

*Supplementary information to the manuscript “Unraveling Amazon tree community assembly using Maximum Information Entropy: a quantitative analysis of tropical forest ecology”.*

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## BOX S1

**Entities:**

*The basic unit of the MEF model which can exist in different states. Here, this constitutes a collection of genera existing at a site, hence each entity can be considered a single genus.*

**States:**

*Classification of different ways any entity can exist. Within the system, states of each entity describe their specific abundance at that site.*

*Microstates constitute the spatial and temporal composition for the states of the entities in the system. Macrostates depict the entities of a system independent of the spatial or temporal composition, e.g., the overall relative abundance distribution but not including processes leading to this distribution (such as dispersal).*

**Traits or properties:**

*The measurable attributes for each entity, of which the values can be different for each entity. For example, genera differ in average wood density, seed mass, height etcetera. Here defined by the functional traits as described in the main text.*

**Maximally uninformative prior:**

*All the information regarding the states before specific constraints are introduced. Described as maximally uninformative as all empirical information should be introduced in the form of constraints quantify the maximal gain of information regarding the different constraints (e.g. traits or prior distribution in this case).*

**Prior distribution:**

*The expected states for the entities, here either constituted by the observed relative abundance of each entity in the summed sample (i.e. summed abundances describing the metacommunity) or by a maximally uninformed (uniform) distribution (see above). The former would be a neutral prior (expected local abundance is equal to the abundance in the larger metacommunity).*

**Community-weighted mean or variance:**

*The mean or variance of genus-level trait value over all constituent present species (for each entity) weighted by the relative abundance of each entity at a specific site.*

**Box S1. Different ingredients necessary for analyses using MEF.** Definitions of the most important terms used in the MEF analyses and throughout the main text to provide the necessary framework of understanding, adapted from [1].

## BOX S2

<p>The Maximum Entropy Formalism as applied here works based on a conceptual model called CATS (<i>Community Assembly by Trait Selection</i> [1–3]) and makes use of three inputs:</p> <p>i) A <b>trait matrix</b> containing the measured functional traits of each of the <math>S</math> total genera in the total regional pool, these can be of either discrete or continuous form.</p> <p>ii) A <b>vector of <math>n</math> community weighted trait values</b>, estimating the average trait value over all individuals in the local community for each of the traits</p> <p>iii) A <b>prior probability distribution</b> specifying the regional abundance distribution, quantifying potential contributions of the regional pool of recruits to the structure of local communities. Using these three sources of information, the model predicts relative abundances (<math>p_i</math>) in the form of Bayesian probabilities for each genus in each local community without assuming any a priori relations or processes. This is achieved by finding the vector of relative abundances maximizing entropy:</p> $1) RE = - \sum_{i=1}^s p_i \ln \left( \frac{p_i}{q_i} \right)$ <p>with <math>q_i</math> the regional species pool abundance of species <math>i</math> and <math>RE</math> (Relative Entropy) subject to the known constraints for <math>j</math> traits and <math>i</math> species.:</p> $2) \bar{t}_j = \sum_{i=1}^s o_i t_{ij} \text{ and } 3) \sum_{i=1}^s p_i = 1$ <p>The solution is a generalized exponential distribution where the <math>\lambda</math> values measure the importance of each trait when all other traits are constant:</p> $4) p_i = \frac{q_i e^{\sum_{j=1}^n \lambda_j t_{ij}}}{\sum_{i=1}^s q_i e^{\sum_{j=1}^n \lambda_j t_{ij}}}$ <p>Note that when all <math>\lambda</math> values are zero, i.e. there is no trait based selection, <math>p_i = q_i</math></p>	<p>The final step is to measure the proportion of total deviance accounted for between observed and predicted relative abundances for each of the four-step solution. These are the <math>R^2_{KL}</math> values, a generalization of the classic <math>R^2</math> index of maximum likelihood estimation using the Kullback-Leibler index [4,5]:</p> <p>i) <math>\bar{R}^2_{KL}(\mathbf{u})</math>: fit of model bias, the model null hypotheses given a uniform prior (i.e. equal distribution in the regional pool of recruits).</p> <p>ii) <math>R^2_{KL}(\mathbf{u}, \mathbf{t})</math>: fit using again a uniform prior but including traits as constraints.</p> <p>iii) <math>\bar{R}^2_{KL}(\mathbf{m})</math>: fit using the metacommunity prior but excluding traits as constraints</p> <p>iv) <math>R^2_{KL}(\mathbf{m}, \mathbf{t})</math>: fit using the metacommunity prior and including traits as constraints</p> <p>The general form of the <math>R^2_{KL}</math> divergence is calculated by:</p> $5) R^2_{KL} = 1 - \frac{\sum_{k=1}^c \sum_{i=1}^s O_{ik} \ln \left( \frac{O_{ik}}{P_{ik}} \right)}{\sum_{j=k}^c \sum_{i=1}^s O_{ik} \ln \left( \frac{O_{ij}}{Q_{i,0}} \right)}$ <p>With the following parameters:</p> <p><math>O_{ik}</math> as the observed relative abundances of the <math>i^{th}</math> genus in the <math>k^{th}</math> community,</p> <p><math>P_{ik}</math> the accompanying predicted values for the specific model of the four solution step as described in the main text and,</p> <p><math>Q_{i,0}</math> the predicted relative abundances given only the maximum uninformative prior.</p> <p>Further details on the calculation of all separate <math>R^2_{KL}</math> values and accompanying pure trait, pure metacommunity, joint information and biologically unexplained information can be found Box S3.</p>
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**Box S2. Mathematical description of the Maximum Entropy Formalism for the four-step solution.** Left panel shows necessary ingredients and formulation of the Maximum Entropy Formalism. Right side panel shows decomposition of the proportion of total deviance accounted for between observed and predicted relative abundances for each of the four-step solution, adapted from [5].

## BOX S3

The purpose of using MEF is to decompose the deviance between observed and predicted relative abundances using the four-step solution as described in the main text. The values generated are described below. The  $R^2_{KL}$  value is a generalization of the classic  $R^2$  index of maximum likelihood estimation using the Kullback-Leibler index for a non-linear regression including a multinomial error structure [2,4,5]. In essence, it is a way of measuring the proportion of total deviance accounted for by that specific model from one of the four steps:

$\bar{R}^2_{KL}(\mathbf{u})$ : fit of model bias, the model null hypotheses given a uniform prior and permuted traits

$R^2_{KL}(\mathbf{u}, \mathbf{t})$ : fit using a uniform prior but including observed traits as constraints

$\bar{R}^2_{KL}(\mathbf{m})$ : fit using the metacommunity prior but excluding observed traits as constraints

$R^2_{KL}(\mathbf{m}, \mathbf{t})$ : fit using the metacommunity prior and including observed traits as constraints

1) The increase in the explained deviance due to traits can be calculated either by

$$\Delta R^2_{KL}(\mathbf{t}|\boldsymbol{\varphi}) = R^2_{KL}(\mathbf{u}, \mathbf{t}) - \bar{R}^2_{KL}(\mathbf{u})$$

Increase in explained deviance due to traits beyond that due solely to model bias

$$\text{or } \Delta R^2_{KL}(\mathbf{t}|\mathbf{m}) = R^2_{KL}(\mathbf{m}, \mathbf{t}) - \bar{R}^2_{KL}(\mathbf{m})$$

Increase in explained deviance due to traits beyond contributions made by the meta-community

2) The increase in explained deviance due dispersal mass effects via the metacommunity can be calculated by either:

$$\Delta R^2_{KL}(\mathbf{m}|\boldsymbol{\varphi}) = \bar{R}^2_{KL}(\mathbf{m}) - \bar{R}^2_{KL}(\mathbf{u})$$

Increase in explained deviance (if any) due to the metacommunity beyond that due to model bias

$$\text{or } \Delta R^2_{KL}(\mathbf{m}|\mathbf{t}) = R^2_{KL}(\mathbf{m}, \mathbf{t}) - R^2_{KL}(\mathbf{u}, \mathbf{t})$$

Increase in explained deviance due to the meta-community given traits, relative to the explained deviance due only to the traits: i.e. information unique to neutral prior

3) And finally the joint information and the biologically unexplained information:

$$\Delta R^2_{KL}(\mathbf{m}+\mathbf{t}) = \Delta R^2_{KL}(\mathbf{m}|\boldsymbol{\varphi}) - \Delta R^2_{KL}(\mathbf{m}|\mathbf{t}) = \Delta R^2_{KL}(\mathbf{t}|\boldsymbol{\varphi}) - \Delta R^2_{KL}(\mathbf{t}|\mathbf{m})$$

Joint information gain, or increase in explained deviance due to both the metacommunity prior and the constraints based on the traits

$$1 - \Delta R^2_{KL}(\mathbf{m}, \mathbf{t})$$

Biologically unexplained variation

*From these values the pure trait, pure metacommunity, joint effect and biologically unexplained variation can be calculated by the following calculations:*

$$\text{Pure trait effects: } \Delta R^2_{KL}(\mathbf{t}|\mathbf{m}) / (1 - \bar{R}^2_{KL}(\mathbf{u}))$$

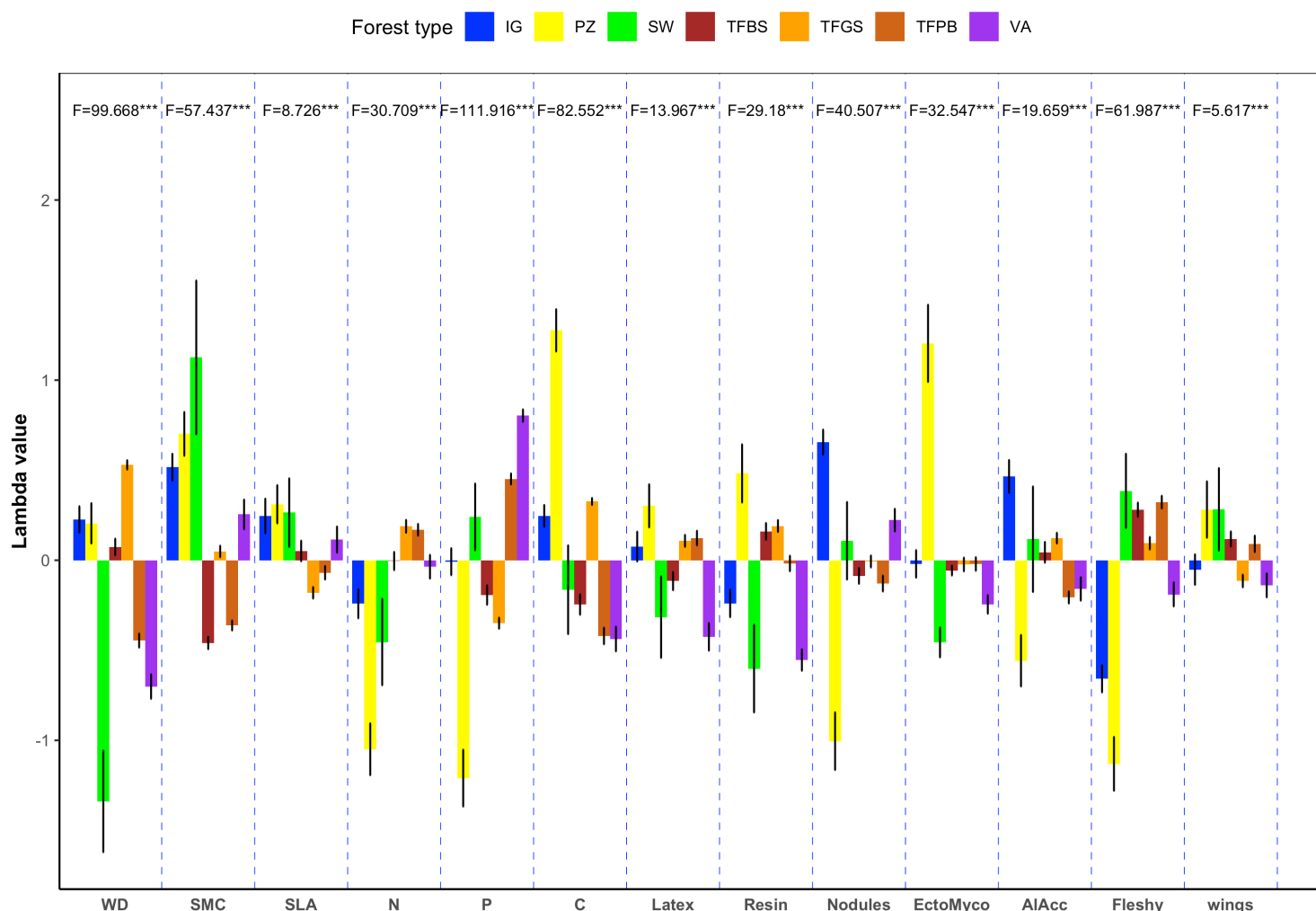
$$\text{Pure metacommunity effects: } \Delta R^2_{KL}(\mathbf{m}|\mathbf{t}) / (1 - \bar{R}^2_{KL}(\mathbf{u}))$$

$$\text{Joint metacommunity and trait effects: } \Delta R^2_{KL}(\mathbf{m}+\mathbf{t}) / (1 - \bar{R}^2_{KL}(\mathbf{u}))$$

$$\text{Unexplained effects: } 1 - \Delta R^2_{KL}(\mathbf{m}, \mathbf{t}) / (1 - \bar{R}^2_{KL}(\mathbf{u}))$$

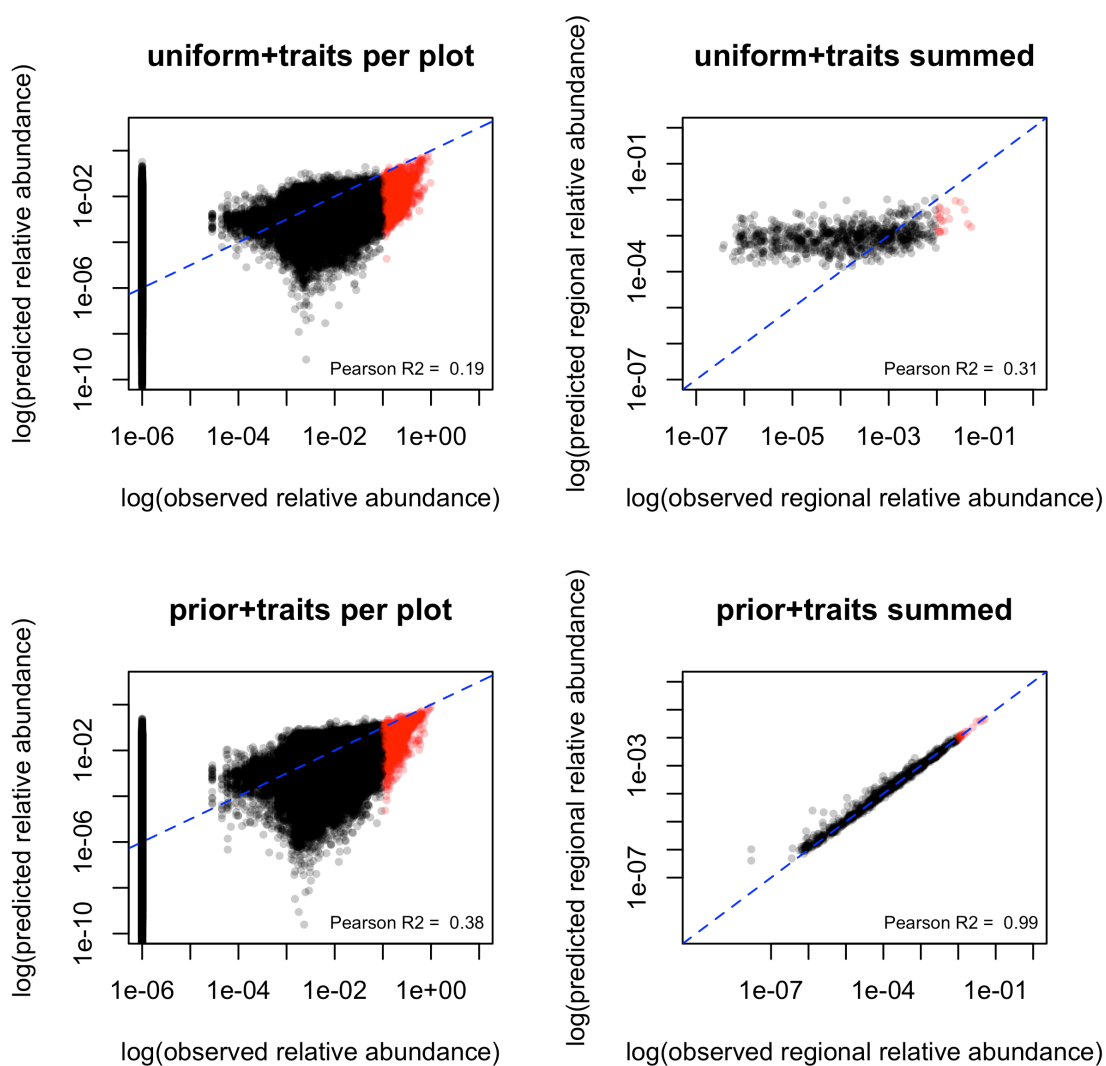
**Box S3. Detailed decomposition of the four-step solution from the MEF.** Mathematical description of the decomposition based on the constraints and prior distributions (both uniform and neutral) for each of the steps from the four-step solution to measure the proportion of total deviance accounted for by each specific model from one of the four steps, adapted from [5].

FIGURE S1



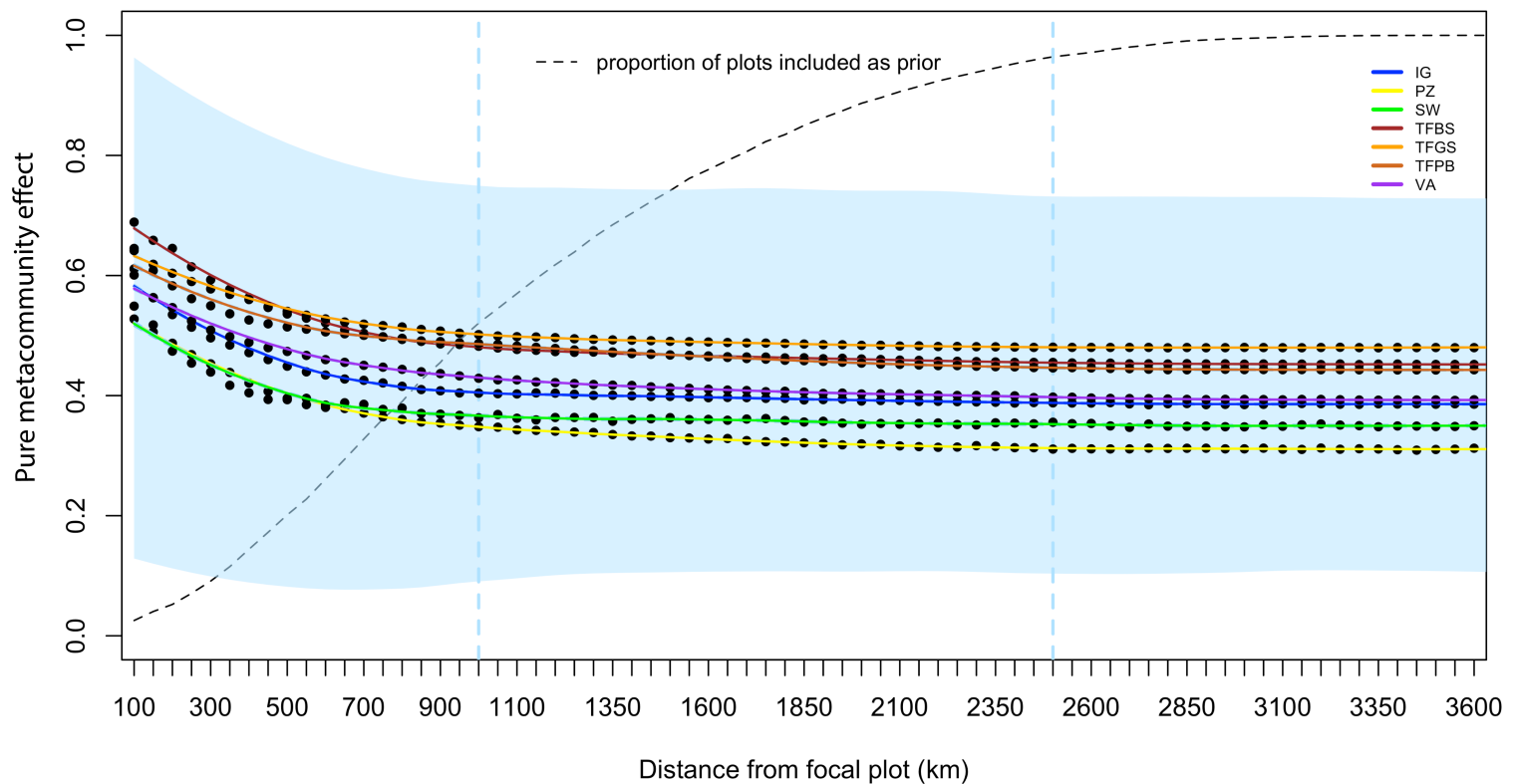
**Fig. S1. Mean lambda values with standard error bars for each functional trait and compared between forest types.** Forest type abbreviations are *igapó* (IG), podzol (PZ), swamp (SW), Brazilian shield *terra firme* (TFBS), Guiana Shield *terra firme* (TFGS), Pebas *terra firme* (TFPB) and *várzea* (VA). Positive values indicate positive selection, reflective of a strong association between higher trait values and higher abundances, negative values reflect the opposite with high trait values associated with lower abundances. Differences between forest types were tested with a one-way analysis of variance with significance levels corresponding to: ns non-significant, \*  $p < .05$ , \*\*  $p < .01$  and \*\*\*  $p < .001$ . Abbreviations indicate functional traits: wood density (WD), seed mass class (SMC), specific leaf area (SLA), nitrogen (N), phosphorus (P) and carbon (C) leaf content. Further traits include the presence/absence of Latex, Resin, Nodules, Ectomycorrhiza (EctoMyco), the ability to accumulate aluminium (AlAcc), and the presence/absence of fleshy fruits (Fleshy) and winged seeds (Wings).

FIGURE S2



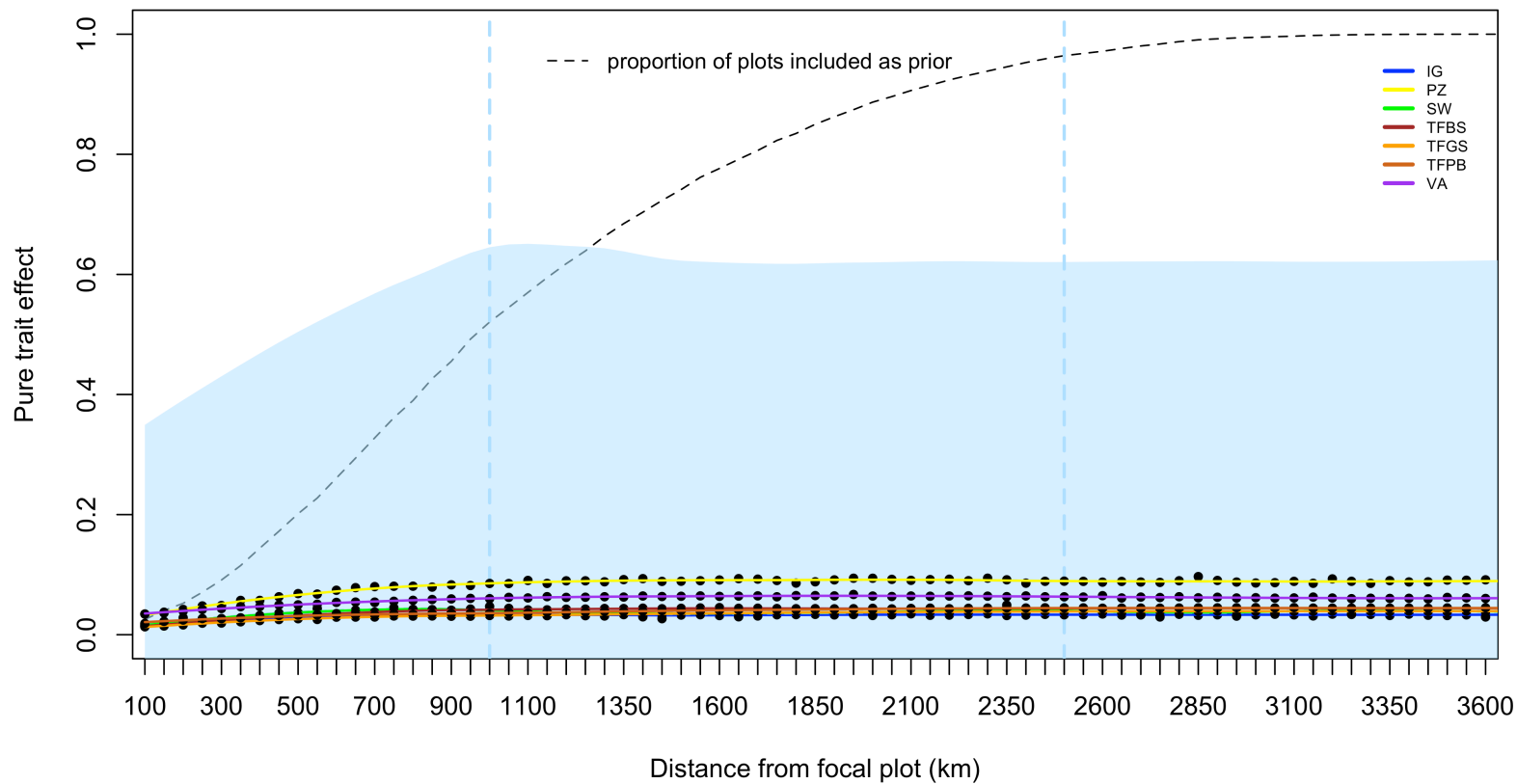
**Fig. S2.** Observed relative abundances for each genus in all plots plotted against predicted relative abundance per plot (left) and summed (right) using only the traits as constraints in combination with a uniform prior (top) or the hybrid model using both traits and the metacommunity relative abundance as prior (bottom) on a log-log scale. Top figures show predictions using only a uniform prior, left separate for all plots and right for all genera summed over all plots. Bottom figures show predictions using the regional prior, again separate for all plots and genera (left) and summed over all plots for each genus (right). Red points indicate taxa with observed relative abundances over 1e-1. Lines show the  $x=y$  prediction and  $R^2$  values correspond to the Pearson's correlation coefficient.

FIGURE S3



**Fig. S3. Distance decay of pure metacommunity effect.** X-axis represents radius of metacommunity prior; i.e. first 100 km consists of just a few plots and at 3800 km all plots are taken into account with dashed line indicating the mean number of plots for that distance included as metacommunity prior. Y-axis represents the pure metacommunity effect, i.e. the increase in explained deviance due to the metacommunity (given traits), but relative to the explained deviance due only to the traits. It is the information unique to neutral prior taken relative to the model bias. Solid lines indicate predictions from loess regression based on all points with different colors indicating the forest types with abbreviations as in main text. Blue vertical lines indicate 1000 and 2500 km boundary points. Blue shading reflects minimum and maximum loess regression predicted values.

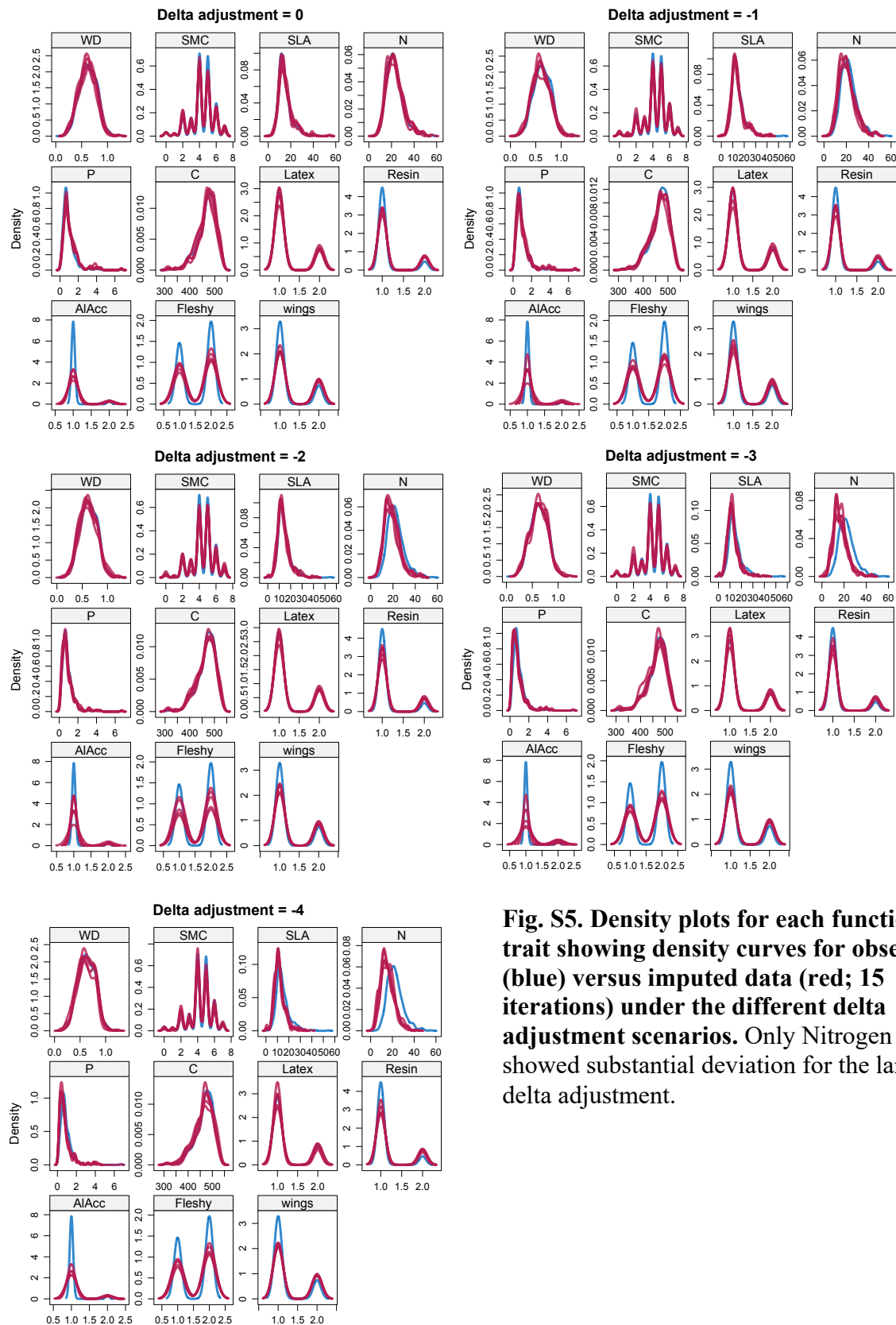
FIGURE S4



**Fig. S4. Distance decay of pure trait effect for each forest type separately and the overall dataset.** X-axis represents the radius of the metacommunity prior; i.e. the first 100 km consists of just a few plots and at 3800 km all plots are taken into account. Y-axis represent the pure trait effect, i.e. the increase in explained deviance due to traits beyond contributions made by the meta-community and relative to the model bias (see also Box S2). Colors indicate the different forest types with abbreviations as in main text. Lines indicate the predictions following from the loess regression based on all points. Blue vertical lines indicate the 1000 and 2500 km boundary points. Blue shading reflects maximum values for that distance of the whole dataset.

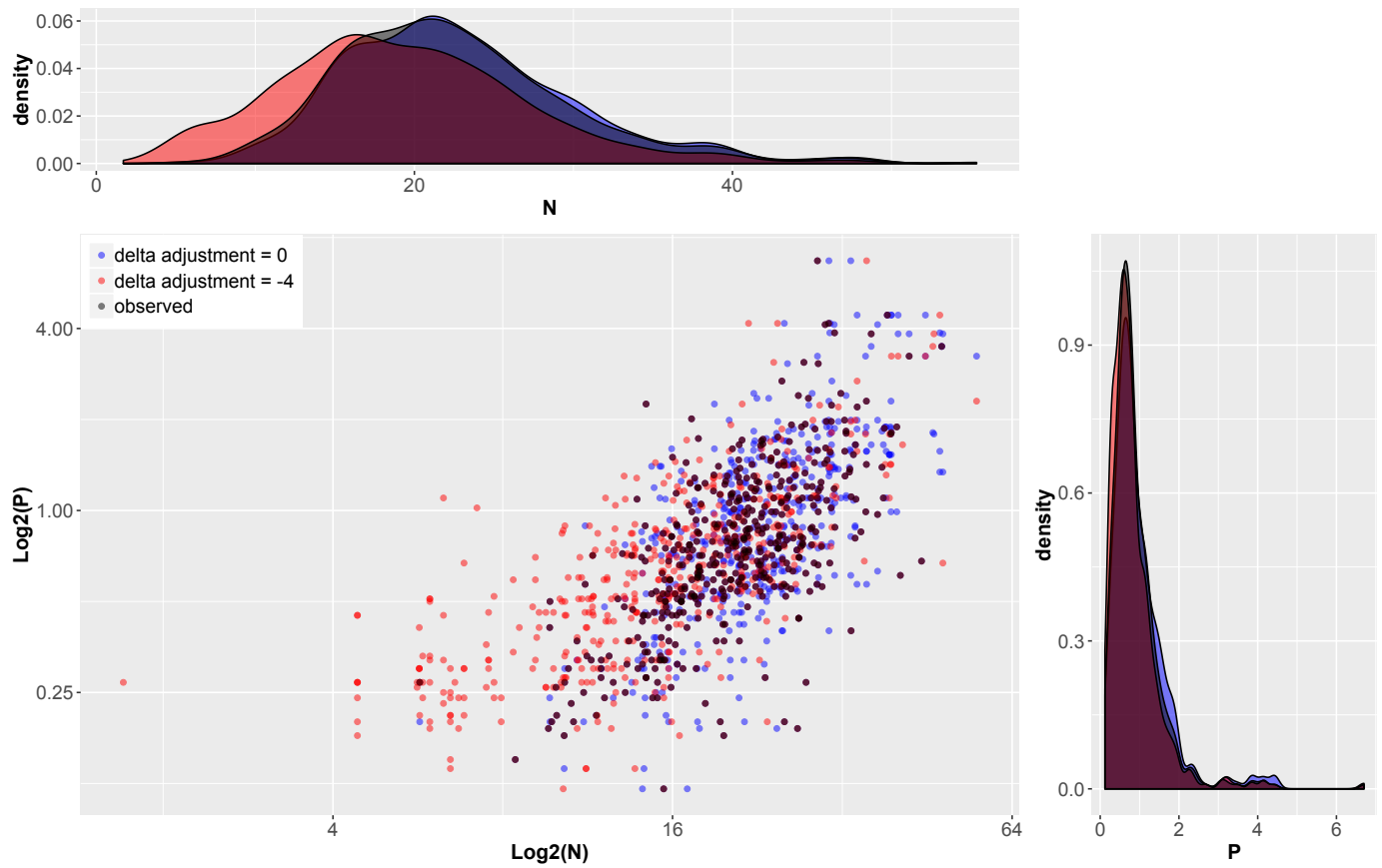


FIGURE S5



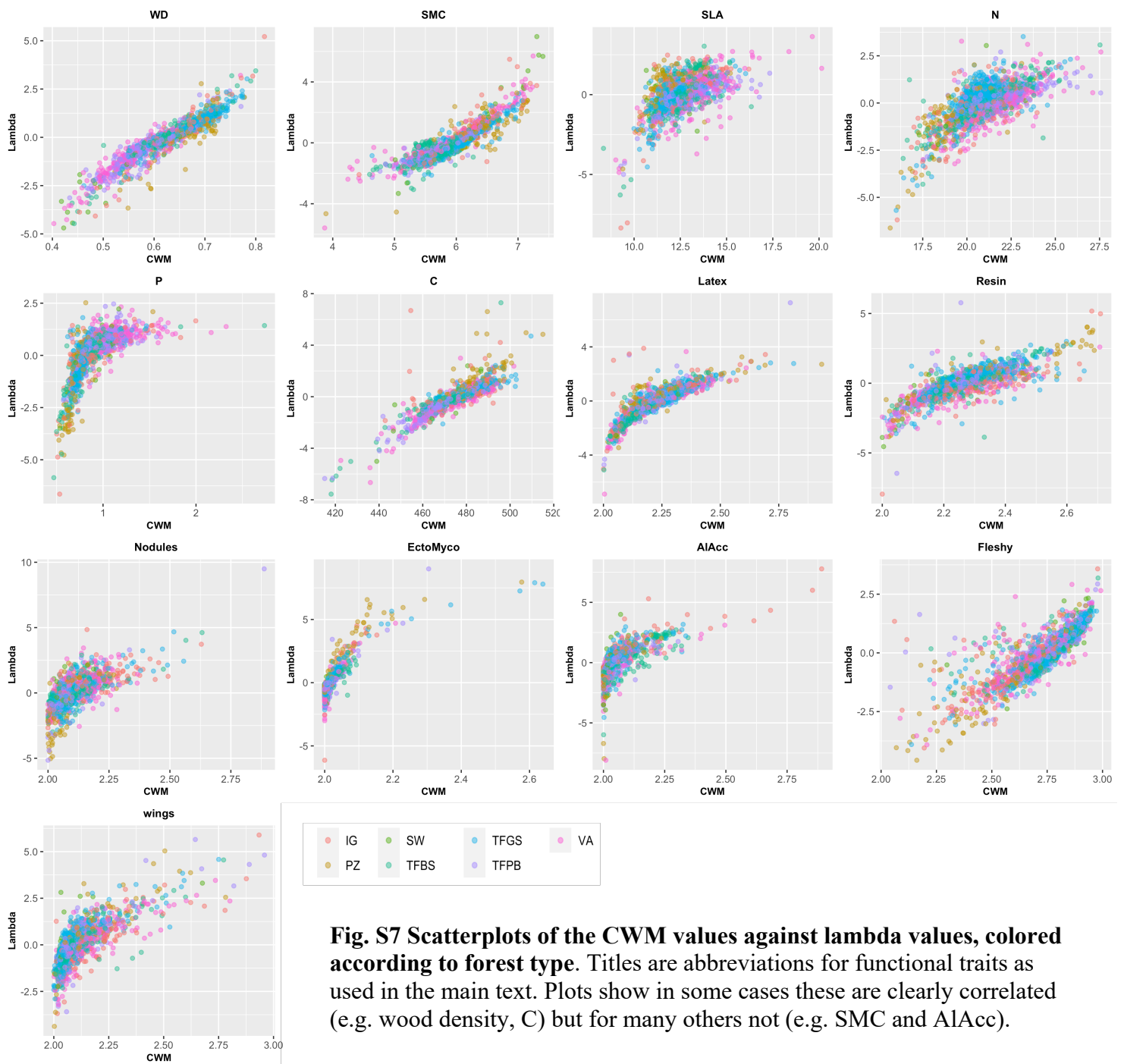
**Fig. S5. Density plots for each functional trait showing density curves for observed (blue) versus imputed data (red; 15 iterations) under the different delta adjustment scenarios. Only Nitrogen showed substantial deviation for the larger delta adjustment.**

FIGURE S6



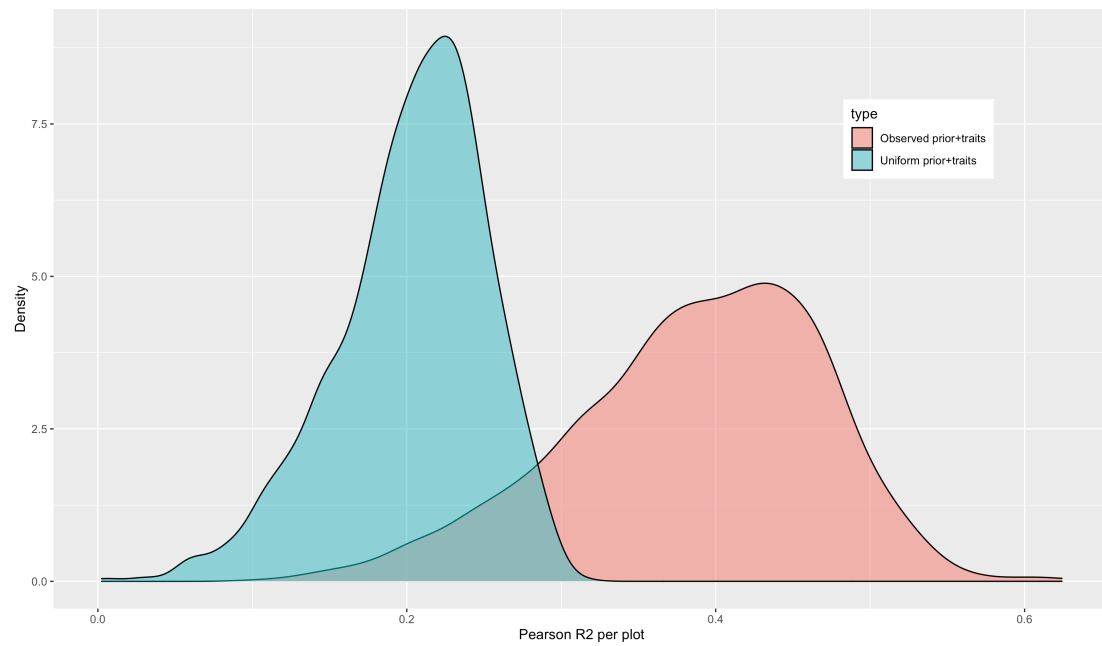
**Fig. S6. Scatterplot of observed vs. imputed leaf nitrogen and phosphorus content under different delta adjustment scenarios.** As Leaf Nitrogen content showed substantial deviation in the larger delta adjustment scenario it was here plotted versus Leaf Phosphorus content, which showed hardly any deviation.

FIGURE S7



**Fig. S7 Scatterplots of the CWM values against lambda values, colored according to forest type.** Titles are abbreviations for functional traits as used in the main text. Plots show in some cases these are clearly correlated (e.g. wood density, C) but for many others not (e.g. SMC and AlAcc).

FIGURE S8



**Fig. S8 Density plot of the per-plot-Pearson correlation coefficient between predicted relative abundances of each genus.** Models either used a uniform prior and functional traits (blue) or the actual observed prior and functional traits (red), results show a large increase in accuracy for the latter.

TABLE S1

**Table S1. Decomposition of results from the various maximum entropy models, combined and separated by forest type (PZ podzol, IG igapó, VA várzea, SW Swamp, TF terra firme with subregions BS (Brazilian Shield), GS (Guyana Shield) and PB (Pebas formation)).** Top rows indicate estimated proportions ( $R^2_{KL}$ ) of total information reflective of variation in local relative abundance explained for by the various models. Middle rows indicate the specific information gain from any one of the used models relative to the model bias. Bottom rows show the actual effects of traits, the metacommunity and the joint information relative to the model bias.

Explained proportions	Forest types							Combined
	PZ	VA	IG	SW	TFBS	TFGS	TFPB	
$\bar{R}^2_{KL}(u)$ <i>model bias fit</i>	0.17	0.11	0.12	0.19	0.08	0.08	0.06	0.09
$\bar{R}^2_{KL}(m)$ <i>pure neutral model fit</i>	0.51	0.51	0.52	0.55	0.55	0.62	0.55	0.56
$R^2_{KL}(u,t)$ <i>pure trait model fit</i>	0.34	0.25	0.23	0.34	0.21	0.24	0.20	0.23
$R^2_{KL}(m,t)$ <i>hybrid model fit</i>	0.59	0.57	0.55	0.57	0.59	0.66	0.59	0.60
<b>Increase in explained deviance</b>								
$\Delta R^2_{KL}(m \phi)$ <i>metacommunity effect beyond model bias</i>	0.35	0.40	0.40	0.36	0.47	0.54	0.48	0.47
$\Delta R^2_{KL}(t \phi)$ <i>trait effect beyond model bias</i>	0.17	0.14	0.11	0.15	0.13	0.16	0.14	0.14
$\Delta R^2_{KL}(t m)$ <i>trait effect beyond metacommunity effect</i>	0.07	0.05	0.03	0.02	0.04	0.04	0.04	0.04
$\Delta R^2_{KL}(m t)$ <i>metacommunity effect relative to trait effects</i>	0.25	0.32	0.32	0.23	0.38	0.42	0.39	0.37
$\Delta R^2_{KL}(m+t)$ <i>joint effect of metacommunity and traits</i>	0.10	0.08	0.08	0.13	0.09	0.12	0.09	0.10
$1 - \Delta R^2_{KL}(m,t)$ <i>unexplained effects</i>	0.41	0.43	0.45	0.43	0.41	0.34	0.41	0.40
<b>Biologically relevant information</b>								
Pure trait effect <i>Information from traits, relative to bias</i>	0.09	0.06	0.04	0.03	0.05	0.04	0.05	0.05
Pure metacommunity effect <i>Information from metacommunity, relative to bias</i>	0.30	0.36	0.37	0.26	0.42	0.45	0.41	0.40
Joint effect <i>Information from joint effect, relative to bias</i>	0.11	0.09	0.09	0.17	0.09	0.13	0.10	0.11
Unexplained information <i>Left over information not explained, relative to bias</i>	0.49	0.49	0.51	0.54	0.44	0.38	0.44	0.44

TABLE S2

**Table S2. Summary statistics overview for the linear models of the various scenarios under the delta adjustment technique as described in the main text.** Rows indicate the different delta adjustments used with the columns representing the standard summary statistics of the linear model comparing the imputed versus observed trait values. Results showed similar patterns with each imputation scenario, indicating a robust imputation procedure.

Scenario	Summary statistics linear model $lm(\text{imputed} \sim \text{observed})$						
	Intercept	Std. error	T value	Pr.	R <sup>2</sup>	Adj. R <sup>2</sup>	Sigma
<i>Delta 0</i>	-.33	.07	-4.85	1.42e-06	.32	.33	.63
<i>Delta -2.5</i>	-.34	.06	-5.93	4.31e-09	.37	.37	.58
<i>Delta -5</i>	-.16	.04	-3.57	3.77e-04	.40	.40	.53
<i>Delta -7.5</i>	.64	.09	-7.33	5.18e-13	.42	.42	.88
<i>Delta -10</i>	0.09	.04	3.17	1.57e-03	.47	.47	.48

## S-A Ecological interpretation of the MEF results

Signals of quantitative environmental selection were found to be highest for podzol forests, whereas its counterpart in the form of the dispersal mass effect from the regional pool of genera had the second lowest value. Podzol forests, having extremely nutrient poor soils could reflect a much stronger selective environment than any of the other forest types. *Terra firme* forests, presumably reflective of a less strong selective environment in terms of resource availability, showed the opposite, with approximately half of the pure trait effect in comparison with podzol forests (even when rarefied to accommodate for different sample sizes). Traits associated with protection against herbivores such as latex [7] and high leaf carbon content showed higher values associated with greater abundance on podzol soils, whereas traits indicative of investment in growth and photosynthetic ability such as high foliar concentrations of P and N [8] showed strong negative associations on nutrient poor soils. The ability to accumulate aluminium was also strongly positively associated with relative abundance on *igapó* forests, which can potentially be richer in aluminium. Lambda values also showed strong negative lambda values for wood density in swamp and forests, fitting high tree mortality and many individuals belonging to pioneer species in especially the western Amazonian swamp forests. *Várzea* and Pebas *terra firme* forests showed a similar response. As the Pebas consists mainly of Andean sediments it has higher nutrient content, promoting lower wood density, supported by our results whereas *várzea* forests are also often flooded. There were also traits that showed no specific (strong) signal of selection on certain forest types (either positive or negative), such as latex on *igapó* and ectomycorrhiza on terra firme forests (see Fig. S1 for all lambda values). Interestingly, terra firme forests in general showed the smallest lambda values overall (positive or negative). This may be indicative of either more pronounced demographic stochasticity or ecological drift eliminating the association between traits and relative abundance. Lower effects of selection in general or more (random) variation due to the larger species pool in comparison with other forest types, however, could also be the result of mixing heterogeneous microenvironments into a single environmental class. Support for such heterogeneity within terra firme forests having influence on distribution of functional traits on valleys or plateaus has recently been found [9]. In addition, natural but also anthropogenic [10] disturbance history affects biotic community composition and can lead to changes in tree community through time, blurring relationships between traits and relative abundances. It should further be noted that, although for terra firme forests we were able to make a distinction by subregion, true within forest type heterogeneity was not taken into account. This might cause an underestimation of the deterministic effect but as of yet cannot be corrected for on this scale and is worth to be investigated in future studies. In addition, podzol forests have a smaller connected surface area and accompanying smaller number of genera in comparison with terra firme forests, adding to the calculated stronger trait effects [11,12]. When more detailed understanding and knowledge of these functional traits would be provided, this would most likely increase the explanatory power of the MEF. The fact, however, that we do not have a very specific knowledge of these interactions and specific traits is precisely the reason why the MEF can provide additional insight.

It should be noted that for species level analyses any micro environmental gradients might prove to also show (stronger) selection at local scales [13,14], as it has been shown that most variation in community composition, due to selection in regard to habitat filtering and niche conservatism, is found at lower taxonomic levels, such as between species within genera [15,16]. In contrast, theoretically it has been shown and tested that immigration numbers are actually very robust across taxonomic scales [17], validating our results of the metacommunity importance using genus level taxonomy. Spatial patterns of metacommunity effects showed shallowest declines in the centre, supporting the suggestion that high diversity of the Amazonian interior could be explained by influx of recruits due to large (overlapping) ranges. This mid-domain effect [18], however, would also predict lower species richness for the edges due to lower range overlap, assuming a closed community. This is not the case, as there is a strong species richness gradient from West (rich) to Eastern Amazonian forests (poor) [19]. The lower metacommunity effect for the edges then is most likely not due to less absolute influx of genera, but rather less influx from the Amazonian tree community. Influx from the species-rich Andes could account for the high diversity [20], yet low Amazonian metacommunity effect for Western Amazonian forests. In contrast, South-eastern parts of Amazonia receive influx from tree species-poor biomes (i.e. the Cerrado) resulting in lower diversity but also low metacommunity effect for Amazonian trees in this region.



## **S-A2 List of packages used in addition to standard R [1] preloaded packages**

*Vegan* Jari Oksanen, F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, Eduard Szoecs and Helene Wagner (2020). *vegan: Community Ecology Package*. R package version 2.5-7. <https://CRAN.R-project.org/package=vegan>

*FD* Laliberté, E., and P. Legendre (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299-305.

*FD* Laliberté, E., Legendre, P., and B. Shipley. (2014). *FD: measuring functional diversity from multiple traits, and other tools for functional ecology*. R package version 1.0-12.

*Fields* Douglas Nychka, Reinhard Furrer, John Paige, Stephan Sain (2021). "fields: Tools for spatial data." R package version 13.3, <https://github.com/dnychka/fieldsRPackage>

*Binr* Sergei Izrailev (2015). *binr: Cut Numeric Values into Evenly Distributed Groups*. R package version 1.1. <https://CRAN.R-project.org/package=binr>

*doParallel* Microsoft Corporation and Steve Weston (2020). *doParallel: Foreach Parallel Adaptor for the 'parallel' Package*. R package version 1.0.16. <https://CRAN.R-project.org/package=doParallel>

*Itertools* Steve Weston and Hadley Wickham (2014). *itertools: Iterator Tools*. R package version 0.1-3. <https://CRAN.R-project.org/package=itertools>

*Reshape* Hadley Wickham (2007). Reshaping Data with the reshape Package. *Journal of Statistical Software*, 21(12), 1-20. URL <http://www.jstatsoft.org/v21/i12/>.

*Ggplot2* H. Wickham. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York, 2016.

*Plotrix* Lemon, J. (2006) *Plotrix: a package in the red light district of R*. *R-News*, 6(4): 8-12.

*Mice* Stef van Buuren, Karin Groothuis-Oudshoorn (2011). *mice: Multivariate Imputation by Chained Equations in R*. *Journal of Statistical Software*, 45(3), 1-67. DOI 10.18637/jss.v045.i03.

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- [6] H. ter Steege, N. C. a Pitman, O. L. Phillips, J. Chave, D. Sabatier, A. Duque, J.-F. Molino, M.-F. Prévost, R. Spichiger, H. Castellanos, P. von Hildebrand, and R. Vásquez, *Continental-Scale Patterns of Canopy Tree Composition and Function across Amazonia.*, *Nature* **443**, 444 (2006).
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