Author response to reviewer 2

Reviewer comments in black
Author responses in blue

I first want to apologize for the long delay in reviewing this manuscript. When I started reading it, I already realized why it is difficult to review this MS - it in principle deals with a relevant topic, it could have interesting insights, but the way it is organized and written, it is very difficult for me to follow and make sense out of it, sometimes things are being repeated, and overall, it misses a focus on what the goal of the whole manuscript is.
What is actually the hypothesis that is being evaluated? Why is this hypothesis relevant? These aspects do not seem to be addressed at all, rather, different fitting equations are presented, and the results of the fitting exercise are described. The data sources are not well described, the climatological forcing comes from an obscure data source that I have never heard before. And in my view, there is too much description of statistical fitting and too little scientific explanations/interpretation.

I thank the reviewer for the helpful comments and appreciation that the manuscript could have interesting insights.

I propose to rewrite and reorganize the manuscript as explained below. First, I interpret the relevant sections of the manuscript, indicated by line numbers, regarding the reviewers' comments. Second, I present the new text in the letter type of the original manuscript.

Regarding the reviewer's comments 'in my view, there is too much description of statistical fitting and too little scientific explanations/interpretation': I hope that the proposed changes to the text, particularly in the introduction and discussion sections, will provide the desired scientific explanations/interpretations and less focus on statistical descriptions. Also, the relatively large focus on statistical aspects compared to scientific explanations is related to the thermodynamic nature of the EBD model. As is possible with thermodynamic models, the EBD model describes the mathematical relationship between observations without explanatory (sub)models of the underlying processes (see the chapter Discussion).

Regarding the reviewer's comment, 'The data sources are not well described': this response provides additional information regarding my response to Reviewer 1.

At the end of this response the new references compared to the preprint of 9 October 2025 are added.

Chapter Introduction.
This chapter is rewritten and replaces the preprint of 9 October as well as my response to reviewer 1.

Lines 21 to 51, my interpretation: the research subject requires further introduction at the beginning, (too) much attention for statistical fitting as related to different values of the exponent in literature and without a focus on the goal of the manuscript. I propose to rewrite these sections with the note that Eq. 1 in the original manuscript will be removed and all equations are renumbered accordingly:

Competition among plants results in an allometric size-density relationship, where the average size of plants scales as a negative exponent of plant density. Theoretical mechanisms that explain the wide variation in empirically estimated values of the exponent are of interest because of the ubiquity of size-density relationships and practical significance for forestry and ecosystem management. Here, the size-density relationship is considered for the allometric relationship between average live aboveground biomass per tree in area $\bar{M}$ (g) and the number of trees in that area N (m^{-2}), with the aim of developing a better explanatory model for the much-discussed variation in the exponent, after which the model is tested for interspecific density series of forests at broad spatial scale.

The allometric mass-density equation is traditionally written as (Yoda et al., 1963; Westoby, 1984):

$$\bar{M} = kN^{-\beta'} \tag{1}$$

where -β' is the scaling exponent and k the scaling coefficient. This equation can also be written as:

$$\log\bar{M} = \log k - \beta'\log N \tag{2}$$

where -β' is the slope and log$k$ the y-intercept of the regression line through datapoints in a log-log plot of average tree mass against tree density.

The exponent was some time thougt to converge to -3/2 in intraspecific as well as interspecific mass-density relationships, also referred to as the 'self-thinning rule' (Yoda et al., 1963; Gorham, 1979; Westoby 1984, White, 1985), until scrutiny showed that the slopes of the regression lines of time and density series vary much more (Weller 1987a; Li et al., 2005, 2006). 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 (Weller, 1989; Lonsdale, 1990; 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 model approaches 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 -β', but it remains problematic to predict the slopes of empirically obtained mass-density relationships (Reynolds and Ford, 2005).

Lines 52 to 72, my interpretation: These paragraphs discuss the light dependent normalization constant. The focus should be on the gradients in energy use in time series and density series of forests and not on the interpretation of light experiments. The light experiments will be interpreted in the Methods section. The paragraphs are replaced by the following text:

Here, an alternative approach is proposed to estimate the exponent value in forest mass-density relationship, with a focus on the intercept log$k$, also referred to as a normalization constant that adjusts the general relationship across environments and species. The normalization constant is generally assumed to be a measure of whole stand resource use including light and reflects the assumption of a constant high rate of energy use in interspecific density series of crowded stands (Enquist et al., 1998; Deng et al., 2012). However, this assumption can be questioned in two ways. Firstly, it is commonly believed that the total leaf area of forest stands, measured as the leaf area index (*LAI*, m^2 m^{-2}), is constant when self-thinning occurs in dense stands, although *LAI* varies with stand age and thus stand density (Ryan et al., 1997; Holdaway et al., 2008). This means that gradients in resource use can occur in time series of single stands and density series of spatially separated stands, as *LAI* is a proxy for the resource use of forests including light (Jump et al., 2017). Secondly, forest 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). This means that the light dependent constant k, equal to $\overline{M}N^{\beta'}$ according to Eq. 1, increases with decreasing latitude, together with an increase in the sum of available solar energy use over the growing season E_{sglob} (GJ m-2 yr-1). The consequence is that gradients in energy use can be expected in density series of forests at broad spatial scales.

After line 72: Inserted are the objective of the investigation (comment reviewer 1), as well as the hypothesis that is being evaluated and the reason that the hypothesis is relevant (reviewer 2):

The objective of this investigation is to develop an energy-biomass-density model (EBD) that uses a light absorption function including LAI and E_{sglob} instead of the normalization constant, enabling to account for gradients in energy use in density series of forests. Hamilton et al. (1995) reason 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 LAI in the light absorption function links both energy and nutrient use to the forest mass-density relationship.

The hypothesis evaluated in this article is that the wide variation in the exponent in interspecific mass-density relationships can be reduced to the self-thinning rule in the EBD because the light absorption function accounts for possible gradients in LAI and E_{sglob} within density series of relatively undisturbed forests. The possibility that forest mass and density together strive for the same dynamic equilibrium with the regime of light absorption on broad spatial scales, which manifests in a single value of the exponent in the new model, would contribute considerably to a better understanding of the wide variation in empirically estimated mass-density relationships used in forestry (Vanderschaaf and Burkhart, 2007) and suitability of forest demographic models for Earth System Models (ESMs; Fisher and Serbin, 2017), leveraging the advancement in field measurements and remote sensing techniques to estimate LAI.

Line 73 to 92: These paragraphs are largely maintained, but the order is changed. The -1/2 self-thinning rule and the use of the dataset of Deng et al. (2012) are added. Two sentences have been added to highlight the relatively strong focus on statistical accountability compared to scientific explanations and interpretations. The paragraphs are replaced with the following text:

The hypothesis is evaluated for relatively undisturbed forests, because the incorporation of a light absorption function assumes 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). The validity of the hypothesis is investigated by introducing the LAI and E_{sglob} separately and together in the light absorption function that replaces the normalization constant k. This results in three energy–biomass–density relationships or EBDs that enable to examine how the interspecific mass–density relationship varies along 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 a possible gradient in 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 self-thinning equation applied to forests. Additionally, we examine the extent to which the regression coefficients support the conclusions regarding the development of the exponent in the EBDs.

This article puts forward a thermodynamic interpretation of the EBD model, presenting it as a mathematical relationship between observations without the need for explanatory (sub)models of underlying processes (see Discussion). This results in a relatively stronger focus on statistical justification than on scientific explanations and interpretations. It has to be noticed that in this introduction is referred to the allometric mass–density relationship using $\overline{M}$, 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}) for statistical reasons, which means that the -3/2 self-thinning rule becomes a -1/2 self-thinning rule, while k stays the same (see section 2.1). The dataset of relatively undisturbed forests to validate the hypothesis is selected from the compendium of Cannell (1982) that comprises standardized tabulations of field and experimental data of forests of approximately 600 reports worldwide (see 'Methods'). An indication of the representativeness of the selected stands is obtained by comparing the allometric mass-density relationship with a much larger data set of natural forests without LAI data (Luo, 1996; Cannell, 1982) used by Deng et al. (2012).

Chapter Methods

Section 2.1, my interpretation:

More scientific explanation and interpretation are needed.

Lines 95 and 96, the first sentence is replaced by the text:

The introduction of a light absorption function begins with the formulation of a balance equation underlying the self-thinning equation. The self-thinning equation is used to describe the self-thinning process in time series of single plant populations. However, it is also applied to intraspecific and interspecific density series of spatially separated forests. This implicitly assumes a space-for-time approach, reflecting resource availability and functional differences among forest stands (Yu et al., 2024).

Line 114:

Insert after 'balance equation': (Eq. 4)

Lines 114 to 117, replace this sentence with the text:

Here, the exponent is expected to converge to the self-thinning rule, which shows in light experiments on monospecific even-aged plant populations, comparing self-thinning trajectories for different but constant levels of illumination. The exponent remains at a value of approximately -1/2 at each level of illumination, except for populations grown under deep shade. Meanwhile, the intercept of the thinning lines or normalization constant decreases as shade increases. 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 (Hiroi and Monsi, 1966; Lonsdale and Watkinson, 1982, 1983; Hutchings and Budd, 1981; Westoby and Howell, 1981; Westoby, 1984). The normalization constant, i.e. the integration constant in Eq. 2A, is not suitable to capture different levels of light absorption within time series or density series, which is adressed by the introduction of gradients in leaf area and the available solar radiation separately and together in the right-hand zero term of the balance equation (Eq. 4).

Section 2.2, my interpretation:
More scientific explanation and interpretation are needed.

Lines 123 to 125 are replaced by the text:
The LEBD is developed by introducing light capture in the balance equation, using the leaf area index or *LAI* of the forest stand (leaf area per unit of ground area in m^2 m^{-2}, one-sided for broadleaved trees and the projected leaf area for coniferous trees). Light availability within a canopy declines exponentially with increasing *LAI*, which implies that total light absorption is non-linearly related to total *LAI*. Light capture is calculated using *LAI* and the light extinction coefficient ε (dimensionless) in the adoption of Beer's Law (Monsi and Saeki, 1953):

Lines 147 and 148, this sentence is replaced by the text:

This means that only forests with *LAI* >1 will be included in the LEBD (Binckley et al., 2013). On the other hand, an upper limit for *LAI* may also be applicable because leaves in dim light environments can have very low assimilation rates close to their compensation points and therefore contribute little to the stand structure, as defined by the allometric mass-density relationship (Parker, 2020). An upper limit for LAI will be discussed in section 2.6. The validation of the LEBD against field data of forests results in values of the light extinction coefficient that are compared with literature values to determine whether the chosen mathematical approach and the data are appropriate to test the hypothesis (see Results).

Section 2.3, my interpretation:
More scientific explanation is needed, in addition to the response to reviewer 1.

Line 159, insert after 'latitude,':
altitude and hillshade,

Section 2.4, my interpretation: the scientific explanation is presented in the 'Introduction'. The scientific interpretation is presented in the 'Discussion'.

Section 2.5, my interpretation: The presentation of the fitting procedure for the different equations can be improved by using separate paragraphs.

Line 182: insert before starting a new paragraph in this line:
The equations are calculated using various statistical techniques.

Line 184: start a new paragraph in this line.

Line 186: start a new paragraph in this line.

Line 188: start a new paragraph in this line.

Line 192: start a new paragraph in this line.

Line 196: The reviewer comments that ‘the climatological forcing comes from an obscure data source that I have never heard before.’
I suppose the source for climatological forcing data is unknown because it is primarily designed for companies. I have no indication that the data are insufficiently accurate for use in this study. I propose to add an explanatory text from the website on the first page of the Supplementary Material after https://www.soda-pro.com/web-services/meteo-data/monthly-means-solar-irradiance-temperature-relative-humidity:
The SoDa Service originates from a European project funded by the European Commission in 1999. A multi-disciplinary consortium has been assembled, which gathers companies and researchers with the necessary expertise in solar radiation and information and communications technologies. Customers and potential users are also represented as partners in the consortium via the involvement of commercial private vendors of solar radiation databases and of representatives of large international or local environmental research and development programs. The consortium:

1. ARMINES (administrative co-ordinator) *France*
2. MINES ParisTech - ARMINES - Centre Energétique et Procédés - Groupe Observation Modélisation et Décision (scientific co-ordinator) *France*
3. MINES ParisTech - Les Presses MINES ParisTech *France*
4. European Commission - Joint Research Centre *Italy*
5. Meteorologiai Szolgalat - Meteorological Satellites Dpt *Hungary*
6. METEOTEST *Switzerland*
7. Carl von Ossietzky Universität Oldenburg Faculty of Physics *Germany*
8. ICONS Srl *Italy*
9. University of Manchester Institute of Science and Technology - Department of Physics *United Kingdom*
10. Università degli Studi di Genova - Dipartimento di Fisica *Italy*
11. CNRS - ENTPE - Département Génie Civil et Bâtiment *France*
12. Fraunhofer - Institut fuer Solare Energiesysteme (ISE) *Germany*

Section 2.6, my interpretation: I suppose the comment ‘The data sources are not well described’ relates to this paragraph. The following adjustments are proposed:

Line 202: the following text is inserted before this line, with the second paragraph already suggested in response to reviewer 1:
The forest field and experimental data in Cannell’s compendium (Cannell, 1982) include biomass data abstracted from about 600 publications (up to mid-1981), describing more than 1200 forest stands in 46 countries. The data are used in many biomass-density studies cited in this article (Weller, 1987a; Weller, 1989; Lonsdale, 1990; Enquist et al., 1998; Deng et al., 2012), with the difference that in this study the LAI data from Cannell's compendium are required for the LEBD and GEBD. The reliability of *LAI* data varies due to, for instance, the number of sample trees in the experimental plots. The validity of the data, of which especially reliable estimates of *LAI* are difficult to obtain (Bréda, 2010), can be assessed by the coefficient of determination in the model regressions and by comparing the extinction coefficient in the LEBD with literature values.

The data on *LAI* of the selected stands were measured using litter traps, allometry based on sample trees or destructive methods, with the note that not all publications describe the measurement method. 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 209 and 210: the sentence beginning and ending in these two lines is replaced with the text:

Forests for which LAI was only estimated globally, for which different LAI values were estimated for the dry and wet seasons, or for which LAI was unclear due to a lack of distinction between trees and other plants, such as shrubs and undergrowth, were omitted. Stand data only obtained from published regressions elsewhere were also a reason for omission, especially as reliable estimates of LAI are difficult to obtain (Bréda, 2003). Only stands with an LAI > 1.0 were selected to stay within the validity limits set by the application of Beer's Law.

Line 211: insert after 'unclear':

(see section 2.2)

Line 218: the following text is added to the end of this line (this is also the response to reviewer 1):

Most of the data are from broadleaved forests, which can be considered a limitation. 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 an altitude between 1500 and 2740 m.

Section 2.7: this section is already presented in response to reviewer 1. The second sentence in this response is replaced by the second and thirth sentence in the text hereafter:

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 subset of natural forests in Deng's dataset S1 comprises 1109 forests from the Chinese Forest Biomass Dataset (Luo, 1996) and 241 forests from Cannell's (1982) compendium. Indicated are forest type, age, aboveground biomass, stand density, annual rainfall, annual mean temperature, potential evapotranspiration, altitude, latitude and longitude. 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 used to compare the slopes and intercepts of these three groups of forests with the data of the broadleaved and coniferous dataset of in total 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 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.

Chapter Results

Section 3.1: The focus on the hypothesis is introduced in this section.

Lines 229 and 230, this sentence until ‘is lower’ is replaced by the text:

Based on the model results for the broadleaved dataset in Table 1, we can validate the hypothesis that the exponent in the EBDs converges to 0.50 when gradients in LAI and E_{sglob} are introduced stepwise in the light absorption function. In the interspecific mass-density relationship of Eq. 2A (Table 1, Fig. 1), the 0.22 exponent value

Line 246, insert after the period:

This is close to the hypothesised value of 0.50.

Lines 252 and 253, replace the sentence after ‘and’ with the text:

indicates that the mathematical design of the LEBD and stand data are apropppriate to correct for changes in the light capture of stands in the trajectory of decreasing stand density.

Section 3.2: The focus on the hypothesis is introduced in this section.

Lines 270, insert before this line the text:

The hypothesis that the exponent of N converges to 0.50 in the EBDs is evaluated in the same way for both the coniferous and broadleaved datasets.

Line 281, insert after the period:

The exponent of 0.50 corresponds exactly to the hypothesised value.

Line 286 to 291, replace the text after ‘Table 1’ with:

corresponds with literature (Parker, 2020). The ε value decreases with increasing solar zenith angle (0 directly overhead) due to the generally planophile leaf canopies, compared to broadleaved forests with more random foliage orientation (Chen et al., 1997). The ε value is also lower because the light absorption capacity of the canopy is more affected by shoot clumping, i.e. leaves are more clumped on shoots compared to broadleaved forests (Kim et al., 2011). The close alignment of the extinction coefficient with values reported in the literature indicates that the mathematical design of the LEBD and stand data are appropriate to correct the density series for gradients in energy use.

Chapter Discussion

My interpretation: more scientific explanation and interpretation are needed, with a focus on the hypothesis of the investigation. The presented text below replaces my response to reviewer 1.

Line 328 to 336, these lines until the period in line 336 are replaced with the text:

To get an indication of whether the datasets of broadleaved and coniferous forests are representative, they are compared with each other as well as with the much larger data set of 1350 natural forests without LAI data used by Deng et al. (2012).

Line 349 to 354, this paragraph is replaced with the text:

In the AEBD of Eq. 13 $\log(MN^{\alpha'})$ is expected to increase with increasing E_{sglob} due to largely latitudinal gradients in global radiation. In the coniferous dataset, however, altitudinal gradients may also influence 13 stands between 1500 and 2740 m. The expected increase of $\log(MN^{\alpha'})$ is confirmed by the broadleaved and coniferous forests separately and together (Table 1) and is also visible in the intercepts of the mass–density relationships in Fig. 4, where the $\log k$ values increase in the order of boreal/alpine, temperate and (sub)tropical forests. The exponent values of α’ = 0.56 and α’ = 0.47 for the broadleaved and coniferous datasets, respectively, and α’ = 0.52 for all stands together are not far from the self-thinning rule. The lower regression coefficient of f = 0.14 for the coniferous dataset compared to $f = 0.30$ for the broadleaved dataset may be due to the lower competitive ability of many coniferous tree species at higher values of E_{sglob}. However, more data is needed to support this suggestion.

Line 371, add to this paragraph:

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.

Line 372 to 417, replace these paragraphs with the text that follows:

The hypothesis that the exponent in the EBD model converges to the self-thinning rule is not tested for intraspecific forest mass-density relationships, such as time series of single forest stands and intraspecific density series of neighbouring forests with a corresponding species composition. However, the self-thinning rule in its original interpretation as the upper boundary of mean plant biomass for a give plant density (Yoda et al., 1963; Osawa and Sugita, 1989) and the light experiments on monospecific even-aged plant stands cited before confirm the self-thinning rule for constant levels of light absorption at and below the upper boundary (see Sect. 2.1). Correcting deviations from the self-thinning rule due to light absorption gradients within time and density series using the light absorption function gives the exponent a completely different meaning.

The exponent -β 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 (Eq. 3). Variations in the exponent in time series of largely undisturbed forests have been shown to be a function of variations in environmental drivers, resource conditions (that might also change with forest development), and forest properties (Yu et al., 2024). The variation in the value of the normalization constant among thinning lines has received relatively little attention (Dillon et al., 2019), but is correlated with the estimate of the exponent in the log - log relationship of Eq. 3 (Westoby, 1984). The normalization constant is described as a measure of a constant whole stand energy use (e.g., Westoby, 1984; White et al., 2007; Deng et al., 2012), with variations due to differences in resource use through time that are much stronger than variations in the exponent (Deng et al., 2006; Dai et al., 2009). This means that both the exponent and the normalization constant in the allometric mass-density relationship are a function of stand and environmental drivers, while in the EBDs the exponent is supposed to converge to a single value, the self-thinning rule, and only the light absorption function is a function of stand and environmental parameters.

This raises the question of how the introduction of a relatively simple light absorption function in the allometric mass-density relationship can reflect the myriad processes that affect the self-thinning process. A thermodynamic view on self-thinning can throw new light on this question, as thermodynamics can deal with the mathematical relationship between observations, without (sub)models of the underlying processes. The thermodynamic nature of the EBD model shows in natural forests, where individuals of all age classes are present simultaneously. Here, a steady state may ultimately be reached where the net production is equal to the losses, and changes in biomass tend to be zero. This means that the energy budget, as the sum of the ingoing and outgoing energy fluxes, is also zero, and it is not appropriate to specify the energy term log$k$ in the mass-density relationship. However, from a thermodynamic point of view, entropy production is as important as energy. Following a further determination of the regression coefficients in the GEBD, the entropy production can be introduced into the GEBD, using the strong linear association with E_{ssol} (e.g., Aoki, 1987, 1989; Brunsell et al., 2011), which allows the development of a physically correct thermodynamic equation. The thermodynamic equation describes the dynamic equilibrium of forest biomass and density together, as defined by the self-thinning rule, with the regime of entropy production. Time does not enter into the dynamic equilibrium described with the model, because the rate of biomass accumulation over time is not described (Westoby, 1984). The dynamic equilibrium can be seen as an attractor for forest succession after human, biotic and abiotic disturbances.

Deviations from the self-thinning rule may indicate 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. The use of EBDs and growth models together 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 (Yu et al., 2024). The 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).

In forestry, the EBD model offers perspectives to further explain the variation in empirically determined self-thinning lines for different species/region combinations in relation to light (and nutrient) use, contributing to the reduction of errors in growth and yield models that are constrained by maximum size-density boundary lines (Vanderschaaf and Burkhart, 2007). 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 light experiments and the EBD model. Although the thermodynamic interpretation of the EBD model and the mechanistic models cited in this article represent different scales of inquiry and different scientific approaches, they can inform one another to obtain more insight into the common processes underlying these theories (Price et al., 2010).

New references compared to preprint of 9 October 2025:

Hamilton, N.S., Matthew, C. and Lemaire, G.: 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.

Osawa, A., Sugita, S.: The self-thinning rule: Another interpretation of Weller's results. Ecology, 70, 279–283, https://doi.org/10.2307/1938435, 1989.

Parker, G.G.: Tamm review: Leaf Area Index (LAI) is both a determinant and a consequence of important processes in vegetation canopies. Forest Ecol. Manag. 477, 118496, http://dx.doi.org/10.1016/j.foreco.2020.118496, 2020.

VanderSchaaf, C.L. and Burkhart, H.E.: Comparison of methods to estimate Reineke's maximum size-density relationship species boundary slope. For. Sci., 53 (3), 435–442, https://doi.org/10.1093/forestscience/53.3.435, 2007.

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.: 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.