

The creation of an improved power law equation that incorporates available radiation and leaf metrics is necessary, given the advancement in technology to estimate leaf area index (either through field measurements or remote sensing techniques). This paper provides new insights into how we build mass-density relationships in forest ecology and includes new variables to improve our biomass models.

I thank the reviewer for her helpful comments and appreciation of the contribution of this work. In the responses below I set out the approach to address the comments.

However, the document requires substantial revision before it can be accepted. In particular, more details about data collection methods and the main objectives of the manuscript need to be clearly stated.

The Yoda power law discussion creates confusion, as it seems this can only be applicable in monospecific forest plantations with well-established designs. At some points in the introduction, the manuscript addresses this as a real limitation of the equation (e.g., Lines 47 or 57). However, in other sections, the text seems to dismiss these limitations simply because the logic behind the equation appears intuitive (Line 70). This may create the misconception that these equations could predict forest biomass globally. The manuscript later acknowledges its limitations at the end of the introduction when indicating that only "undisturbed stands" will be included in the model testing. Therefore, it would be wise to clearly distinguish between the actual application of the equation and the broader theoretical implications.

The objective of the manuscript is not clearly stated in either the introduction or the abstract. As I understand it, the objective is to develop a model for the mass-density relationship that uses a light absorption function instead of a normalization constant. This should be explicitly stated in the document for better clarity.

The abstract and introduction are substantially revised to clearly state the objectives and clearly distinguish between the actual application of the equation and the broader theoretical implications. The text has been rearranged. The item about the Yoda power law has been replaced to the Discussion. Equation 1 has been removed, which means that all equations in the text have been renumbered. Two new references are included. The full text of the abstract and introduction are presented below. The most significant changes to the text are indicated in bold letter type.

Abstract. Forest stand mass scales with varying values of the exponent of tree density for compilations of forest communities on different spatial scales, being the slope of the regression line in a log–log plot, where the intercept is a normalization constant reflecting the assumption of a constant rate of energy use by the species and environments involved. **The objective of this article is to develop a model, using a light absorption function instead of a normalization constant**, to investigate how the interspecific forest mass-density relationship varies along spatial, largely latitudinal gradients of leaf area and the sum of global radiation over the growing season for relatively undisturbed forests **distributed across biomes in the Northern Hemisphere**. The test of the model shows the highest explained variance when both gradients are included in the light absorption function, meaning that the exponent is determined not only by the rate but also the sum of energy use over the growing season. The exponent of tree density converges to 1/2, which deviates from an expected 1/3 value based on mass-density scaling of large compilations of plant communities on a continental or global scale. The 1/2 value corresponds

with the so-called self-thinning rule that applies to the self-thinning line constructed as the upper boundary of mass–density points for monospecific even-aged plant stands, where gradients in energy use can be neglected. The results demonstrate the appropriateness of replacing the normalization constant with a light absorption function, suggesting a thermodynamic interpretation that may be of interest to other plants and even animals when gradients in energy use similarly affect the intercept and slope of the interspecific mass–density relationship.

1 Introduction

In order to predict climate-induced changes in forest ecosystem processes at different spatio-temporal scales, it is crucial to understand how available resources (i.e. energy, nutrients and water) interact with forest structure dynamics (i.e. size and density) and forest functions that affect carbon stocks and fluxes. The allometric relationship between the average live aboveground biomass per tree in an area \bar{M} (g) and the tree number in that area N (m⁻²) links forest structure to forest functions for relatively dense stands, with the underlying rationale that an increase in the average biomass per tree is associated with tree mortality due to competition for the available resources (Westoby, 1984; Yu et al., 2024). However, the mathematical expression does not include resource variables, which makes it difficult to understand the interaction of the mass-density relationship with (gradients in) resource use in density series of stands at different spatial scales. Here, the allometric mass-density relationship is adjusted by including the resource variable light and testing the model for interspecific density series of relatively undisturbed forests with negligible drought stress at broad spatial scale, starting from the equation:

$$\bar{M} = kN^{-\beta'} \quad (1)$$

where $-\beta'$ is scaling exponent and k the scaling coefficient or normalization constant that adjusts the general relationship across environments and species. For statistical reasons \bar{M} is written as a function of N , because the number of trees in an area can be determined much more accurately as the independent variable in a linear regression model where the general mass-density equation is plotted on logarithmic axes:

$$\log \bar{M} = \log k - \beta' \log N \quad (2)$$

where $-\beta'$ is the slope of the regression line and $\log k$ the y-intercept.

The exponent $-\beta'$ was for a time thought to converge to $-3/2$ (the ‘self-thinning rule’, Yoda et al., 1963; Westoby, 1984; White, 1985), but closer examination revealed that the slope and intercept vary considerably when the equation is applied to intraspecific and interspecific density series of plant stands at different spatial scales (Weller 1987a, 1987c; Lonsdale, 1990). Only for large interspecific datasets of plant communities at continental and global scales, where N is the critical density of maximally packed individuals where all resources are used, an exponent value of $-4/3$ (or $-3/4$ as the exponent of \bar{M} , using \bar{M} as the independent variable in Eq. 1) is reasonably well founded (Deng et al., 2012; White et al., 2007). **However, the generalisation of this value to mass-density relationships of tree-dominated communities of boreal, temperate, subtropical and tropical biomes separately seems to be unwarranted, as shown for the Chinese Forest Biomass Dataset (Luo, 1996, Li et al., 2006).**

Mechanistic models based on geometric, allometric and dynamic growth arguments (e.g., Weller, 1987b; Adler, 1996; Enquist et al., 1998; Li et al., 2000; Deng et al., 2012) reproduce the general mass-density equation well, with plausible values of $-\beta'$, but it remains problematic to predict the slopes of empirically obtained mass-density

relationships. In most of these models, the constant k is assumed to be a measure of a constant whole stand rate of resource use, including light (e.g., Westoby, 1984; White et al., 2007; Deng et al., 2012), with variations between mass-density relationships that can be stronger than variations in the exponent (Deng et al., 2006; Dai et al., 2009). However, the variation in k has received relatively little attention (Dillon et al., 2019), although the estimate of the variation is correlated with the estimate of $-\beta'$ in Eq. 2 (Westoby, 1984).

The objective of this investigation is to develop a model that uses a light absorption function instead of the normalization constant, with the purpose of incorporating gradients in total energy use in the general mass-density equation. The model is tested for interspecific density series of relatively undisturbed forests, where energy use is expected to be in a dynamic equilibrium with the living aboveground biomass and tree density. Two common assumptions are investigated with the new model: 1) the assumption that the rate of energy use is constant, while stand leaf area varies with stand age (Ryan et al., 1997; Holdaway et al., 2008) and 2) the assumption that the rate of energy use drives self-thinning (e.g. Deng et al., 2012), while gradients in the sum of energy use over the growing season can also be considered. The impact of the first assumption emerges in light experiments on monospecific even-aged plant populations, comparing self-thinning trajectories for different but constant levels of illumination. The intercept of thinning lines is lowered with increasing shade, while the scaling exponent at each level of shade is maintained at a value of approximately $-3/2$, except for populations grown under deep shade (Hiroi and Monsi, 1966; Lonsdale and Watkinson, 1982, 1983; Hutchings and Budd, 1981; Westoby and Howell, 1981; Westoby, 1984). This suggests that reduced light absorption due to a lower total leaf area, rather than increased shade, also results in a lower intercept of the thinning line, but only a different slope if light absorption is not constant throughout the trajectory of self-thinning. The effect of gradients in total leaf area, and thus light absorption, on the exponent of N in the forest mass–density relationship is investigated by developing a light absorption function that includes total leaf area, **measured by the Leaf Area Index or LAI (m^2m^{-2}) of the forest stand, to replace the normalization constant k .**

The investigation of the second assumption is intuitively justified by the finding that tree density increases with decreasing latitude to approximately 25° , while the total aboveground biomass is supposed to be constant (Enquist and Niklas, 2001) or increases, apart from the spatially restricted temperate rainforests (Pan et al., 2013). Therefore, the light dependent constant k , equal to $\bar{M}N^{\beta'}$ according to Eq. 1, increases with decreasing latitude, together with an increase in the sum of available solar energy use over the growing season, here investigated by including this gradient in a light absorption function, separately from and in addition to leaf area. The leaf area and the available solar radiation over the growing season are introduced stepwise in the light absorption function that replaces the scaling coefficient k , to correct for gradients in the total energy use of forests. This results in three energy–biomass–density relationships or EBDs that are used to examine how the interspecific mass–density relationship of relatively undisturbed forests varies along spatial, largely latitudinal gradients of leaf area and available solar energy separately and together. In addition to the three EBDs, the bivariate mass–density relationship and the relationship between leaf area and stand density are calculated, giving insight into how the slope of the mass–density line relates to the gradient in total leaf area. The analysis focuses on the development of the exponent of N because this is a central issue in the debate on the mathematical form of the mass-density equation applied to forests. In addition, we examine the extent to which the regression coefficients support the conclusions with respect to the development of the exponent in the EBDs. **In a follow-up paper the model will be applied to density series of neighbouring stands with similar species composition, which contributes to a**

better understanding of the relationship between interspecific and intraspecific scaling for relatively undisturbed forests and of the interaction of resource use with forest structure and forest functions for separate species and habitats.

In this introduction is referred to the allometric mass–density relationship using \bar{M} , conform most cited studies, but the model development in this paper will be based on equations written in terms of the total living aboveground biomass M (g m^{-2}), because the calculation of \bar{M} as M/N from the available field data introduces artificially inflated correlations (Weller, 1987a). The use of M leads to an exponent $-\beta = -\beta' + 1$, while k stays the same (see Methods). The EBDs assume a constant regime of light absorption over the years that is long enough to establish a dynamic equilibrium with the aboveground living biomass and tree density. Human, biotic and abiotic disturbances like thinning (not self-thinning), insect diseases and drought stress can lead to deviations in leaf area from this dynamic equilibrium, due to functional responses of forests to disturbances (Jump et al., 2017). Therefore, only relatively undisturbed stands are included in the test of the model equations. The model equations are applied to the field data of forest biomass and density in the compendium of Cannell (1982) that comprises standardized tabulations of field and experimental data of forests of approximately 600 reports worldwide.

New references:

Hamilton, N.S., Matthew, C. and Lemaire, G. (1995). In defense of the $-3/2$ boundary rule: A re-evaluation of self-thinning concepts and status. *Ann. Bot.* 76, 6, 569–577, <https://doi.org/10.1006/anbo.1995.1134>. 1995.

Yu, K., Chen, H.Y.H., Gessler, A., Pugh, T.A.M., Searle, E.B., Allen, R.B., Pretzsch, H., Ciais, P., Phillips, O.L., Brienen, R.J.W., Chu, C., Xie, S., Ballantyne, E.P., 2024. Forest demography and biomass accumulation rates are associated with transient mean tree size vs. density scaling relations. *PNAS Nexus* 3: 1–9, <https://doi.org/10.1093/pnasnexus/pgae008>, 2024.

The final five paragraphs of the discussion focus on limitations and scope of the results. However, the potential applications of the results are missing from the last paragraph. It would be better to conclude the discussion with the manuscript's conclusions, though this may be challenging without a clear explanation of the objectives.

The first paragraph and the first three of the last five paragraphs of the discussion have been revised. The new text of the first paragraph is presented below. The first three paragraphs of the last five paragraphs have been rewritten and are presented also. The last two paragraphs have been maintained. The most significant changes to the text are indicated in bold letter type.

The first paragraph of the discussion:

In this article the interaction of resource use (i.e. light) and stand structure dynamics of relatively undisturbed forests at broad spatial scales is investigated by replacing the normalization constant in the forest mass-density scaling relationship with a light absorption function, distinguishing between two assumptions. The first common assumption in interspecific mass-density scaling relationships is that the scaling coefficient represents a limiting use of resources supplied to an area at a fixed rate, here assumed to be solar radiation (Deng et al., 2012), which is examined by introducing LAI into the light absorption function. **The second assumption** examines the possibility that the scaling coefficient depends not only on the rate of solar energy use, but also on the sum of solar radiation over the growing season, which is investigated by including both LAI and E_{sglob} in the light absorption function. **In the investigation of the assumptions, using the data of 199 relatively undisturbed forest communities selected from Canell (1982), a comparison is made with a much**

larger dataset of 1350 natural forests obtained from Deng et al. (2012), where *LAI* data are generally missing (see section 2.7).

The first three of the last five paragraphs of the discussion have been replaced by the text (most significant changes in bold letter type):

The GEBD calculates the scaling exponent correctly, but the regression coefficients in the GEBD are attenuated, due to measurement errors in the *LAI* and E_{sglob} (Aiken and West, 1991). This will be addressed in a forthcoming paper by analysing the structure of the underlying data, using intraspecific time and density series of forests with little or no biotic, abiotic and human disturbances. The use of EBDs to analyse intraspecific data will also provide more information on the theoretical aspects and potential applications of the EBD model discussed below.

The results of the GEBD suggest that deviations from the 0.50 exponent in bivariate interspecific scaling of relatively undisturbed forests at broad spatial scales can be attributed to gradients in the sum of energy use over the growing season. This is consistent with the classic 'self-thinning rule', which was once thought to predict a 0.50 exponent of tree density for interspecific and intraspecific density series (Westoby, 1984). Currently the rule is considered to describe only the upper boundary of data points in a $\log M - \log N$ plot of crowded even-aged monospecific plant populations, where the datapoints are often obtained from stands in the same region (Hamilton et al., 1995). Here, the gradients in *LAI* and E_{sglob} are negligible small, so the GEBD is expected to converge to the mass-density relationship of Eq. 2A, with the light absorption function equal to $\log k$, representing the energy use at the ceiling leaf area. The absence of gradients in energy use is much less likely in other types of intraspecific density series, which argues in favor of applying the EBDs. The application of EBDs to intraspecific mass-density relationships can provide more insight into the relationship between interspecific and intraspecific scaling.

The EBDs show how the interspecific forest mass-density relationship interacts with the resource energy (i.e. light), but the question is how it interacts with the resource nutrients for relatively undisturbed forests with negligible drought stress. The *LAI* is central to answering this question, because it can be seen as a proxy of functional responses of forests to the resource availability of e.g. energy and nutrients (Jump et al., 2017). Hamilton et al. (1995) reasons that competition for light, rather than nutrients, causes mortality and an increase of leaf area shifts the limiting thinning line upwards. An increase of the nutrient supply increases the rate of progression of the thinning line, without changing the position of the line (Yoda et al., 1963; White and Harper, 1970). The evidence that nutrients also alter the position of the line (Westoby, 1984; Morris and Myerscough, 1991) is ambiguous. If nutrients change the position of the line, there may be an indirect effect on the leaf area and thus the capacity of plant stands to absorb light (Hamilton et al., 1995). This reasoning suggests that the *LAI* in the light absorption function links both energy and nutrients to the forest mass-density relationship.

The exponent $-\beta$ in the general mass-density relationship (Eq. 2A) reflects the ratio of the relative growth rate and the relative mortality rate of the forest stand (RGR/RMR ratio, Eq. 3). A more negative value, or steeper slope in a $\log M - \log N$ plot, implies a larger RGR/RMR ratio, i.e. the biomass accumulation rate increases when the mortality rate is constant, or the mortality rate decreases when the biomass accumulation is constant. As the exponent becomes less negative, the reverse reasoning applies (Yu et al., 2024). The bivariate mass-density relationship is not suitable for determining whether the variation in exponent values is associated with light and nutrient use or other environmental drivers, but the GEBD is, because gradients in light and nutrient use are included in the light absorption function, not in the exponent value that converges to 0.50. Deviations from the 0.50 exponent may indicate other environmental or vegetation property changes like, for instance, disturbances that prevent the forest structure to be in a dynamic

equilibrium with the use of energy and nutrients as formulated with the light absorption function. In this way, the EBDs can provide further information on the interaction of changing environmental conditions with forest demography and carbon sequestration at different spatio-temporal scales, using the advancement in technology of field measurements and remote sensing techniques to estimate leaf area index and other stand indices like tree density and size. A better insight in LAI and E_{sglob} as predictors of stand structure and growth (see also Parker, 2020), together with high-resolution satellite or aerial remote sensing data at broad spatial scales, contributes to the inclusion of size-structured forest demographic models in Earth System Models (ESMs; Fisher and Serbin, 2017).

The EBDs are also of importance for forestry practice, where self-thinning lines are used with the idea that all stands should eventually approach and track along the same maximum size-density relationship (MSDR) boundary for a particular species/region combination (Vanderschaaf and Burkhardt, 2007). The EBDs allow investigating of how spatio-temporal variation in MSDRs across regions and species relates to gradients in light (and nutrient) use, helping to reduce the empirical nature of MSDRs and hence errors in growth and yield models constrained by MSDR boundary lines (Vanderschaaf and Burkhardt, 2007).

In the interspecific GEBD, gradients in E_{sglob} are associated with shifts in species composition between the forest communities involved, making it difficult to predict the impact of climate-induced longer growing seasons on forest structure. Application of the EBD model to long-term trial plots is recommended, provided reliable LAI data are available. Self-thinning lines of Norway spruce, European beech (Pretzsch et al., 2014) and *Pinus sylvestris* (Toraño Caicoya et al., 2024) do not show trends in time due to climate change-induced longer growing seasons, only the growth rate increases. However, the intercepts of the self-thinning lines of *Pinus sylvestris* in Europe increase with decreasing latitude (Toraño Caicoya et al., 2024) and with increasing E_{sglob} , which is associated not only with a longer growing season but also with an increase in the intensity of solar radiation. This may lead to an increase in the intercept that is consistent with the results of light experiments (see Introduction).

Line 123: Where did you obtain the leaf area index data? It would be surprising if it came from the Cannell database. This should be detailed in the materials and methods section as it is not a standard variable. In line 203, you mention obtaining it from the Cannell database, but could you elaborate on how this variable was measured? If obtained through remote sensing, this should be explicitly stated, as mixing estimated and field data could be a limitation of your work. After reviewing the supplementary material, the LAI values seem unusually high. Typically, these values range from 4 to 6, meaning the canopy cover is 4-6 times higher than the projected ground area. With your reported LAI values, it's surprising that any light reaches the soil. As someone with field experience measuring LAI , values above 3 indicate dense forest canopies. Your database shows no values under 1, suggesting your equation may only be applicable to very dense forests or forest canopies. Please explain how the LAI measurements were conducted.

Indeed, as indicated in line 209: Stands with an LAI less than 1.5 were removed from the database to stay within the validity limits set by the application of Beer's Law. Also, most of the stands in the database have relatively high LAI values. I think the high LAI values of most stands are due to the selection of relatively undisturbed forests with negligible drought stress. The application of the equations to intraspecific density series of neighbouring tree stands with a corresponding species composition in a follow-up paper can give more information on the validity range of the light absorption function (see Discussion). The following text with respect to the measurement methods is inserted between the two sentences in line 209:

The data on *LAI* of the selected stands were measured using litter traps, allometry based on sample trees or destructive methods. An example of the use of litter traps is the deciduous woodland in Sweden (p. 222 Cannell, Supplementary Table 1), where the *LAI* value was averaged over a three-year measurement period. An example of the use of allometry are *Pinus resinosa* plantation forests in the U.S.A., New York (p. 314 Cannell, Supplementary Table 2), with 5 sample trees per plot in 4 plots and 3 sample trees in one plot. The *LAI* values were derived from regressions on breast-height diameter *D*. Examples of destructive methods are the *Abies alba* forest and deciduous forest in Czechoslovakia (p. 57 Cannell, Supplementary Table 1, 2). The *LAI* values were derived by multiplying the means of 5 sampled dominant trees, 5 co-dominants and 5 subdominants by the numbers of trees in each of these classes.

Line 49: Should this have an additional reference, or is this information contained in (Weller, 1987a)?
This sentence is not included in the new text.

Line 61: The manuscript mentions "leaf area," but it seems to refer to "total leaf area," as individual tree leaf area doesn't vary significantly. This distinction should be clarified in the introduction. While the authors later refer to leaf area index as a measure of total leaf area for their calculations, greater precision in terminology would be helpful.
This is clarified in the previously presented new introduction.

Line 131: Is the first "and" necessary?
"and" will be removed

Line 159: Consider mentioning hillshade as a factor influencing seasonal global radiation.
After latitude has been inserted 'and hillshade'

Line 217: Since most of your data comes from broadleaved trees, this should be mentioned as a limitation.
At the end of line 218 is added: Most of the data are from broadleaved forests, which can be considered a limitation.

Table 1: Consider adding a column at the beginning with equation names (e.g., "AEBD model" or "LEBD model").
In the first column the name will be added. For instance: 'Equation 14' becomes 'AEBD Eq. 13'.
Note that Eq. 1 is removed, so Eq. 14 becomes Eq. 13.

Line 231 & 271: How can you explain the lower scaling exponent due to reduced leaf area if this variable isn't used in the equation? This appears to be an educated guess rather than a direct result from your model. Consider adding "Possibly" at the beginning of the sentence in Line 271.
Line 231: 'This can be explained by a reduction in leaf area with decreasing tree density *N*' will be replaced by 'A plausible explanation is a reduction in leaf area with decreasing tree density'.
Line 271: 'Possibly' will be added at the beginning of the sentence.

Line 234: Is it valid to compare scaling exponents when the equations are fundamentally different?
The mass-density Eq. 2A can be considered as a special case of EBDs, namely when gradients in *LAI* and E_{sglob} are negligible. So, these equations can be compared. See also the new text of the Discussion (second paragraph of the new text that replaces three of the last five paragraphs).

Line 235: Figures should appear in the document in the order they are referenced. Asking readers to check figures 1c, 2c, and 3c makes the flow difficult to follow.

The sentence 'Note that the regression coefficients of Eq. 11 are calculated from the regression results presented in Fig 1(c), Fig 2(c) and Fig 3(c), where LAI is the dependent variable' will be included in the legend of Table 1.

Line 287: A map showing plot locations (with different colors for each forest type) is necessary, especially given that you explain results based on geographic distribution.

This map will be included in the Supplementary Material.

Line 349: A "second alternative premise" is mentioned, but this doesn't appear to be an original objective of the paper. Again, the objectives should be clearly stated in the introduction.

Furthermore, it's surprising that a proper latitudinal analysis isn't included in the methods or results, yet a new figure appears in the discussion.

In the new 'Introduction' and 'Discussion' presented before two 'assumptions' instead of 'premises' are considered. The latitudes of the 199 selected forests with LAI data are considered at the end of section 2.6. The next sentences are added:

The latitude of the broadleaved forests varies between ca. 2° and ca. 56° N, with an average latitude of ca. 36° N. The latitude of the coniferous forests varies between ca. 32° and ca. 58° N, with an average latitude of ca. 41° N. The coniferous dataset includes thirteen forests with a latitude between 1500 and 2740 m NAP.

The latitudes of the boreal/alpine, the temperate and the (sub)tropical dataset are considered in the new section 2.7, presented below:

2.7 Notes on data from Deng et al. (2012)

Dataset S1 from Deng et al. (2012) is used to obtain an indication of whether the selection of 199 forest stands with *LAI* data from Cannell (1982) is representative of a larger selection of forests for which *LAI* data are generally missing (see Discussion). The dataset includes a subset of 1350 natural forests from the Chinese Forest Biomass Dataset (Luo, 1996) and the Cannell (1982) compendium, of which 1109 forests are from the Luo database and 241 are from Cannell (1982). The Luo database includes 6 forest biomes across the entire country. The 6 biomes are: boreal/alpine, temperate deciduous broadleaved, temperate coniferous, subtropical evergreen, subtropical coniferous and tropical rainforest/monsoon forest. Here, the 1350 forests are grouped into a boreal/alpine, temperate and subtropical/tropical group of forests, which are expected to differ in E_{sglob} due to latitudinal and altitudinal gradients. The interspecific forest mass-density relationship (Eq. 2A) is applied to compare these groups with the 199 forests including *LAI* data (see Discussion). The equation is also applied to all 1350 forests together. The boreal/alpine subgroup includes 252 coniferous and 13 broadleaved forests, the temperate subgroup 389 broadleaved and 219 coniferous forests and the (sub)tropical subgroup 335 broadleaved and 142 coniferous forests. The latitudes of the boreal/alpine subgroup (between ca. 27°-64° N) and the temperate subgroup (between ca. 27°-56° N) are about the same on average (ca. 40° N), but E_{sglob} of the boreal/alpine subgroup is smaller on average due to the relatively short growing season of 166 alpine forests with a latitude between 27°-40° N and an altitude of ca. 2000 m NAP or higher. So, the gradient in energy use is also related to an altitudinal gradient. The average latitude of (sub)tropical forests (between ca. 7°-38°) is about 28°. This includes forests in the southern hemisphere also.

Line 357: The location of dataset S1 from Deng et al. (2012) and its relationship to your equation in Table 1 needs clarification. The data, analysis, and reasoning behind Figure 4 are completely missing

from the document. It's problematic that the largest figure in the manuscript appears without proper context or explanation.

The data, analysis and reasoning are now included in the Introduction, section 2.7 and the Discussion.