, hydrological, and soil fertility variation, which is expressed in shift-community composition: I really think that you are entering here in some degree of speculation when assume that floristic changes are related to canopy reflectance. Due to you are no testing that, I would recommend to focus your conclusions on the structural properties evaluated rather than including claims still under debate. In fact, the work that claimed the existence of a fine-grain relationship between canopy reflectance and plant species composition is the Tuomisto et al. (1995) paper, and not the reference employed by the authors (Tuomisto et al. 2003).

We did not intend to say that floristic changes occurred along our gradient, since we did not look at floristics. We rephrased as “This finding may also link to reports of widely varying community composition, productivity, and carbon storage throughout the western Amazonian lowlands (Quesada et al., 2009;Asner et al., 2012;Higgins et al., 2012;Aragão et al., 2009;Girardin et al., 2013;Carvalho et al., 2013;Tuomisto et al., 1995).”

Reviewer 2

Remote sensing may offer a unique opportunity to extent detailed but spatially limited field measurements to study environmental controls on tropical forest growth and mortality. The objective of the study was to demonstrate the utility of novel remote sensing tools (lidar and imaging spectroscopy) to characterize changes in forest structure and function along an elevation gradient in Peru. I particularly liked the correlation analysis between structure metrics and spectral metrics and with elevation. The manuscript (although long) is well written, and, I believe, a useful contribution to the ecological

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literature. I am sure it will inspire future research activities. At the same time, I wish the author's would have provided a more critical examination of the potentials and limitations of these tools. I don't believe in easy answers; and some of the ecological conclusions drawn in this study require more careful examination. For example, the study seeks to confirm results from another field-based study that found biomass turnover rates were constant across the same elevation gradient. However, the results of the study under review, which are based on a lidar-derived gap-size frequency metric, are inconclusive. There are probably a variety of good reasons for that, e.g. difference in plot size, but these should not be overlooked. This is important, as other studies have argued that biomass turnover rates are linked to primary productivity across the observed ecological gradients.

We understand the reviewer's concern. By reconsidering the Girardin et al papers, and combining those with the Moser et al paper, we developed a clearer take-home message for our results. From their previous plot-based work, we see that biomass and NPP decrease with increasing elevation, and biomass turnover rates remain nearly constant. Our goal was to assess aspects of this at a larger (25 ha) scale. We did find nearly constant gap-scaling patterns, despite gross differences in gap size frequencies. This is suggestive of near constant aboveground biomass turnover rates, and thus our results indeed corroborate earlier plot-based results. This is now clearer in the introduction and discussion.

Similarly, the advantages and limitations of NDVI are well documented in the remote sensing literature, and the authors acknowledge that. Yet, their conclusion as a 'proxy for production at steady state' seems overly optimistic to me. This came to a surprise to me considering the author's expertise with sophisticated methods like lidar and imaging spectroscopy. My concern is that ecologists less familiar with remote sensing get the wrong message. I recommend the authors address my concerns prior to publication, which should not be too difficult with careful editing.

We no longer indicate this as our interpretation.

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15416/10: Please make clear that canopy gap and understory were estimated with lidar, e.g. lidar-based canopy gap density and understory cover.

Done.

15416/12: Elevation was negatively related to vertical profile. What specifically do you mean with vertical profile here, canopy depth?

Yes, clarified as the vertical partitioning of vegetation in the canopy.

15418/28: Is there room for alternative hypotheses? Studies in temperate forests have found a clear trend with elevation (Stephenson & Mantgem, 2005).

We have rephrased this entire paragraph.

15419/7-10: This is an important statement, but it is not quite clear. Are you trying to answer the question or question it? If canopy gap fraction is an indicator of forest turnover rates, than your analysis could help reveal trends with elevation. You can then compare and contrast them to field-based measurements. But how would you use your analysis to explore why biomass turnover is constant while NPP decreases with higher elevation?

We have completely revised the way we are describing this issue, to be more clear.

15418/7: Please see also Moser et al. (2011). Their analysis of belowground and aboveground carbon pools on an elevational gradient in Ecuador indicated a transition from light to nitrogen limitation with increasing elevation and decreasing temperatures.

We have incorporated the Moser et al study throughout the paper, in both the Introduction and Discussion. Indeed their results corroborate ours.

15419/11: Which unknowns?

Removed this phrase because it was vague.

15427/22: This normalization of the lidar height profile adjusts for horizontal variations

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in the sampling density but it does not adjust for vertical canopy occlusion. Detection probabilities decrease exponentially with increasing canopy depth and LAI. Thus, the cover estimates of sub-canopy voxels are not unbiased estimates of understory cover. There are ways to correct for occlusion and convert lidar height profiles to canopy height profiles, e.g. see Lefsky et al. (1999). I am not suggesting this has to be done. The general trends found in this study may not change. However, it has to be made clear that the understory cover estimates are in fact pure, unvalidated lidar metrics and should be interpreted with caution.

This is true, but the degree to which this occurs is also based on laser power and beam divergence. The CAO lidars are designed for maximum canopy penetration by maintaining a wide beam divergence (0.56 mrad 1/e), very high power (18 watts), and digitization of portions of the return beam (Asner et al. 2012 - RSE). As a result, our vertical profiles do approach canopy profiles at the reporting voxel resolution of 5 m x 5 m. Nonetheless, we added this caveat as requested in the Methods (Data Processing section).

15428/23: It is curious that you do not find an elevational trend with fiPAR but with NDVI and PV. fiPAR (and fPAR) is a much more direct measure of canopy traits and photosynthetic capacity than the spectral measures NDVI and PV. The saturation of a simple metric like NDVI is not surprising, but that it is more sensitive than your spectroscopy based fiPAR estimate makes me wonder about the meaning of your observed relationships. Often a linear relationship between fPAR and NDVI is assumed where background reflectance is negligible. Your correlation between fiPAR and NDVI is indeed higher than between NDVI and PV. On the other hand there is no correlation between fiPAR and PV, which again seems counterintuitive. Note, Table 3 shows a negative correlation between NDVI and fiPAR. Shouldn't it be positive?

We carefully checked the data, and indeed fiPAR is saturated while NDVI is not. fiPAR very easily saturates in densely foliated tropical forests since it includes only 400-700 nm light, which is readily absorbed by these canopies. In contrast, the NDVI is more

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sensitive to near-infrared light reflected from canopies, even while the visible light remains almost fully absorbed.

PV from imaging spectroscopy is sensitive to the later cover (top layer of foliage), and not to the vertical density of foliage (e.g., LAI or fiPAR) (see Asner et al. RSE 2005 and others). We are thus not surprised to see a decoupling of the NDVI from PV or the NDVI from fiPAR.

Yes, the NDVI-to-fiPAR relationship is positive, but not significantly so. We corrected the typographical error.

15429/2: Table 3 shows non-significant correlation coefficients (e.g. fiPAR\_NDVI: -0.66) that are higher than significant correlation coefficients (e.g. PV\_P:H = 0.53). How is that possible when the sample size is equal? Is it not?

Corrected – the PV vs PH was not significant. We also checked the others for errors.

15430/10: Although you sampled a wide range of different landscape types, it is not clear that these generalized conclusions are properly justified. Also, this finding is only based on the spectral metrics; the lack of correlation with fiPAR is ignored here.

We removed this statement.

15431/11: I am somewhat surprised that this study only reports results from remote sensing analysis. A more direct comparison with field data may have revealed interesting synergies and limitations between field measurements and remote sensing. Field data seems to exist for the studied locations.

Field data do not exist for any of our remotely sensed measurements at 25 ha scale. The only measurements taken in the field that would match our study would be canopy height, but those have been done on a portion of the trees in the center 1-ha. The point of our study is to provide a new set of measurements, and at a scale that can't be achieved easily in the field.

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15431/13: Please explain this in more detail. A decrease in aboveground biomass can be associated with a decrease in stand height and/or density. But how does that explain a constant turnover rate? Other studies suggest a relationship between NPP and turn over rates (e.g. Stephenson & Mantgem, 2005).

Yes, we agree and have rephrased and explained this in more detail.

15431/18: I am confused. It seems you observed a weak but significant decrease in turnover rates (gap-size scaling) ( $r=0.3$ ). You mention landslides as a potential cause. But your argument is no convincing. Is there no reason to believe that the observed trend is true? There are certainly good reason why 1-ha plot studies do not match 20-ha plot studies. I think a more comprehensive discussion on the sources of error, both, for the field and remotes sensing analysis is needed, before such important conclusion can be drawn.

Although aboveground biomass and NDVI decrease with increasing elevation, we computed a near-constant gap-size scaling parameter throughout the elevation gradient (Fig. 3). This parameter is a quantitative index often used to compare and contrast biomass turnover rates in tropical forests. Our results thus suggest that turnover is relatively constant when ascending from the lowlands into the montane. Not only do our results corroborate previous plot-based studies of nearly constant turnover, they suggest that we may be able to use airborne remote sensing of gap-size frequency to map relative rates of turnover in large forested regions of Amazonia. Doing so will improve our understanding of the spatial distribution of growth and mortality at much broader ecological scales than can be achieved with field plots. We clarified this in the discussion.

15432/4-15: Here you partly address one of my earlier comments regarding the negative correlation between NDVI and fIPAR. Your explanation is that NDVI is influenced by regrowth vegetation in canopy gaps, which is a reasonable explanation, though an "increase in greenness" should increase NDVI with elevation not decrease. An increase in

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shadow fraction with increasing gap fractions may be an alternative explanation. However, the statement that 'NDVI is more sensitive to turnover' is an oversimplification of a simple spectral metric that cannot be easily generalized. An increase/decrease of NDVI can be caused by several different factors that are usually not known a priori. Otherwise, this would suggest that NDVI can replace lidar metrics, which I don't believe is the authors' intent. I strongly suggest to clarify the limitations of NDVI (which are well documented in the remote sensing literature) to avoid confusion with readers less experienced with remote sensing.

We were able to avoid this issue by rephrasing as shown above.

15432/16: You seem to be using the term disturbance synonymously to tree mortality or turn over rate here. I think there needs to be a clear distinction between these different processes. Elsewhere in the manuscript you bring up the concept of equilibrium turnover rates, which assumes that the sites are undisturbed.

We rephrased as “gap formation patterns” rather than as disturbance.

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