Ecology and Evolution
Open Access

Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits

Journal:	*Ecology and Evolution*
Manuscript ID	ECE-2016-03-00280.R1
Wiley - Manuscript type:	Original Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Musavi, Talie; Max-Planck-Institute for Biogeochemistry Jena, Biogeochemical Integration Migliavacca, Mirco; Max-Planck-Institute for Biogeochemistry Jena, Biogeochemical Integration van de Weg, Martine Janet; Vrije Universiteit Amsterdam, Amsterdam Global Change Institute Kattge, Jens; Max-Planck-Institute for Biogeochemistry Jena, Biogeochemical Integration; German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig Wohlfahrt, Georg; University of Innsbruck, Institute of Ecology van bodegom, Peter; Leiden University, Institute of Environmental Sciences Reichstein, Markus; Max-Planck-Institute for Biogeochemistry Jena, Biogeochemical Integration; German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig Bahn, Michael; University of Innsbruck, Institute of Ecology Carrara, Arnaud; Mediterranean Center for Environmental Studies (Foundation CEAM) Domingues, Tomas; Ciências e Letras de Ribeirão Preto, Depto. de Biologia, Faculdade de Filosofia Gavazzi, Michael; Eastern Forest Environmental Threat Assessment Center, USDA Forest Service Gianelle, Damiano; Research and Innovation Center, Fondazione Edmund Mach, Department of Sustainable Agro-Ecosystems and Bioresources; Foxlab Joint CNR-FEM Initiative Gimeno, Cristina; Mediterranean Center for Environmental Studies (Foundation CEAM) Granier, André; INRA, Ecologie et, Ecophysiologie Forestierès Gruening, Carsten; European Commission, Joint Research Centre, Institute for Environment and Sustainability Havránková, Kateřina; Global Change Research Institute CAS, Department of Matters and Energy Fluxes Herbst, Mathias; Johann Heinrich von Thünen Institute, Federal Research Institute for Rural Areas, Forestry and Fisheries Hrynkiw, Charmaine; National Hydrology Research Centre (NHRC) Kalhori, Aram; San Diego State University, Department of Biology Kaminski, Thomas; The Inversion Lab Klumpp, Katja; INRA, Grassland Ecosystem Research

	Kolari, Pasi; University of Helsinki, Department of Physics Longdoz, Bernard; INRA, Ecologie et, Ecophysiologie Forestierès Minerbi, Stefano; Provincia Autonoma di Bolzano Servizi Forestali Montagnani, Leonardo; Provincia Autonoma di Bolzano Servizi Forestali; Libera Universita di Bolzano, Faculty of Science and Technology Moors, Eddy; Alterra Green World Research Oechel, Walter ; San Diego State University, Department of Biology; The Open University Walton Hall, Department of Environment, Earth and Ecosystems Reich, Peter; University of Minnesota Twin Cities, Department of Forest Resources; University of Western Sydney, Hawkesbury Institute for the Environment Rohatyn, Shani; Weizmann Institute of Science, Department of Earth and Planetary Sciences; The Hebrew University of Jerusalem, Soil and Water Department Rossi, Alessandra; San Diego State University, Department of Biology Rotenberg, Eyal; Weizmann Institute of Science, Department of Earth and Planetary Sciences Varlagin, Andrej; A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences Wilkinson, Matthew; Environmental and Human Sciences Division, Forest Research Wirth, Christian; Max-Planck-Institute for Biogeochemistry Jena, Biogeochemical Integration; German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig; University of Leipzig, Institute of Special Botany and Functional Biodiversity Mahecha, Miguel; Max-Planck-Institute for Biogeochemistry Jena, Biogeochemical Integration; German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig
Category:	Ecosystem Ecology
Organism:	Ecosystem
Approach:	Method Development
Abstract:	The aim of this study is to systematically analyze the potential and limitations of using plant functional trait observations from global databases versus in-situ data to improve our understanding of vegetation impacts on ecosystem functional properties (EFPs). Using the ecosystem photosynthetic capacity as an example, we first provide an objective approach to derive robust EFP estimates from gross primary productivity (GPP) obtained from eddy covariance flux measurements; Second we investigate the synchrony of EFPs and plant functional traits in time and space to evaluate their relationships, and the extent to which we can benefit from global plant trait databases to explain the variability of ecosystem photosynthetic capacity; Finally we identify a set of plant functional traits controlling ecosystem photosynthetic capacity at selected sites. Suitable estimates of the EFP for ecosystem photosynthetic capacity can be derived from a light response curve of GPP responding to PAR or APAR. Despite the fact that the effect of climate is minimized in the calculation, the estimates indicate substantial interannual variation, even after removing site-years with confounding factors like disturbance. The relationships between foliar nitrogen concentration and ecosystem photosynthetic capacity are tighter when both of the measurements are synchronized in space and time. Considering multiple plant traits simultaneously as predictors for ecosystem photosynthetic capacity variation, the combination of leaf carbon to nitrogen stoichiometry with leaf phosphorus content explains the variance of ecosystem photosynthetic capacity best (adjusted R2 = 0.58). Overall, this study provides an objective approach to identify links between leaf level traits and canopy level processes and highlights the relevance of the dynamic nature of

	ecosystems. Synchronizing measurements of eddy covariance fluxes and plant traits in time and space is shown to be highly relevant to better understand the importance of intra- and interspecific trait variation on ecosystem functioning.

InSitu_Traits.csv
CWMtraits_EFPs.csv
SpeciesComposition.csv

Jena, June, 30th, 2016

Dear Dr. Andrew Beckerman, Editor-in-Chief

Ecology and Evolution Journal,

We are pleased to send you a modified version of the manuscript ID ECE-2016-03-00280, “Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits” by Talie Musavi and co-authors, which has being revised for possible publication in the journal Ecology and Evolution.

We are grateful to the reviewers and the Associate Editor for their comments and remarks that helped to improve the quality of the manuscript and to clarify some important aspects of the analysis overlooked in the first submission.

We carefully revised the manuscript by addressing all the reviewers’ comments and including most of the suggestions. In particular we re-evaluated the manuscript and clarified the concept in the introduction and added a more mechanistic view to our discussion. We made a second data check to prepare tables for publication. In this regard we realized that for one site the data of the *in-situ* year was reported wrong and we corrected for that. As a result, some of the numbers in the results changed a bit. We performed additional analyses based on the ideas of the reviewers in order to confirm the robustness of the results and conclusion (e.g. testing for random effects). In addition, we considered cross-site variation in climate and included the results in the supplementary with a reference in the text.

Please find below the point-by-point response to the reviewers’ comments.

The reviewers’ comments are typed in bold characters, while authors’ replies are in normal characters and the new text included in the revised manuscript is in italics.

We hope to have fully answered all questions and incorporated all the recommendations in the revised version, and we hope that the revised manuscript can be accepted for publication in Ecology and Evolution.

Best regards,

Talie Musavi & co-authors

REPLY TO ASSOCIATE EDITOR

1. **More clarity between concepts/ideas presented in the introduction and the goals/objective of the study. For example, the relevance of synchronizing measurements in space and time is only presented in the methods section.**
2. **Consider framing your analysis around mechanistic hypothesis**
3. **Provide the PFT of a given site and provide more information on the underlying mechanisms of the relationships.**
4. **Test the role of cross-site variation in climate and land management (e.g., fertilization)**

> We re-evaluated the manuscript and clarified the concept better in the introduction, added more mechanistic view to our discussion and clarified methods and concepts when it was not clear to the reviewers. For all the figures we provided the PFTs of the sites by color coding the sites according to their PFTs. This information has also been made available in the tables provided for possible publication. In addition, we considered cross-site variation in climate and included the results in the supplementary with a reference in the text. Based on the comments of the reviewers we conducted a test analyzing the robustness of our results and added that to the text and supplementary information. The test was done using random site-years for Lathuile data compared to *in-situ* N% in order to verify whether the improvement of the relationship when using time-space matched data was by chance.

REPLY TO REVIEWER #1

1. **Musavi et al perform an interesting analysis on inferring ecosystem photosynthetic capacity from leaf traits. They ask the very relevant question of what are the limitations to using ex-situ data to predict processes. The response follows the expectation that better estimates come from in situ and "in tempo" (=same time) data but, to my knowledge, this is the first study quantifying this aspect. In addition, the manuscript also makes an in depth analysis on how to characterize maximum photosynthetic capacity in ecosystems. This is an important contribution to the field and, essentially, I just have a few doubts on things that were not clear to me and that will, hopefully, help the authors improve this very nice manuscript.**

> We are grateful for the positive comments and feedback. Please find below the answers to the questions and comments, and the modification we introduced in the manuscript according to the reviewer's suggestions.

2. **There's a lot of different ideas in the manuscript and it is sometimes difficult to follow what the authors are saying. For instance, I found that mention of EBVs in the intro was more distracting than anything else, as no reference is made to that later on: it's a good idea to think in those terms, but the idea comes too abruptly in the manuscript and it is not developed much. This is just an example and, while I have no other specific suggestions, I**

would encourage the authors to re-read the manuscript and do a bit more of streamlining. Also note that, in addition to environmental response (L116), another paper with A. Richardson shows that biological rhythms are also important drivers of short-term responses (GCB 2012, 18: 1956-1970)

We carefully revised the manuscript and we streamlined the text, in particular as suggested by the reviewer we removed the EBV concept from the introduction. We also modified the introduction in a way that the concepts are introduced less abruptly. The citation suggested was considered very relevant and therefore added (line 120, page 5).

"The short-term (half-hourly to daily) variability of carbon fluxes measured with the EC technique is controlled by meteorological, environmental conditions (Richardson et al., 2007) and, plant rhythms (de Dios et al., 2012). "

3. **Something that may need to be clarified is that the authors claim EFPs to be emergent properties but then they seek to predict GPP from the underlying components... isn't the definition of an emergent property something that cannot be predicted by looking at the underlying components?**

In the manuscript we report the definition of EFP discussed in Reichstein et al., 2014 (PNAS). EFPs are defined as properties of ecosystems related to physical and ecohydrological parameters relevant for land surface–atmosphere interactions. The EFPs – at canopy to ecosystem level- are analogous to ecophysiological characteristics at leaf level, like carboxylation capacity (Vcmax) or the maximum photosynthetic CO_2 uptake at light saturation (i.e. A_{MAX} derived from the light response curve). The word "emergent" in this context was used to identify patterns that emerge from the data measured at ecosystem scales with the eddy fluxes. However, we fully understand the confusion this caused. Therefore, we removed the use of "emergent" in the manuscript as following (line 129:131, page 5):

"The EFPs are ecosystem properties related to physical and ecohydrological parameters relevant for land surface–atmosphere interactions (Reichstein et al., 2014), and are assumed to be affected by vegetation characteristics."

4. **Please explain briefly in the methods how GPP was calculated in La Thuile. Is PAR used to estimate GPP? If not, then please ignore my comment. If yes, then is there any potential circularity in using PAR to estimate GPP and then also in eq. 1?**

PAR is not used for the estimation of GPP. In this study we used Reichstein et al 2005 as method for partitioning NEE into Reco and GPP. The algorithm computes GPP by extrapolating nighttime NEE data (nighttime Reco) using a respiration model based on air temperature data. Moreover, the GPP data used in this analysis are the ones for half hours with high quality measurements of NEE, and therefore not gap-filled. We are confident that there is not spurious correlation between GPP and PAR in the dataset used. We added the explanation to the partitioning method and the reference in the manuscript (lines 197:200, Page 8).

"The GPP values were computed using the commonly used algorithm for flux partitioning, which is based on the extrapolation of nighttime net ecosystem exchange measurements, using an ecosystem respiration model based on air temperature (Reichstein et al., 2005)."

5. **I did not understand how CV was calculated (L298): Along these lines, please explain how IAV was calculated from CV (which indicates intra-annual variability)**

IAV is mostly estimated using standard deviation (SD) or coefficient of variation (CV) – in our study the year to year variation of the ecosystem property (i.e of the 90th percentile of GPP_{sat}). Here we chose CV to consider the site differences and have the SD normalized by the mean. For each site-year we estimated the EFP (e.g. GPP_{sat}). CV is calculated by dividing the standard deviation of annual EFP estimates (GPP_{sat}) by the mean of the annual EFP estimates at the sites. For example if the GPP_{sat} of AT-Neu is 39.43, 33.08, 36.64, 40.45 and 38.99 $\mu molCO_2 m^{-2} s^{-1}$ in 2002, 2003, 2004, 2005, and 2006 respectively, then the CV is 0.08 (2.94/37.72). We added a description and example in the revised manuscript. (line 314:318, page 14)

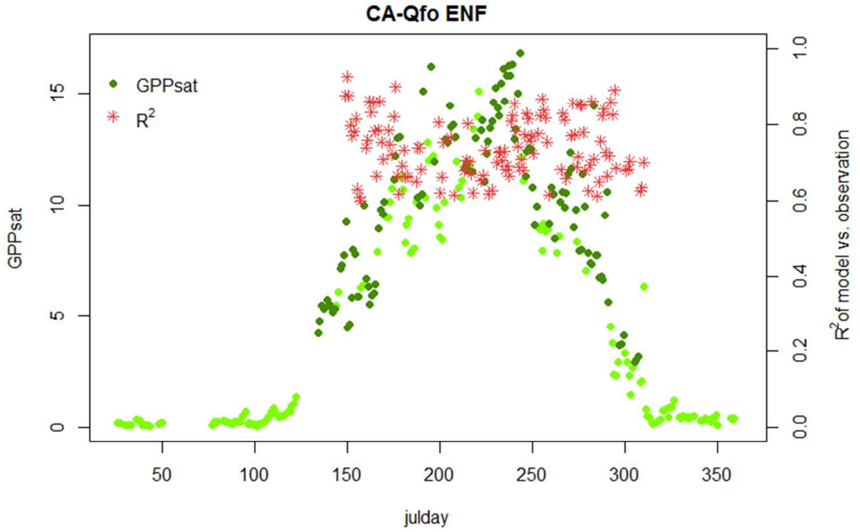
"For example, at each site we computed the annual value for GPPsat (i.e. 90th percentile of GPPsat daily time series). The CV was subsequently computed as the standard deviation of annual GPPsat of all years available, divided by the mean annual GPPsat for all years available at the respective site (CV GPPsat)."

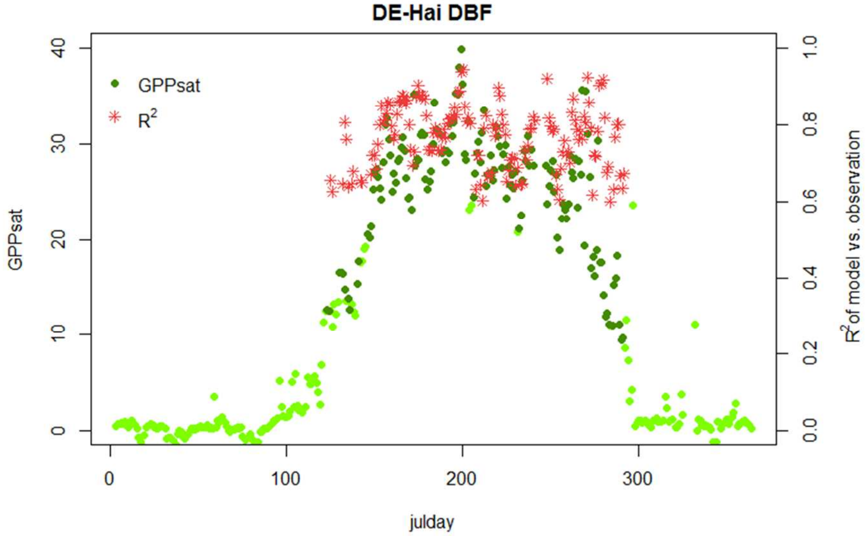
6. **Why use annual, instead of growing season, values? Except in the tropics and relatively aseasonal environments, GPP will always go to 0 at a time or another in the year. Therefore, if site A has Amax=20 and site B has Amax= 5, because they will both have Amin=0 in the winter, then CVs will be higher site A, simply because it has a higher Amax. I realize there's something fundamental I'm missing, as the graph says CV of 0.6 and 0.9 quantile, yet I did not quite understand how the calculation had been made.**

We agree with the consideration of the reviewer. Indeed, in the analysis we used days of the year with a good fit of the light response curve and omitted all days with R^2 of the model fitting < 0.6. By using this method it was not necessary to filter out the data for growing season because the fit of the model (and the uncertainty of the parameters) was usually only good within the growing season. Below we plotted the data of the GPP_{sat} time series. The respective $R^2 > 0.6$ of the light response curve for two different ecosystem types is indicated with red stars. As can be seen from the graphs the days with a good model fit ($R^2 > 0.6$) are in the growing season, which are shown for GPPsat by darker green color. By using this methodology we basically restricted the analysis to the growing season as suggested by the reviewer.

We tried to clarify this aspect in the revised manuscript (line 307:310, page 13, supplementary figure 1).

"In this way we first retain parameters estimated when the performance of the fitting is good, and second we retain data only in the active growing season as the R2 of the model fit of the model was higher than 0.6 only within the growing season (Fig. S1)."





7. **In Fig. 4: is a linear model of application here?**

Indeed relationship in Fig. 4 seems to be non-linear, but we only have 20 sites in our study and none of the previous studies (with more sites) show a non-linear relationship between N% and photosynthesis capacity (Ollinger et al., 2008, Kergoat et al., 2008 and on leaf basis Givnish 1986). Therefore, while keeping the linear model in the Fig. 4 we added the distance correlation (which considers also no-linearity) estimate to Table 2 next to the estimates of the linear model. In addition, we show the same Fig. 4 considering a non-linear model in the supplementary information (Fig. S6 - line 397:399, page 17).

"The fit is even better when a non-linear fit is used for Fig. 4a and Fig. 4b (distance correlation increases from 0.56 to 0.73 for GPPsat and from 0.47 to 0.63 for GPPsat.structure, See also Fig. S6)."

Givnish TJ (1986) On the economy of plant form and function, University of Cambridge

Kergoat L, Lafont S, Arneth A, Le Dantec V, Saugier B (2008) Nitrogen controls plant canopy light-use efficiency in temperate and boreal ecosystems. Journal of Geophysical Research-Biogeosciences, **113**.

Ollinger SV, Richardson AD, Martin ME et al. (2008) Canopy nitrogen, carbon assimilation, and albedo in temperate and boreal forests: Functional relations and potential climate feedbacks. Proceedings of the National Academy of Sciences of the United States of America, **105**, 19336-19341.

8. **How about phylogenetic differences between species?**

I am not completely sure to grasp the request from the reviewer. If I correctly understand the reviewer is asking to account for phylogenetic differences between species in each site. However, we consider that in this study and with this dataset phylogenetic effects are not relevant as we work with site averages and thus community weighted means across several species.

9. **Are there no random effects to be considered?**

Also for this question we are not exactly sure what was meant by the reviewer, but we decided to take the comment as following: In order to test whether the relationship in Fig. 4c is just by chance better than Fig. 4b, we performed a bootstrapping test. For the relationship in Fig. 4b, prior to estimating the mean GPP_{sat} of the sites, we resampled randomly (with replacement) for each site the GPP_{sat} (also $GPP_{sat.structure}$) and then estimated the mean over the years. This was done 100 times and at each step the R^2 and significance (*p*) of the linear regression of the model was computed. In none of the cases using randomly resampled GPP_{sat} the fit was better than the one in Fig. 4c (time and space matched data). Using $GPP_{sat.structure}$ only 1% of the random site-year combination had an R^2 higher than the one in Fg.4c (0.37) with a p-value < 0.05 and a positive slope. Below are the summary of the results from the 100 random fit of Fig. 4b. Thus we think the improvement of the fit when using time and spaced matched data was not random.

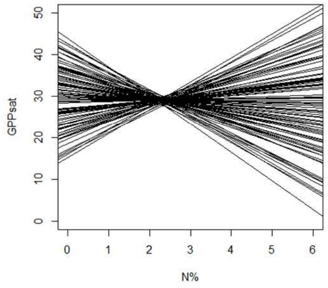
This is also included in the text and supplementary material (line 405:410, page 18, supplementary table 2).

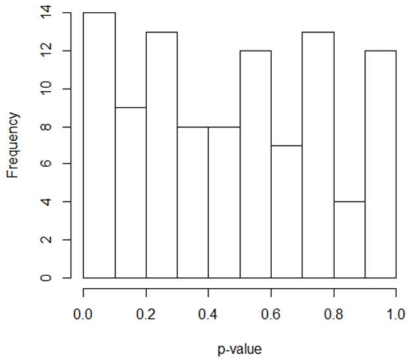
"We also tested whether the improvement of this relationship was due to random. To do this we randomly resampled the annual photosynthetic capacity (specifically GPPsat and GPPsat,structure) to test if the use of corresponding years statistically improves the relationship or not. The results confirm that the best fit is obtained when the N% and the photosynthetic capacity estimate match in time and space (Table S2)."

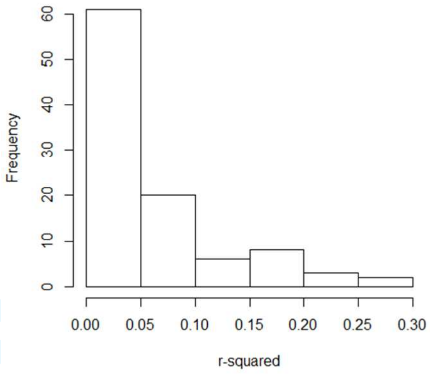
	R^2	*p*	EFP estimate
Min.	0.2683	0.002288	GPP_{sat}
1^{st} Qu.	0.2845	0.004134	
Median	0.3315	0.007891	
Mean	0.3309	0.009602	
3^{rd} Qu.	0.3745	0.015435	
Max.	0.4118	0.019314	
Min.	0.2799	0.002061	$GPP_{sat.structure}$
1^{st} Qu.	0.2967	0.007480	
Median	0.3345	0.009494	
Mean	0.3320	0.011045	
3^{rd} Qu.	0.3514	0.015927	
Max.	0.4369	0.019853	

10. **Overall I was surprised on how well TRY traits worked to predict fluxes (R2=0.27 is still biologically significant). If the authors think it could add some value, I would be interested in seeing what would have happened if Fig. 4 would also compare against a null model? For instance, randomly re-assign N values of one species to another? I realize this may take some extra work, and this is certainly not crucial to the goals of the manuscript (just my personal curiosity), so the authors don't really need to take this suggestion on board unless they feel it can add something.**

We performed the suggested analysis for the in-situ N% and GPP_{sat} of the *in-situ* year, meaning that prior to estimating the community weighted mean of N% for each site the values of the N% for the species were randomly mixed. We repeated this 100 times. The result indicates non-significant linear fits for the 100 tries and as it is seen in the first plot the fit can be in any direction. (Figures show the linear fit, frequency of the *p-value* (minimum 0.02) and R^2 of the fit, respectively.







<u>REPLY TO REVIEWER #2</u>

1. **Overall, I liked this paper. I like papers that try to link whole-ecosystem eddy covariance data to the underlying properties of the vegetation present, such as the leaf traits. There is not enough of this kind of work in the literature, so this is a valuable addition. However, I do have a few suggestions that I think would help to improve the quality of the paper.**

   We are grateful for the positive comments and feedback. Please find below the answers to the questions and comments, and the modification we introduced in the manuscript according to the reviewer’s suggestions.

2. **Number 1 suggestion of course is to publish the data! Please make the data available in as comprehensive a form as possible. I appreciate that the authors sent me the values so readily, and that they said they would publish them. I’d like to suggest that they be made available in a slightly more comprehensive form: in particular, please give the traits broken down by species (along with species information). It is also very useful to see within-species variation. If it were me, I would be publishing the original data, ie all the individual values, not just species averages.**

The data is now available for possible publication. We included the EFP estimates of the fluxnet sites, species composition information from the sites and the averaged traits for each species including also the standard deviation estimate.

3. **I was unsure why GPP-cum was included as a potential measure of ecosystem capacity. It is not defined very clearly and it is not explained what information it would offer that is more useful than GPPsat. There was relatively little comment on it during the results or discussion. Does it really need to be considered, or could you simplify by removing it as an option?**

The cumulative of GPP was used as additional EFP because we wanted to explore different definitions of EFP. Please note that the use of different formulations of EFP was also considered as strength from the other reviewer. However GPP cum turned out to be not the best metric to meet the definition of EFP. We clarified this in the text.

4. **I would really like to see the sites classified by PFT. One reason I asked for the trait data was so that I could assess the extent to which the %N-GPPsat relationship is driven by PFT differences in leaf %N. I believe a lot of the relationship is driven by the fact that conifers tend to have lower leaf %N and lower GPP, than deciduous broadleaf species. It's unclear to me whether that means leaf %N is really implicated as a driving factor (especially given the big differences in SLA) or whether both %N and GPP are being driven by a third factor. I think it is important to classify by PFT here.**

The point raised by the reviewer is indeed very relevant. We followed the suggestions of the reviewer by color coding the plots using a different color for each PFTs. We agree with the concern of the reviewer that the positive relationship could be attributed to mean differences in N between PFTs. Unfortunately it was not possible to statistically test the effects of PFTs because of data scarcity.

For this reason we also conducted a literature review:

In a previous work using AMERIFLUX, Kergoat et al 2008 also found that the relationship between light use efficiency and N is linear within deciduous and evergreen forests. We added this consideration in the manuscript.

In Givnish 1986 (on the economy of plant form and function), plants of different vegetation types are compared for leaf nitrogen and photosynthetic capacity and mentions that "photosynthetic capacity is strongly regulated by leaf nitrogen, without large effects due to habitat, growth form, or interspecies differences" (page 31-32).

Givnish TJ (1986) On the economy of plant form and function, University of Cambridge

Kergoat L, Lafont S, Arneth A, Le Dantec V, Saugier B (2008) Nitrogen controls plant canopy light-use efficiency in temperate and boreal ecosystems. Journal of Geophysical Research-Biogeosciences, **113**.

KERGOAT ET AL.: LIGHT-USE EFFICIENCY AND LEAF NITROGEN

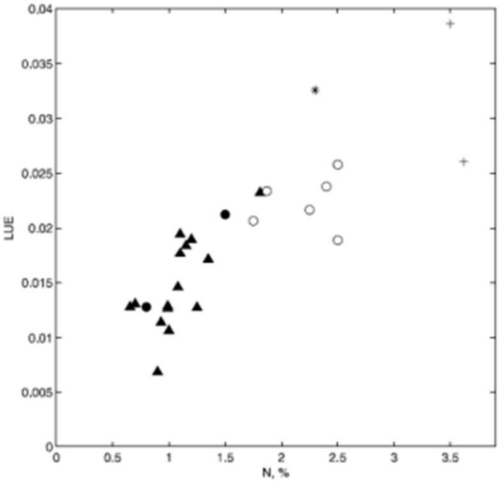
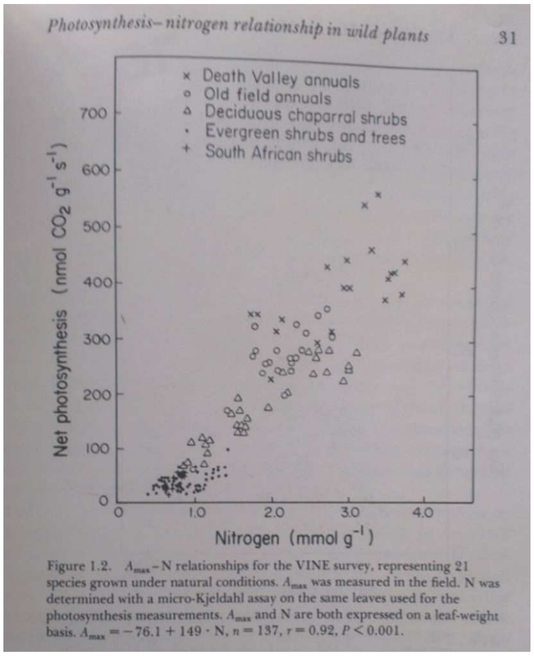


Figure 3a. Optimum daily LUE versus leaf nitrogen content N, mass basis.



Photosynthesis–nitrogen relationship in wild plants 31

Figure 1.2. A_{max} – N relationships for the VINE survey, representing 21 species grown under natural conditions. A_{max} was measured in the field. N was determined with a micro-Kjeldahl assay on the same leaves used for the photosynthesis measurements. A_{max} and N are both expressed on a leaf-weight basis. $A_{max} = -76.1 + 149 \cdot N$, $n = 137$, $r = 0.92$, $P < 0.001$.

5. **I also can see that one of the big differences between TRY and site-specific leaf N values is for the crop site, which has average %N in TRY and very high %N in the site-specific data, suggesting a potential effect of fertilization. The discussion of why site-specific values for traits are better than TRY values centers on community dynamics. I find that discussion to be highly speculative. It would be better if they looked closely at the data that they have and thought carefully about why the values at sites might differ from the values in TRY – such as the possibility that fertilizer has been applied!**

Definitely the fertilization can be an issue, which we missed to mention. We clarified that the potential difference in crops can be imputed to different management between the site included in TRY and the FLUXNET site. (line 506:508, page 22)

"This includes also the effect of fertilization on few sites, which could be one of the reasons why the in-situ N% from the cropland and grasslands are very different from the mean N% from TRY."

6. **The key take-home seems to be "The predictive power of traits for ecosystem photosynthetic capacity substantially improved when intraspecific variability and interannual variability was accounted for, respectively". However, this conclusion has not actually been tested statistically. The authors just note that there is an increase in the R2. But R2 must either go up or down: so there is a 50% chance that it would go up, even if there is no real difference. The authors need to test whether the use of corresponding years statistically improves the relationship or not. Otherwise their conclusion is unsubstantiated.**

Also for this question we are not exactly sure what was meant by the reviewer, but we decided to take the comment as following: In order to test whether the relationship in

Fig. 4c is just by chance better that Fig. 4b) we performed a bootstrapping test. For the relationship in Fig. 4b, prior to estimating the mean GPP_{sat} of the sites, we resampled randomly (with replacement) for each site the GPP_{sat} (also $GPP_{sat.structure}$) and then estimated the mean over the years. This was done 100 times and at each step the R^2 and significance (*p)* of the linear regression of the model was computed. In none of the cases using randomly resampled GPP_{sat} the fit was better than the one in Fig. 4c (time and space matched data). Using $GPP_{sat.structure}$ only 1% of the random site-year combination had an R^2 higher than the one in Fg.4c (0.37) with a p-value < 0.05 and a positive slope. Below are the summary of the results from the 100 random fit of Fig. 4b. Thus we think the improvement of the fit when using time and spaced matched data was not random.

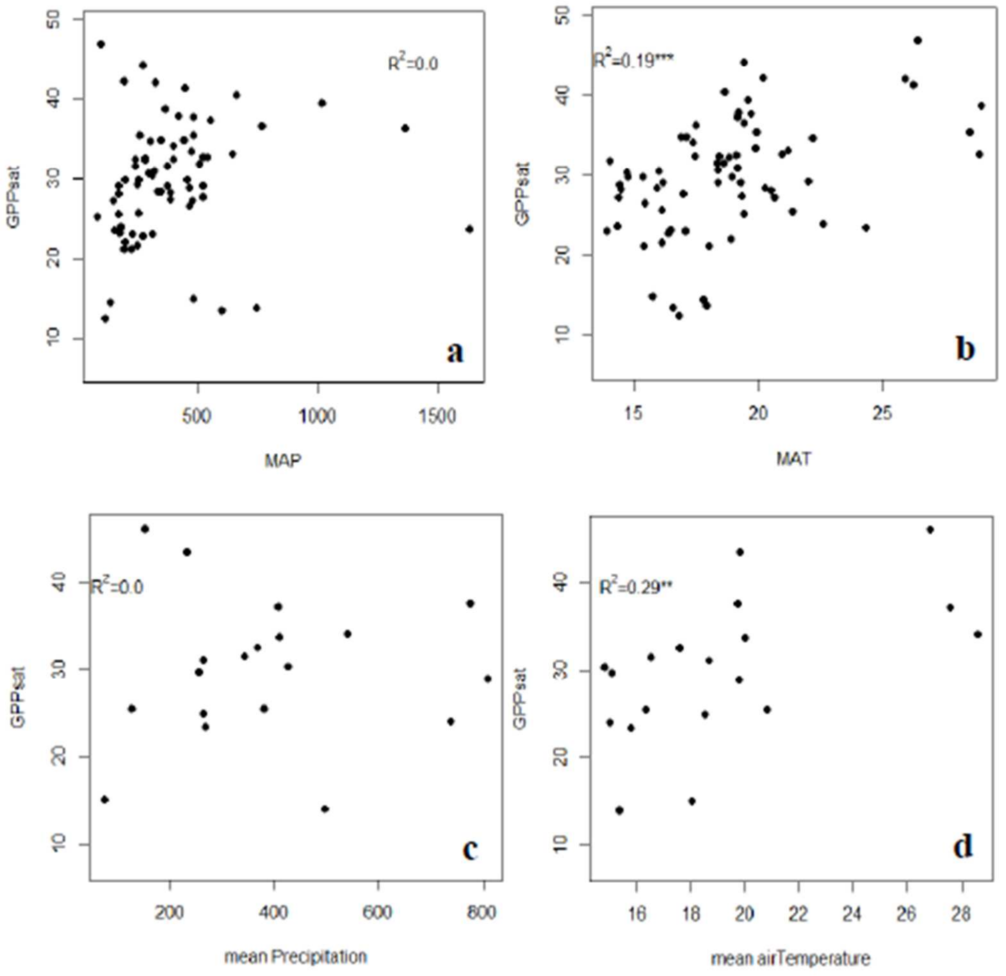
	R^2	*p*	**EFP estimate**
Min.	0.2683	0.002288	**GPP_{sat}**
1st Qu.	0.2845	0.004134	
Median	0.3315	0.007891	
Mean	0.3309	0.009602	
3rd Qu.	0.3745	0.015435	
Max.	0.4118	0.019314	
Min.	0.2799	0.002061	**$GPP_{sat.structure}$**
1st Qu.	0.2967	0.007480	
Median	0.3345	0.009494	
Mean	0.3320	0.011045	
3rd Qu.	0.3514	0.015927	
Max.	0.4369	0.019853	

This is also included in the text and supplementary material (line 405:410, page 18, supplementary table 2).

"We also tested whether the improvement of this relationship was due to random. To do this we randomly resampled the annual photosynthetic capacity (specifically GPPsat and GPPsat,structure) to test if the use of corresponding years statistically improves the relationship or not. The results confirm that the best fit is obtained when the N% and the photosynthetic capacity estimate match in time and space (Table S2)."

7. **The authors seem to ignore the role of cross-site variation in climate. They suggest that their analysis "accounts for the effects of meteorological variables" but I am not really sure what they mean by that. Certainly the value for different sites will be affected by the different climates across sites – values in Finland will correspond to lower temperature than values in Italy, for example – but this effect is not considered in the analysis.**

While many studies show that instant GPP is very strongly correlated to climate variables, the extraction of GPPsat considers the optimal conditions and is thereby less correlated to climate variables. The fact that GPPsat is the potential GPP at light saturation overcomes the direct effects of climate as well. The two figures below indicate that the difference between sites for GPPsat is not related to the mean precipitation and only slightly related to air temperature of the sites. Both climate variables were estimated during the growing season. In a and b the link between the annual average air temperature and cumulative precipitation is shown with annual GPPsat. In c and d the link between mean annual temperature (MAT) and mean annual precipitation (MAP) with the site averaged GPPsat is shown.



This has also been added to the supplementary material with a reference in the manuscript. (Line 384:385, page 17, and line 429:432, page 19, Supplementary figure 8)

"In addition, the estimated parameters e.g. GPPsat are not strongly linked to climate variables (Fig. S8)."

> *“We postulated that the IAV of ecosystem photosynthetic capacity at optimal growth conditions (e.g. at optimal light, temperature and water availability) derived with the proposed methodology and in the absence of disturbances should be low, and we demonstrated that it is not strongly related to climate drivers (Fig. S8).”*

8. **The attempt to find which traits best predict photosynthetic capacity is, in my view, very unsatisfactory. GPPsat is regressed against a bunch of traits, with several transformations possible for each trait. At least one of those traits is likely to turn up significant – but that certainly does not make it a good predictor for GPPsat. This kind of “try everything out and assign meaning to the one thing that comes out significant” approach is not statistically valid. By all means explore the correlation structure among variables but do not attempt to pick which variable is the best predictor!**

> Here we considered plant traits relevant for ecosystem photosynthesis, specifically leaf C/N/P traits. It is not clear how they control photosynthetic capacity (if linearly/with or without interaction), therefore one way to test this is a purely data driven approach with all possible variable combinations and mining for possible explanatory ideas. This is a very simple form of data mining, which explores the full search space and is certainly valid - even if not following classical hypothesis driven research. This debate is general very important today in many branches of science. See the links below and we tend to favor Golub 2010.:
> Point: Hypotheses first (Weinberg R (2010) Point: Hypotheses first. Nature, **464**, 678-678.)
> Counterpoint: Data first (Golub T (2010) Counterpoint: Data first. Nature, **464**, 679-679.)
>
> We tried to clarify this issue and added the reasoning that led us to the application of this methodology (line 353:355, page 15 and line 531:533 page 23).
>
> *“Because the functional relationship between plant traits, their interactions and photosynthetic capacity is not yet completely defined (Sardans & Penuelas 2012), a purely data driven approach was used (Golub et al., 2010).”*
>
> *“We considered leaf traits relevant for photosynthesis and used a data-driven exploratory approach with all combinations of the selected leaf traits, mining for possible functional relationship between photosynthetic capacity and foliar traits (Golub 2010).”*

9. **It would have been good to hear more about the mechanisms. A lot of the trait literature suffers from the “correlate everything with everything else and go with the highest R value”**

philosophy and this work also verges on that error. It would be good to see some more mechanistic hypotheses framing the work.

Thanks for the comment. We have added more material on the mechanism of the finding, throughout the discussion. A paragraph at the end of the section "Linking plant functional traits and EFP estimates", in some lines in the section "Robustness of ecosystem photosynthetic capacity –plant trait relationship to relaxed time-space synchrony of measurements" and a paragraph in the section "Identifying plant traits determining ecosystem photosynthetic capacity", which are all highlighted.

10. **Although, I must say, I'm still kind of surprised by the correlation between N% and GPP. GPP ought to be related to N on an area basis, not on a mass basis, so why is this relationship being observed, I wonder? Ollinger and Kergoat show the same thing, so it is quite consistent, which would be worth pointing out, and then considering what is underlying this relationship.**

Given that Narea (as partly driven by SLA) tends to vary more strongly within the canopy than Nmass (and given that we use canopy-averaged values), this uncertainty leads to extra noise. In addition, the transformation from weight based to area based leaf nitrogen tends to compress the total range of variation in Nmass. Together this caused lower correlations of Narea when plotted against GPPsat.

11. **I'm also started by the relationship with tissue C content. What on earth is driving that? I was not aware that tissue C content had a lot of functional meaning – it is generally assumed constant. How can it explain 40% of cross-site variation?**

The carbon content is related to the dry mass of the leaves and follows the leaf spectrum of fast growing species (shorter leaf longevity) with thin leaves (Low C and higher N) and slow growing species (higher leaf longevity) with thicker leaves (high C low N). This can be seen when looking at the values of leaf C content of PFTs with needle leaves and broadleaved evergreen species having the highest C while grasses and cropland species with lowest C. Leaf C content thus relates to the investment of nutrients into photosynthesis vs storage capacity and is through this mechanism directly related to photosynthesis capacity (as well as indirectly, through the correlation with leaf nutrients). Usually the C content of a given species is less variable (not constant) during growing season in comparison to leaf nutrients such as N and P (e.g. Jayasekera and Schleser 1991, Journal of plant physiology).

Jayasekera R, Schleser GH (1991) Seasonal-Changes in Organic-Carbon Content of Leaves of Deciduous Trees. Journal of Plant Physiology, **138**, 507-510.

12. **Picky notes: Please look closely at your symbols and try to come up with a consistent naming system using subscripts and abbreviations as necessary. GPP yes, AMAX no –should be Amax. Parea no – should be P_{area}. GPPsat,structure is just unwieldy – can you come up with a better name?**

We have changed some of the suggested abbreviations. AMAX to A_{max}. Parea to P_{area}. Narea to N_{area}. Pmass to P_{mass}.

13. In Figure 4c, I think two circles may have been cropped off the top of the graph? Can they be put back in? Same for Figure S3.

Thanks for the remark. We edited the figures accordingly.

14. I suggest Figure 4 should show values coloured by PFT, as could Figure S2.

We edited the figures accordingly.

15. y-axis label in Supp Fig 1 should not have 1000 in it?

Thanks for the remark. We have corrected this figure.

Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits

AUTHORS: Talie Musavi[1*], Mirco Migliavacca[1], Martine Janet van de Weg[2], Jens Kattge[1, 3], Georg Wohlfahrt[4], Peter M. van Bodegom[5], Markus Reichstein[1, 3], Michael Bahn[4], Arnaud Carrara[6], Tomas F. Domingues[7], Michael Gavazzi[8], Damiano Gianelle[9,10], Cristina Gimeno[6], André Granier[11], Carsten Gruening[12], Kateřina Havránková[13], Mathias Herbst[14], Charmaine Hrynkiw[15], Aram Kalhori[16], Thomas Kaminski[17], Katja Klumpp[18], Pasi Kolari[19], Bernard Longdoz[11], Stefano Minerbi[20], Leonardo Montagnani[20,21], Eddy Moors[22], Walter C. Oechel[16,23], Peter B. Reich[24, 25], Shani Rohatyn[26,27], Alessandra Rossi[16], Eyal Rotenberg[27], Andrej Varlagin[28], Matthew Wilkinson[29], Christian Wirth[1,3, 30], Miguel D. Mahecha[1, 3]

AFFILIATIONS:

1. Max Planck Institute for Biogeochemistry, 07745 Jena, Germany
2. Amsterdam Global Change Institute, VU University Amsterdam, The Netherlands
3. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany
4. University of Innsbruck, Institute of Ecology, A-6020 Innsbruck Austria
5. Leiden University, Institute of Environmental Sciences, Leiden, Netherlands
6. Mediterranean Center for Environmental Studies (Foundation CEAM), Valencia, Spain
7. FFCLRP-USP, Ribeirão Preto, Brasil
8. Eastern Forest Environmental Threat Assessment Center, USDA Forest Service, Raleigh, NC 27606, US
9. Department of Sustainable Agro-Ecosystems and Bioresources, Research and Innovation Center, Fondazione Edmund Mach, 38010 S. Michele all' Adige Trento (Italy)
10. Foxlab Joint CNR-FEM Initiative, Via E. Mach 1, 38010 San Michele all'Adige, Italy
11. INRA, UMR 1137 Ecologie et, Ecophysiologie Forestierès, F54280, Champenoux, France
12. European Commission, Joint Research Centre, Institute for Environment and Sustainability, Ispra, Italy
13. Department of Matters and Energy Fluxes, Global Change Research Institute CAS, Brno, 603 00, Czech Republic
14. Johann Heinrich von Thünen Institute, Federal Research Institute for Rural Areas, Forestry and Fisheries, Braunschweig, Germany
15. National Hydrology Research Centre (NHRC), Saskatoon, Saskatchewan, Canada
16. Department of Biology, San Diego State University, San Diego, CA 92182-4614, USA
17. The Inversion Lab, Martinistr. 21, 20251 Hamburg, Germany
18. INRA, Grassland Ecosystem Research (UR874), 5 Ch de Beaulieu, 63039 Clermont Ferrand, France
19. Department of Physics, FI-00014 University of Helsinki, Finland

20. Provincia Autonoma di Bolzano Servizi Forestali, 39100 Bolzano, Italy
21. Faculty of Science and Technology, Free University of Bolzano, Piazza Università 1, 39100, Bolzano, Italy
22. Alterra Green World Research, Wageningen, NL 6700 AA, The Netherlands
23. Department of Environment, Earth and Ecosystems, The Open University Walton Hall Milton Keynes England. U.K. MK7 6AA
24. Department of Forest Resources, University of Minnesota Twin Cities, Saint Paul, Minnesota 55108 USA
25. Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales 2753, Australia
26. Soil and Water Department, Faculty of Agricultural, Food and Environmental Quality Sciences, The Hebrew University of Jerusalem, Rehovot, Israel
27. Department of Earth and Planetary Sciences, Weizmann Institute of Science, Rehovot 76100, Israel
28. A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia 119071
29. Environmental and Human Sciences Division, Forest Research, Alice Holt Lodge, Farnham, Surrey, UK GU10 4LH
30. Institute of Special Botany and Functional Biodiversity, University of Leipzig, 04103 Leipzig, Germany

* To whom correspondence should be addressed. Email: tmusavi@bgc-jena.mpg.de, Phone: +49 3641 576296, Fax: +49 3641 577200

ABSTRACT: The aim of this study is to systematically analyze the potential and limitations of using plant functional trait observations from global databases versus *in-situ* data to improve our understanding of vegetation impacts on ecosystem functional properties (EFPs). Using ecosystem photosynthetic capacity as an example, we first provide an objective approach to derive robust EFP estimates from gross primary productivity (GPP) obtained from eddy covariance flux measurements. Second we investigate the impact of synchronizing EFPs and plant functional traits in time and space to evaluate their relationships, and the extent to which we can benefit from global plant trait databases to explain the variability of ecosystem photosynthetic capacity. Finally we identify a set of plant functional traits controlling ecosystem photosynthetic capacity at selected sites.

Suitable estimates of the ecosystem photosynthetic capacity can be derived from light response curve of GPP responding to radiation (PAR or APAR). Although the effect of climate is minimized in the calculations, the estimates indicate substantial interannual variation of the photosynthetic capacity, even after removing site-years with confounding factors like disturbance such as fire events. The relationships between foliar nitrogen concentration and ecosystem photosynthetic capacity are tighter when both of the measurements are synchronized in space and time. When using multiple plant traits simultaneously as predictors for ecosystem photosynthetic capacity variation, the combination of leaf carbon to nitrogen ratio with leaf phosphorus content explains the variance of ecosystem photosynthetic capacity best (adjusted $R^2 = 0.55$). Overall, this study provides an objective approach to identify links between leaf level traits and canopy level processes, and highlights the relevance of the dynamic nature of ecosystems. Synchronizing measurements of eddy covariance fluxes and plant traits in time and space is shown to be highly relevant to better understand the importance of intra- and interspecific trait variation on ecosystem functioning.

Keywords: ecosystem functional property, plant traits, TRY database, Eddy covariance, FLUXNET, spatio-temporal variability, interannual variability, photosynthetic capacity

INTRODUCTION

Accurate predictions of land-atmosphere feedbacks under climate change require an in-depth understanding of how climatic and other environmental controls on ecosystem functioning are mediated by vegetation characteristics, diversity, and structure (Bonan 2008). Eddy covariance (EC) measurements of carbon dioxide (CO_2), water, and energy fluxes are widely employed to monitor ecosystem processes and functions (Baldocchi *et al.,* 2001). The increase number of EC flux sites contributing to the FLUXNET network allows for monitoring ecosystem processes and responses to environmental conditions for different ecosystems and time scales (Baldocchi 2008). In many applications, both in terrestrial biosphere models and in experimental analyses, the characteristics and structure of the vegetation are given by plant functional types (PFTs), which represent a grouping of functionally similar plant types (Lavorel *et al.,* 1997). However, plant traits and model parameters derived from eddy covariance (EC) data can be highly variable within PFTs and species (Kattge *et al.,* 2011, Alton 2011, Groenendijk *et al*., 2011, Reichstein *et al.,* 2014). Vegetation characteristics and the variation therein are assumed to be determined by the abundance and traits of the respective plant species (Garnier *et al.,* 2004, Lavorel & Garnier 2002). Therefore, both modeling (Van Bodegom *et al.,* 2012, Verheijen *et al.,* 2015, Pappas *et al.,* 2016) and observational efforts (Meng *et al*., 2015) increasingly aim to account for the variation of traits within and between PFTs, in order to better understand the relationship between vegetation characteristics and ecosystem functioning. Most efforts so far have focused on specific regions (e.g. Ollinger *et al.,* 2008), and have not systematically analyzed the importance of spatio-temporal variation in traits and ecosystem function variables for their relationship. Plant traits contribute to different ecosystem processes where our knowledge is often limited. Furthermore, efforts have mostly focused on leaf nitrogen as a functional trait (in relation to ecosystem productivity, e.g. Kattge *et al.,* 2009), whereas other plant traits could also be suitable candidates. Foliar phosphorus for example, improves the model prediction of carbon fluxes as reported by Mercado *et al.,* (2011), Goll *et al.,* (2012) and Yang *et al.,* (2014).

The short-term (half-hourly to daily) variability of carbon fluxes measured with the EC technique is controlled by meteorological, environmental conditions (Richardson *et al.*, 2007) and, plant rhythms (de Dios *et al.*, 2012). In contrast, biotic responses (e.g. temporal variability in plant abundance and traits) seem to be more important than environmental variation for long-term (e.g. annual and more) variation of fluxes (Richardson *et al.,* 2007, Stoy *et al.,* 2009). Evaluating the relationship between plant traits and fluxes is not straight forward because the former is usually measured only a couple of times per year (mostly during the growing season), whereas the latter is measured at half hourly time scale. It is possible to derive so called Ecosystem Functional Properties (EFP) from EC measurements, a concept recently introduced to characterize the long-term patterns underlying carbon, water and energy fluxes (Musavi *et al*., 2015, Reichstein *et al.,* 2014).

The EFPs are ecosystem properties related to physical and ecohydrological parameters relevant for land surface–atmosphere interactions (Reichstein *et al.,* 2014), and are assumed to be affected by vegetation characteristics. Analogous to leaf level ecophysiological characteristics, like carboxylation capacity (Vc_{max}), EFPs are less variable in time than the fluxes themselves, which makes them a suitable quantity to be linked to plant functional traits (Musavi *et al*., 2015, Reichstein *et al.,* 2014). Therefore, EFPs can be used to characterize long-term variation in key process characteristics, like ecosystem photosynthetic capacity and respiration rates under standardized environmental conditions, or they can represent the sensitivity of processes to temperature and light availability (for a more detailed collection; see Table 1, Musavi *et al.,* 2015). Deriving EFP estimates from EC fluxes is not trivial, because they should represent intrinsic ecophysiological properties of the ecosystem; effects of short-term meteorological conditions on functional responses should be factored out.

Another constraint for systematically testing the links between plant traits and EFPs is that so far, measurements of plant functional traits have not yet been carried out systematically at FLUXNET sites. Consequently, the number of studies linking plant traits and EFPs using a wide range of ecosystems are few (e.g. Kergoat *et al.,* 2008). Although plant trait data from FLUXNET sites are currently limited, the global database of plant traits - TRY (Kattge *et al.,* 2011) - facilitates the identification of many different traits for most of the plant species present at FLUXNET sites, which could potentially help testing such relationships. However, the use of trait values derived from such broad-scale databases may suffer from inaccuracies, when trait values for a particular site deviate from those reported in databases, which may hamper deducing the patterns of plant traits influences on EFPs. Hence, it is important to test the potentials and limitations of using plant functional traits derived from a global database (e.g. TRY) versus *in-situ* measurements obtained from the sites to infer the impact of plant traits on ecosystem processes derived from EC flux data. We still do not know how temporal and spatial variations in both EFPs and plant functional traits affect their link. Likewise the uncertainties of the relationship between EFPs to plant functional traits related to the temporal dynamics of both ecosystem functioning and traits have not been evaluated before. This is the first time to our knowledge that the relationship between an EFP (here ecosystem photosynthetic capacity) derived from EC CO_2 fluxes and plant traits and the associated uncertainties have been systematically investigated for spatio-temporal variation and the relevance of synchronized observations. Using ecosystem photosynthetic capacity as an example for an EFP derived from selected FLUXNET sites, the goals of this study were:

1) Providing an objective approach to characterize ecosystem photosynthetic capacity from different estimates of gross primary productivity (GP) derived from EC measurements.

2) Assessing how relaxing the time-space synchronization of ecosystem photosynthetic capacity estimates and plant functional trait measurements introduces uncertainty to the relationships between ecosystem photosynthetic capacity and relevant plant traits (with a particular focus on leaf nitrogen content per leaf mass).

3) Identifying (a set of) plant traits that control the spatial variability of ecosystem photosynthetic capacity.

MATERIAL & METHODS

The overall methodological approach consisted of comparing different ways to estimate ecosystem photosynthetic capacity at each FLUXNET site. Ecosystem photosynthetic capacity is an EFP related to the photosynthetic processes at ecosystem scale. It is computable from estimates of GPP from EC, incoming shortwave radiation and the fraction of absorbed photosynthetically active radiation (FAPAR) retrieved from remote sensing. Given the attempt to characterize properties related to long-term variation of ecosystem function that are not affected by short –term meteorological variability, the ecosystem photosynthetic capacity estimates with the least inter annual variation (IAV) were assumed as the most appropriate to characterize the EFP. The most appropriate estimates of ecosystem photosynthetic capacity were then correlated to leaf nitrogen content per leaf mass (N) measured *in-situ* or derived from the TRY database to identify the relevance of time and space synchronizing measurements of EC data and plant traits. Finally, ecosystem photosynthetic capacity was correlated to a suite of other photosynthesis-related plant traits to identify those that control its spatial (i.e. across site) variability.

Eddy covariance flux measurements

The analysis used data from the FLUXNET La Thuile database (Baldocchi 2008), referred hereafter as 'La Thuile'. Very dry sites and forest site-years with disturbances (i.e. forest thinning, harvesting and planting, etc.) were removed opting for optimal conditions to avoid confounding factors. For the remaining dataset, 20 sites responded to a request for providing leaf traits sampled in 2011/2012 (for some sites trait measurements from the years before was used) and the flux data from the year of sampling. Depending on the site, different years of flux data were available in the LaThuile database in addition to the fluxes from the sampling year 2011/2012.

To characterize ecosystem photosynthetic capacity, we used half-hourly values of GPP (µmol CO_2 m^{-2} s^{-1}) and the corresponding photosynthetically active radiation (PAR, µmol m^{-2} s^{-1}). The GPP values were computed using the commonly used algorithm for flux partitioning, which is based on the extrapolation of nighttime net ecosystem exchange measurements, using an ecosystem respiration model based on air temperature (Reichstein *et al.,* 2005). Since PAR was not always available at the selected sites, we derived PAR by multiplying global incoming shortwave radiation (Rg, W m^{-2}) by 2.11 (Britton & Dodd 1976).

Only GPP data derived from measured net ecosystem exchange were used for the analysis and gap-filled values were omitted. In addition, only day-time GPP data were used (Rg > 10

Wm^{-2}). For each site-year we estimated the number of days with more than 80% gaps in half-hourly net ecosystem exchange measurements during the period from April to September. Site-years with more than 25% of such days were excluded.

MODIS TIP- FAPAR and Leaf Area Index (LAI) - vegetation quantity/structure

For the selected sites, estimates of FAPAR and LAI (see Pinty *et al*., 2011a,b) derived at 1 km spatial resolution by the JRC-TIP (Pinty *et al.,* 2007) from the MODIS broadband visible and near-infrared surface albedo products (Schaaf 2002) were used to quantify the phenology of vegetation and changes in the structure of the ecosystem (Musavi *et al*., 2015, Fig. 1). The FAPAR product covers a sequence of 16 days periods with 1 km spatial resolution. We used the FAPAR time series of the pixels where the towers of FLUXNET sites were located. To fill gaps in FAPAR and LAI, we performed a distance correlation between the time series of all pixels around the central pixel for each flux site (Szekely *et al.,* 2007). We subsequently chose pixels with a correlation of $r > 0.75$ with the central pixel. Afterwards, we used the data of those pixels to fill the gaps in the central pixel, prioritizing the pixels with highest correlation. In case where gaps remained after this procedure, we used a spatiotemporal gap-filling approach for the remaining gaps (v. Buttlar *et al.,* 2014). To derive daily time-series of FAPAR a smoothing spline approach was used to derive daily time-series of FAPAR (see also Migliavacca *et al*., 2011, Filippa *et al.,* 2016). FAPAR was then used to compute half-hourly APAR (absorbed photosynthetic active radiation) values (μmol m^{-2} s^{-1}). Annual maximum LAI was derived by using the 90th percentile of the satellite retrieved estimates of LAI from JRC-TIP of the same year of sampling (Pinty *et al.,* 2011).

Plant functional trait collection - vegetation characteristics

Plant traits known to be relevant for photosynthesis at ecosystem scale, specifically leaf nutrient contents and stoichiometry of the nutrients were determined (Sardans & Penuelas 2012): leaf nitrogen content per dry mass (Nmass or per 100gram leaf dry mass- N%), leaf nitrogen content per leaf area (N_{area}, g m^{-2}), leaf phosphorus content per leaf dry mass (P_{mass}, mg g^{-1}) and per leaf area (P_{area}, g m^{-2}), leaf carbon content per leaf dry mass (C, mg g^{-1}), leaf C/N ratio (C/N, g/g), leaf stable isotope concentration ($\delta^{13}C$) and specific leaf area, (SLA, mm mg^{-1}).

In-situ leaf samples from the selected sites were collected in the period 2011-2012 (except for two sites in 2003 and in 2004). The leaf sampling protocol was based on “Protocols for Vegetation Sampling and Data Submission” of the terrestrial carbon observations panel of the global terrestrial observing system (Law *et al.,* 2008). Samples were collected from the dominant species present in the footprint of the flux-towers (defined by the site’s principal investigator). Depending on accessibility, multiple individuals per species were sampled. Sampling was done mostly at peak growing season on fully developed and non-damaged leaves and, from different levels of the canopy (top, middle and bottom, representing fully sunlit and shaded leaves). For forest sites, the understory vegetation was not sampled.

After grinding the dried leaves, total carbon and nitrogen concentrations were determined by dry combustion with an elemental analyzer (Perkin Elmer 2400 Series II). Phosphorus concentrations were determined by digesting ground leaf material in 37% HCl: 65% HNO_3. Phosphorus was subsequently measured colorimetrically at 880 nm after a reaction with molybdenum blue. Leaf carbon stable isotope values ($\delta^{13}C$) were determined by an elemental analyzer (NC2500, ThemoQuest Italia, Rodana, Italy) coupled on-line to a stable isotope ratio mass spectrometer (Deltaplus, ThermoFinnigan, Bremen, Germany). Leaf area was calculated with the ImageJ freeware (http://rsb.info.nih.gov/ij/).

Species abundance information was collected for each site, or if not available (one tropical forest site), all species were considered equally abundant. Abundance information for each species was used to calculate the community weighted means (CWM, Garnier *et al.,* 2004) of the different plant traits considered in the analysis: foliar N, P, and C concentration of leaves, specific leaf area (SLA), and leaf carbon stable isotope values (δ^{13}C). Plant trait data were also extracted from the TRY global database (Kattge *et al*., 2011). Species mean values were calculated from the observed plant trait values included in TRY, which were subsequently used to compute CWM trait values at each site. TRY data used in this study based on the following references: Atkin *et al*., 1997, Bahn *et al.,* 1999, Campbell *et al*., 2007, Cavender-Bares *et al*., 2006, Coomes *et al.,* 2008, Cornelissen 1996, Cornelissen *et al.,* 2003a, Cornelissen *et al.,* 1996, Cornelissen *et al.,* 2004, Cornwell *et al*., 2008, Craine *et al.,* 2009, Craine *et al.,* 2005, Diaz *et al*., 2004, Freschet *et al.,* 2010, Fyllas *et al*., 2009, Garnier *et al.,* 2007, Han *et al*., 2005, Hickler 1999, Kattge *et al.,* 2011, Kattge *et al*., 2009, Kazakou *et al*., 2006, Kerkhoff *et al.,* 2006, Kleyer *et al.,* 2008, Laughlin *et al.,* 2010, Louault *et al.,* 2005, Loveys *et al.,* 2003, Medlyn *et al.,* 1999, Messier *et al.,* 2010, Meziane & Shipley 1999, Niinemets 2001, Ogaya & Penuelas 2003, Onoda *et al.,* 2011, Ordonez *et al*., 2010, Poorter *et al.,* 2009, Poschlod *et al*., 2003, Quested *et al.,* 2003, Reich *et al.,* 2009, Reich *et al.,* 2008, Sack *et al*., 2003, Sack *et al.,* 2006, Shipley 1995, Shipley 2002, Shipley & Vu 2002, Vile 2005, White *et al.,* 2000, Willis *et al.,* 2010, Wright *et al.,* 2007, Wright *et al.,* 2004, Wright *et al.,* 2010.

Estimates of ecosystem photosynthetic capacity

To estimate the ecosystem photosynthetic capacity, we used ecosystem level light response curves, using half-hourly GPP estimates and a variety of radiation data. The resulting six different formulations of ecosystem photosynthetic capacity estimates are reported in Table 1, and described in the following.

We fitted non-rectangular hyperbolic light response curves (Gilmanov *et al.,* 2003):

$$GPP = \frac{1}{2\theta}\left(\alpha Q + A_{max} - \sqrt{(\alpha Q + A_{max})^2 - 4\alpha A_{max}\theta Q}\right) \qquad \text{EQ.1}$$

where ***α*** is the initial slope of the light response curve, ***θ*** is the curvature parameter (ranging from 0 to 1), A_{max} is the plateau of the light response curve, *GPP* is the half-hourly GPP values, *Q* is the incoming radiation used to drive the model. Specifically two different estimates of radiation were used (PAR, and APAR): in the estimation of the EFPs, APAR was used to account for seasonal and across-site variations in canopy structure (e.g. LAI) as it stand for the amount of light that is absorbed by the leaves of the ecosystem.

The ecosystem photosynthetic capacity values were estimated by using a 5-days moving window. The parameters of the light response curves were estimated and attributed to the day at the center of the window (Fig. 1a). The parameters were estimated by minimizing the model-observation residual sum of square with the Quasi-Newton method that allows box constraints (Byrd *et al.,* 1995). To this purpose we used the *optim* function implemented in R (http://CRAN.R-project.org/). For comparison a Michaelis-Menten based light response curve (Hollinger *et al.,* 2004) was used. Results were comparable with the non-rectangular hyperbolic light response curve (data not shown).

Each light response curve fitting was used to derive the A_{max} parameter, the value of GPP at light saturation and the integral of the light response curve at light saturation (Falge *et al.,* 2001). For light saturation we defined a threshold of Rg of 1000 Wm^2 (corresponding to PAR of 2110 µmol m^{-2} s^{-1}) (see also Jacobs *et al.,* 2007). This resulted in 6 different estimates describing ecosystem photosynthetic capacity: 1) A_{max}: parameter of the Eq. 1; 2) $A_{max.structure}$: parameter of Eq. 1 but with APAR as driving radiation to account for canopy structure; 3) GPP_{sat} : GPP at light saturation using PAR as driving radiation 4) $GPP_{sat.structure}$: as GPP_{sat} but with APAR as radiance variable; 5) GPP_{cum} : integral of the fitted light response until light saturation and 6) $GPP_{cum.structure}$: as GPP_{sat} but using APAR as radiation until light saturation (Fig. 1a, Table 1).

A time series of daily values of A_{max}, $A_{max.structure}$, GPP_{sat}, $GPP_{sat.structure}$, GPP_{cum}, and $GPP_{cum.structure}$ was then derived for each year. In Fig. 1b GPP_{sat} is shown as an example. Daily parameters were retained for further analysis only if the R^2 of the fit of light response curve was higher than 0.6. In this way we first retain parameters estimated when the performance of the fitting is good, and second we retain data only in the active growing season as the R2 of the model fit of the model was higher than 0.6 only within the growing season (Fig. S1).

To extract the corresponding annual ecosystem photosynthetic capacity for each site-year, maximum and different percentiles (90th to 60th) of the time series of the estimated parameters were computed. Finally, the coefficient of variation (CV, Everitt 1998) of the annual ecosystem photosynthetic capacity estimates was computed for each site. For example, at each site we computed the annual value for GPP_{sat} (i.e. 90^{th} percentile of GPP_{sat} daily time series). The CV was subsequently computed as the standard deviation of annual GPP_{sat} of all years available, divided by the mean annual GPP_{sat} for all years available at the respective site (CV GPP_{sat}). The CV was used as a measure of the interannual variability (IAV) of the ecosystem photosynthetic capacity estimates. Low IAV (i.e. the lowest CV) was used as criteria to identify the most appropriate estimates to characterize the ecosystem photosynthetic capacity at ach site. This was repeated for both ecosystem photosynthetic capacity estimates with and without the effect of canopy structure included (i.e. using PAR and APAR, respectively. This comparison was done using sites with at least five years of data. The average of annual ecosystem photosynthetic capacity of the selected estimates was used to relate to leaf functional traits.

Relationship between ecosystem photosynthetic capacity and leaf nitrogen concentration

This study evaluates the relevance of synchronizing measurements of plant functional traits and EFPs in space and time for joint analyses. We analyzed the relationship between the best estimates for ecosystem photosynthetic capacity selected as described above, and CWM of plant traits e.g. N%. N% is chosen here, since the relationship between N% and photosynthetic processes is well established (e.g. Field & Mooney 1986, Reich et al 1997) at the leaf scale and to a lesser extent at ecosystem scale (e.g. Kergoat *et al.,* 2008, Ollinger *et al.,* 2008). The relationship with other traits is included in the supplementary material (Fig. S2). Three different combinations of synchronizing ecosystem photosynthetic capacity and N% were tested:

1) Ecosystem photosynthetic capacity derived from the La Thuile database and species CWM N% derived from TRY (no synchronization in space and time). 2) Ecosystem photosynthetic capacity derived from the La Thuile database and the N% sampled at the FLUXNET sites (*in-situ*, synchronization in space). 3) Ecosystem photosynthetic capacity derived for the same year of trait sampling and N% *in-situ* (synchronization in space and time).

For each combination of ecosystem photosynthetic capacity and N%, the slope and R^2 of the linear regression were determined. Distance correlation was computed as well, since it accounts for non-linear relationships (Szekely *et al.,* 2007). In order to evaluate the predictive capacity of the selected model a leave-one-out cross-validation was performed. Modeling efficiency (EF; Loague & Green 1991) and relative root mean square error (RRMSE) were computed to test the performances of the relationships. An analysis of covariance (ANCOVA) was conducted to statistically test the differences of regression slopes in the three relationships. In addition, to assess the significance of canopy structure in the relationship of plant traits and ecosystem photosynthetic capacity, we evaluated the information that LAI, representing the canopy structure, provides to the relation of N% and photosynthetic capacity estimated using GPP and PAR.

Identifying plant functional traits controlling ecosystem photosynthetic capacity

Because the functional relationship between plant traits, their interactions and photosynthetic capacity is not yet completely defined (Sardans & Penuelas 2012), a purely data driven approach was used (Golub et al., 2010). To identify the main explanatory variables (plant functional traits and LAI) of ecosystem photosynthetic capacity we used a stepwise multiple regression for variable selection based on the Akaike's Information criterion (AIC;

Yamashita *et al.,* 2007). Plant traits used in this context include N%, N_{area}, P_{mass} and P_{area}, C, $\delta^{13}C$ and SLA. We allowed the variables (traits and LAI) to be raised to the half and second power and also included the logarithm and ratios of all predictors to account for non-linear relationships and interactions as well.

RESULTS

Identifying robust estimates to characterize ecosystem photosynthetic capacity

Among the different percentiles that were used for the extraction of annual ecosystem photosynthetic capacity estimates, the 90th percentile is the one that minimizes the CV (i.e. the IAV) of most estimators (Fig. 2). The maximum values show the highest IAVs, and therefore are not considered appropriate estimates of ecosystem photosynthetic capacity. The use of the 60th percentile for the extractions shows slightly higher IAV than the 90th percentile. Other percentiles such as 85, 80, 75, and 70 are also tested and have similar results to the 60 percentile (data not shown). However, considering that we are interested in the annual maximum photosynthetic rates the 90th percentile of the different parameters was selected for further analyses.

Among the different estimators for ecosystem photosynthetic capacity (Table 1), A_{max} and $A_{max.structure}$ have the highest IAV regardless of how they are extracted annually. GPP_{cum} and GPP_{sat} have the lowest IAV, even though a detailed analysis revealed a substantial IAV for both estimators at some La Thuile sites (Fig. 3). While GPP_{cum} is related to the whole growing season, GPP_{sat} is related mostly to the peak of growing season. However, GPP_{cum} and GPP_{sat} are strongly correlated (Table S1). $GPP_{cum.structure}$ and $GPP_{sat.structure}$, accounting for canopy structure, show slightly higher IAV than GPP_{cum} and GPP_{sat}. Since we aim at developing a method to derive maximum ecosystem photosynthetic capacity robust to meteorological variability, we assess the impact of excluding from the analysis site-years with documented extreme events, such as the heat wave of 2003 in Europe (Fig. S3). Removing the year 2003 from the European sites-years does not change the results (Fig. S4). In addition, the estimated parameters e.g. GPP_{sat} are not strongly linked to climate variables (Fig. S8).

We conclude that the 90th percentile of GPP_{cum} or GPP_{sat} parameters of non-rectangular hyperbolic light response curves (either with or without structural information included) is an appropriate approach to characterize ecosystem photosynthetic capacity.

Relationship between ecosystem photosynthetic capacity and plant functional traits

Using a linear relationship, the CWM N% based on data from the TRY database explains 27% of the variance of site averaged GPP_{sat} (20% of $GPP_{sat.structure}$) (Fig. 4a, Table 2). CWM N% derived from TRY and *in-situ* were strongly correlated (Fig. S5), and the R^2 of the relationship between N% and GPP_{sat}, and $GPP_{sat.structure}$ improves from 0.27 to 0.39 and from 0.20 to 0.32, respectively when *in-situ* N% was used (Fig. 4b, Table 2). When additionally site averaged estimates of GPP_{sat} and $GPP_{sat.structure}$ were replaced by GPP_{sat} and $GPP_{sat.structure}$ from the years of *in-situ* sampling R^2 increases to 0.50 and 0.37, respectively (Fig. 4c, Table 2). The fit is even better when a non-linear fit is used for Fig. 4a and Fig. 4b (distance correlation increases from 0.56 to 0.73 for GPP_{sat} and from 0.47 to 0.63 for $GPP_{sat.structure,}$ See also Fig. S6). An ANCOVA test reveals that the relationship between ecosystem photosynthetic capacity and N% is significantly different between the levels of synchronization when GPP_{sat} (significantly different in slope and intercept, $p < 0.01$) or

$GPP_{sat.structure}$ (only significantly different intercept, $p < 0.05$) is used to characterize ecosystem photosynthetic capacity. Similar improvements of the relationship of CWM traits to GPP_{sat} and $GPP_{sat.structure}$ were realized using other plant traits and synchronizing the plant traits with the ecosystem photosynthetic capacity estimates in time and space (Fig. S2). We also tested whether the improvement of this relationship was due to random. To do this we randomly resampled the annual photosynthetic capacity (specifically GPP_{sat} and $GPP_{sat,structure}$) to test if the use of corresponding years statistically improves the relationship or not. The results confirm that the best fit is obtained when the N% and the photosynthetic capacity estimate match in time and space (Table S2).

Since species abundance information at the FLUXNET sites can be a relevant source of uncertainty we also calculated site-level species-averaged N% without accounting for differences in abundance. The results of the R^2 decreases but only by about 0.05 (Fig. S7).

Part of the unexplained variance may be due to the fact that we use leaf level N%, while not accounting for differences in LAI. Indeed, although N% and LAI are highly correlated, the combination of N% and LAI leads to a better explanation of the variability of $GPP_{sat,}$ (adjusted $R^2 = 0.56$, $R^2 = 0.64$) than N% ($R^2 = 0.50$) or LAI ($R^2 = 0.28$) alone (Table 3 - for 19 sites with available LAI).

Essential plant traits for ecosystem photosynthesis capacity

The variable selection analysis conducted with the stepwise regression using time-space synchronized data of ecosystem photosynthetic capacity estimates and *in-situ* measured plant traits and LAI shows that the variability of GPP_{sat} and $GPP_{sat.structure}$ between sites is best explained by leaf C/N ratio and $P_{area}{}^2$ (considering AIC as the selection criteria). However, only C/N is a significant predictor for both of the ecosystem photosynthetic capacity estimates. The selected model explains 61% and 54% of the variance of GPP_{sat} and $GPP_{sat.structure}$, respectively (Table 4).

DISCUSSION

Determining robust estimates of an EFP

We postulated that the IAV of ecosystem photosynthetic capacity at optimal growth conditions (e.g. at optimal light, temperature and water availability) derived with the proposed methodology and in the absence of disturbances should be low, and we demonstrated that it is not strongly related to climate drivers (Fig. S8). Additionally, assuming that the variation of plant traits across years is relatively low, this would allow for coupling ecosystem photosynthetic capacity estimates at any year, or averaged over several years, to species traits collected at the respective site (typically sampled during peak growing season).

Based on these criteria, the use of the light response curve was suitable as it accounts for variation in radiation, which is one of the important parameters explaining variation in GPP (van Dijk *et al.,* 2005). The estimation of the parameters using a moving window approach was also suitable because it accounts for variation in meteorological variables such as temperature and vapor pressure deficit. Among the parameters derived from the light response curve, A_{max} (or $A_{max.structure}$) had the largest IAV and was therefore the least suitable estimator for ecosystem photosynthetic capacity. This may have several reasons: The response of GPP to PAR/APAR does not exhibit a clear saturation and still tends to increase at high PAR/APAR and reaches A_{max} outside the range of PAR/APAR measurements.

Therefore, small changes in the slope at high PAR/APAR may cause large deviations in A_{max} (Gilmanov *et al*., 2003). In periods of the year when the PAR/APAR is not high, or the numbers of data points at high PAR is limited, the A_{max} parameter is poorly constrained. In this case the fit can be affected by random flux uncertainty that scales with the magnitude of fluxes and is not easily constrainable (Richardson *et al.,* 2012). GPP_{sat} or GPP_{cum} showed much smaller IAV and therefore we suggest the use GPP_{sat} or GPP_{cum} derived with PAR or APAR (Falge *et al.,* 2001, Lasslop *et al.,* 2010, Ruimy *et al.,* 1995) as more robust estimators of ecosystem photosynthetic capacity than A_{max}. Our results also demonstrate that the use of higher percentiles (i.e. 90th) rather than the maximum for EFP extraction should be preferred as it was more robust to outliers.

Linking plant functional traits and EFP estimates

EFPs are whole-ecosystem properties and thus depend on both ecosystem structure and function (Reichstein *et al*., 2014). Since GPP depends on both the efficiency with which the absorbed energy is converted to chemical energy at leaf level (Monteith 1972) and the canopy structure, GPP_{sat} variability ultimately depends on the variability of FAPAR (Reichstein *et al.,* 2014). In this study we accounted for this aspect by using APAR in Eq 1 for the estimation of $GPP_{sat\text{-}structure}$. APAR accounts for the seasonal and canopy structural (e.g. LAI) variability of the different ecosystems (Wang & Jarvis 1990). In extreme combinations, it is possible for an ecosystem to maintain a high LAI but low N% and vice versa (McMurtrie *et al*., 2008, Fig. S9). However, due to the smoothing and reconstruction of time-series of daily FAPAR from 16-days data (e.g. Kandasamy *et al.,* 2013), and the spatial mismatch between satellite pixel and the eddy-covariance footprint (Cescatti *et al.,* 2012, Jung *et al.,* 2008, Roman *et al.,* 2009), the EFP estimates using APAR exhibited larger uncertainties that more likely is reflected in the higher IAV compared to using PAR. The FAPAR product that we used for our estimates has a high temporal resolution (16 days) but its spatial resolution (1km) makes it uncertain; the footprints of FLUXNET sites are often smaller than a 1km grid-cell, and sites located in heterogeneous grid-cells have higher uncertainties in FAPAR as a consequence (Cescatti *et al.,* 2012). Nevertheless, the relationships of the estimates of photosynthetic capacity to plant traits were consistent, whether PAR or APAR was used. Our results also indicate the importance of accounting for canopy structure (Baldocchi & Meyers 1998, Reich 2012). The LAI-N% interaction contributes to the explanatory power of the model for predicting GPP_{sat}, as it shows how N% has an approximately linear relationship with GPP_{sat} (i.e. the GPP at light saturation without accounting for canopy structure) while the impact of LAI saturates.

A critical aspect when comparing leaf level attributes and EFPs is scaling these traits from leaf to canopy level. Based on the hypothesis that the dominant species are most adapted to their ambient environment (Vile et al., 2006), also known as "dominance hypothesis" (Grim 1998), we used CWM estimates of traits from dominant species at the sites. Here we considered sites with different vegetation types and environments (e.g. climate), where differences between the locations and vegetation types are large enough to ignore intraspecific trait variability, this allows us to use averaged trait values from TRY database in this study and in likewise global scale analyses (see Albert et al., 2011).

Robustness of ecosystem photosynthetic capacity –plant trait relationship to relaxed time-space synchrony of measurements

Here we show that the general pattern of the relationship between ecosystem photosynthetic capacity and plant traits (slopes of the linear regression, Fig. 4) is apparently independent using locally measured traits (*in-situ*) or species mean values from the TRY database. In addition, the relationships are independent of whether all data corresponded to the same year or the ecosystem photosynthetic capacity represented the multi-year averages of ecosystem photosynthetic capacity we used (most cases, Fig. S2). However, we observed a strong degradation of the explained variance when the synchronization in time and space was relaxed. The predictive power of plant functional traits for ecosystem photosynthetic capacity substantially improved when variation of species abundance, intraspecific variability of plant traits and interannual variability of ecosystem photosynthetic capacity was accounted for.

In part, this variability may be due to community species composition dynamics and competitive interactions that are partly triggered by disturbances or extreme environmental conditions. The study sites were not chosen to be in their late successional stage, and in the course of e.g. ten years of flux measurements, species abundances can change and plant species can be replaced. Site history and aging of the ecosystems contributes to the variability of the plant traits (Becknell & Powers 2014) and EFPs (e.g. Kutsch *et al.*, 2009, Urbanski *et al.,* 2007). This includes also the effect of fertilization on few sites, which could be one of the reasons why the *in-situ* N% from the cropland and grasslands are very different from the mean N% from TRY. Plant traits also have a temporal variability, which can be due to plant development or changes in the environment (e.g. Mickelbart 2010). Plant traits are responsible for the plastic response of an ecosystem to environmental changes and thus influence the interannual variability of ecosystem photosynthesis (Grassi *et al.*, 2005, Ma *et al.,* 2010). Furthermore, it confirms that species signals of some traits, specifically leaf nutrients, are not strong enough (high trait variability) (Kazakou et al., 2014) and this contribute to the uncertainty observed when linking EFPs and trait values derived from data bases. One way to account for intraspecific trait variation is to use trait observations from TRY that were reported from similar climatic conditions to the FLUXNET sites, or to predict intraspecific trait variation (Schrodt *et al.,* 2015). These opportunities are promising for future work, but could not be used here due to data scarcity and insufficient prediction accuracy. It remains to be better understood how the intraspecific variation of plant traits in time contributes to the response of plant communities to hydrometeorological changes and thus how the interannual and long-term variability of ecosystem photosynthetic capacity is mediated by dynamics of the vegetation (Reichstein *et al.,* 2014). A promising approach to monitor long-term variation of plant traits for different FLUXNET sites worldwide is novel remote sensing information (e.g. Asner & Martin 2015, Asner *et al.,* 2015). But, the contribution of physiological vs. structural information in the remote sensing signals needs to be better understood (e.g. Homolova *et al*., 2013, Wong & Gamon 2015). The common protocols developed in initiatives like ICOS - integrated carbon observation system (https://www.icos-ri.eu/) and NEON - national ecological observatory network (http://www.neoninc.org/) might help to overcome such limitations.

Identifying plant traits determining ecosystem photosynthetic capacity

We considered leaf traits relevant for photosynthesis and used a data-driven exploratory approach with all combinations of the selected leaf traits, mining for possible functional relationship between photosynthetic capacity and foliar traits (Golub 2010). Our results are in line with other studies conducted at the leaf-scale showing that C, N and P stoichiometry have a complimentary role in explaining photosynthetic capacity (Sardans & Penuelas 2013, Walker *et al*., 2014, Perez-Priego *et al.,* 2015). While C has low variation during the growing season (e.g. Jayasekera & Schleser 1991, Ma *et al*., 2010, Kattge *et al.,* 2011), N is the main factor driving the C:N ratio and influencing photosynthesis (see also Rong *et al.,* 2015). The N% is related to the chlorophyll content (e.g Houborg *et al.,* 2013) and to the amount of Ribulose-1,5-bisphosphate carboxylase/oxygenase enzymes that ultimately controls the photosynthetic rates and carbon uptake (Kattge *et al*., 2009, Evans 1989). Several studies have also shown this link at the ecosystem level (Kergoat *et al*., 2008, Ollinger *et al.,* 2008, Reich 2012). P is found in adenosine triphosphate molecules (ATP) and nucleotides of Nicotinamide adenine dinucleotide phosphate (NADP), which are involved in carbon fixation reactions. Several hypotheses connect the stoichiometry of leaves with optimum photosynthetic capacity and growth (e.g. growth rate hypothesis) (Elser *et al*., 2000; Sterner & Elser, 2002). In particular, the N/P ratio is related to photosynthetic capacity via the connection between the allocation of P into P-rich ribosomal RNA and of N to protein synthesis (Hessen *et al*., 2007). Since P is also used in carbon fixation as N, it influences the nitrogen-photosynthesis relationship by constraining the response of photosynthesis to N when P is low (Reich *et al.,* 2009, Walker *et al.,* 2014). However, more data are needed to build robust models that predict ecosystem photosynthetic capacity directly from plant functional traits and stoichiometry. Currently no consensus exists on which traits are most important to be measured at the sites in order to monitor the effect of plants on ecosystem functioning in response to their environment. Trait-ecosystem functioning studies with more data are needed to allow for robust conclusion on a suit of traits in this regard.

In conclusion, to quantitatively evaluate the link between ecosystem photosynthetic capacity and plant traits to improve predictions of ecosystem carbon uptake, continuous observations of species composition and plant traits at FLUXNET sites can be the key. We showed that currently the evaluation is limited by the scarcity of observations of both species composition and traits. We therefore suggest systematic sampling of plant traits, species abundance and auxiliary data for up-scaling traits at FLUXNET sites in parallel to flux measurements. In addition, remote sensing can be a solution in the future to acquire canopy level traits, circumventing up-scaling issues of *in-situ* measurements and may contribute to better detection of temporal and spatial variation of ecosystem level plant traits in synchrony with ecosystem photosynthetic capacity.

ACKNOWLEDGEMENTS

We thank all the people who made this study possible by participating in leaf sampling and sharing flux and plant trait data. We appreciate all the good discussions at the Max-Planck Institute of Biogeochemistry. We thank Ulrich Weber for preparing part of the flux and remote sensing data. We thank Jurgen van Hal, and Richard van Logtesteijn at the VU University in Amsterdam for measuring the plant traits and Katrin Fleischer for helping for leaf sampling at NL-Loo site. We also thank Martina Mund for sending us litter fall data from species of DE-Hai from which we estimated the abundances. We thank the anonymous reviewers and the Associate Editor for their constructive comments that improved both the readability and the robustness of the manuscript. The authors affiliated with the MPI BGC acknowledge funding by the European Union's Horizon 2020 project BACI under grant agreement No. 640176. The study has been supported by the TRY initiative on plant traits (http://www.try-db.org), hosted at the Max Planck Institute for Biogeochemistry, Jena, Germany. TRY is currently supported by DIVERSITAS/Future Earth and the German Center for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig. This work used eddy covariance data acquired by the FLUXNET community and in particular by the following networks: AmeriFlux (U.S. Department of Energy, Biological, and Environmental Research, Terrestrial Carbon Program (DE-FG02-04ER63917 and DE-FG02-04ER63911)), AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, CarboMont, ChinaFlux, Fluxnet-Canada (supported by CFCAS, NSERC, BIOCAP, Environment Canada, and NRCan), GreenGrass, KoFlux, LBA, NECC, OzFlux, TCOS-Siberia, and the USCCC. We acknowledge the financial support to the eddy covariance data harmonization provided by CarboEuropeIP, FAO-GTOS-TCO, iLEAPS, Max Planck Institute for Biogeochemistry, National Science Foundation, University of Tuscia, Université Laval, Environment Canada and US Department of Energy and the database development and technical support from Berkeley Water Center, Lawrence Berkeley National Laboratory, Microsoft Research eScience, Oak Ridge National Laboratory, University of California – Berkeley and the University of Virginia, and the IceMe of NUIST. The authors would like to thank all the PIs of eddy covariance sites, technicians, postdoctoral fellows, research associates, and site collaborators involved in FLUXNET who are not included as coauthors of this paper, but without whose work this analysis would not have been possible. K.H. acknowledges funding from the Ministry of Education, Youth and Sports of Czech Republic within the National Sustainability Program I (NPU I), grant number LO1415. T. Musavi acknowledges the International Max Planck Research School for global biogeochemical cycles.

Figures & Tables

Table 1 Definitions of ecosystem photosynthetic capacity estimated using light response curve. In the column 'Radiation' the independent variable used in Eq. 1 is reported.

Ecosystem Photosynthetic Capacity	Radiation	Definition
GPP_{sat}	PAR	GPP at light saturation using PAR as driving radiation and 2110 μmol m^{-2} s^{-1} as saturating light
$GPP_{sat.structure}$	APAR	GPP at light saturation using APAR as driving radiation and 2000 μmol m^{-2} s^{-1} as saturating light
A_{max}	PAR	Light saturated GPP - parameter of Eq. 1 with PAR as driving radiation
$A_{max.sructure}$	APAR	Light saturated GPP - parameter of Eq. 1 but with APAR as driving radiation
GPP_{cum}	PAR	integral of the light curve GPP up to the saturation point 2110 μmol m^{-2} s^{-1} of PAR
$GPP_{cum.structure}$	APAR	integral of the light curve GPP up to the saturation point 2000 μmol m^{-2} s^{-1} of PAR

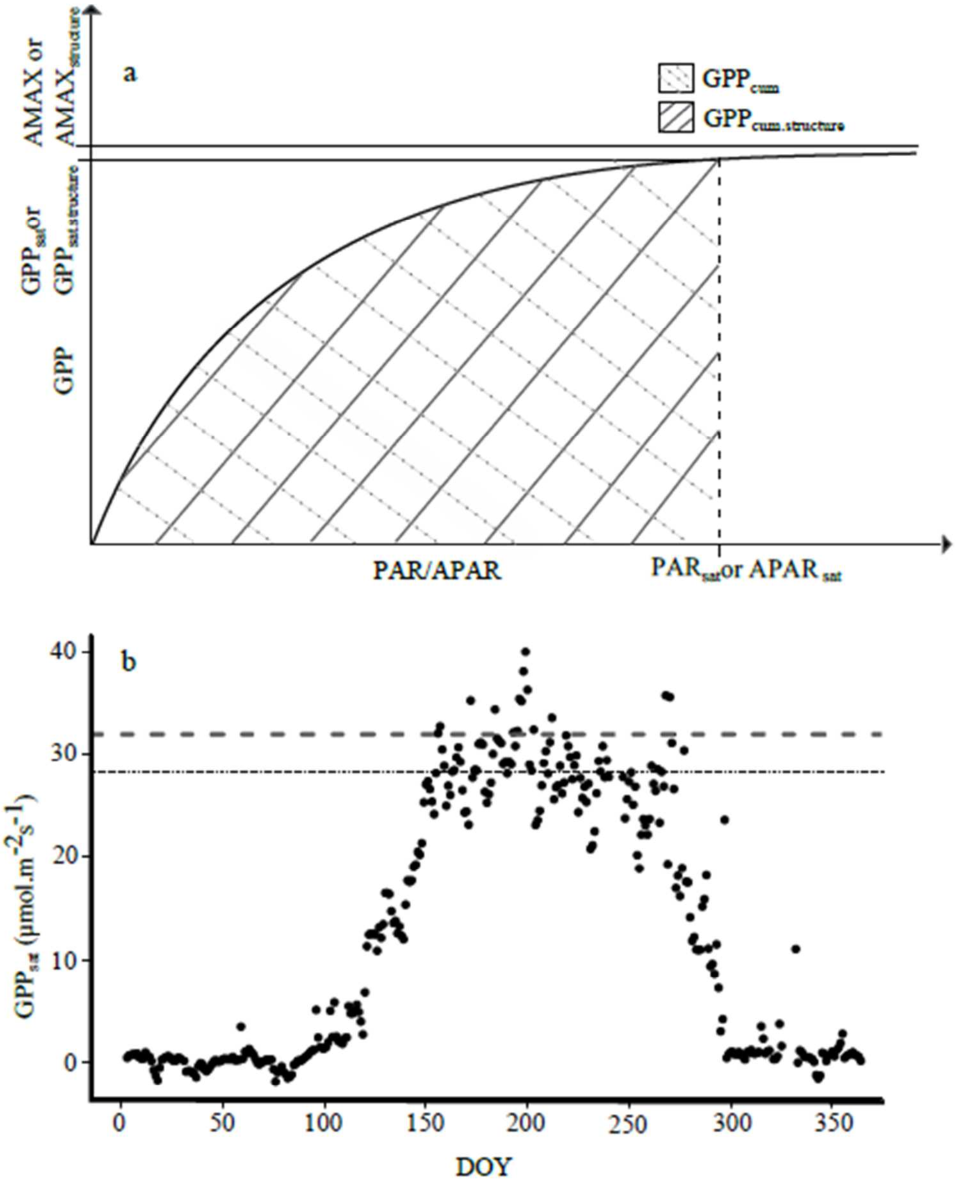


Figure 1 a. Conceptual figure of the different estimates of Ecosystem Functional Property (EFP) related to ecosystem photosynthetic capacity. Light response curves are fitted using GPP flux and PAR or APAR according to Table 1. b. Time series of GPP_{sat} for one year. Higher values of GPP_{sat} occur during the growing season (usually around mid-spring to end-summer). For this

study we use the 90th percentile as the maximum GPP_{sat} of each year, which is indicated with the dashed line. For comparison the 60th percentile of GPP_{sat} is indicated with the dotted line.

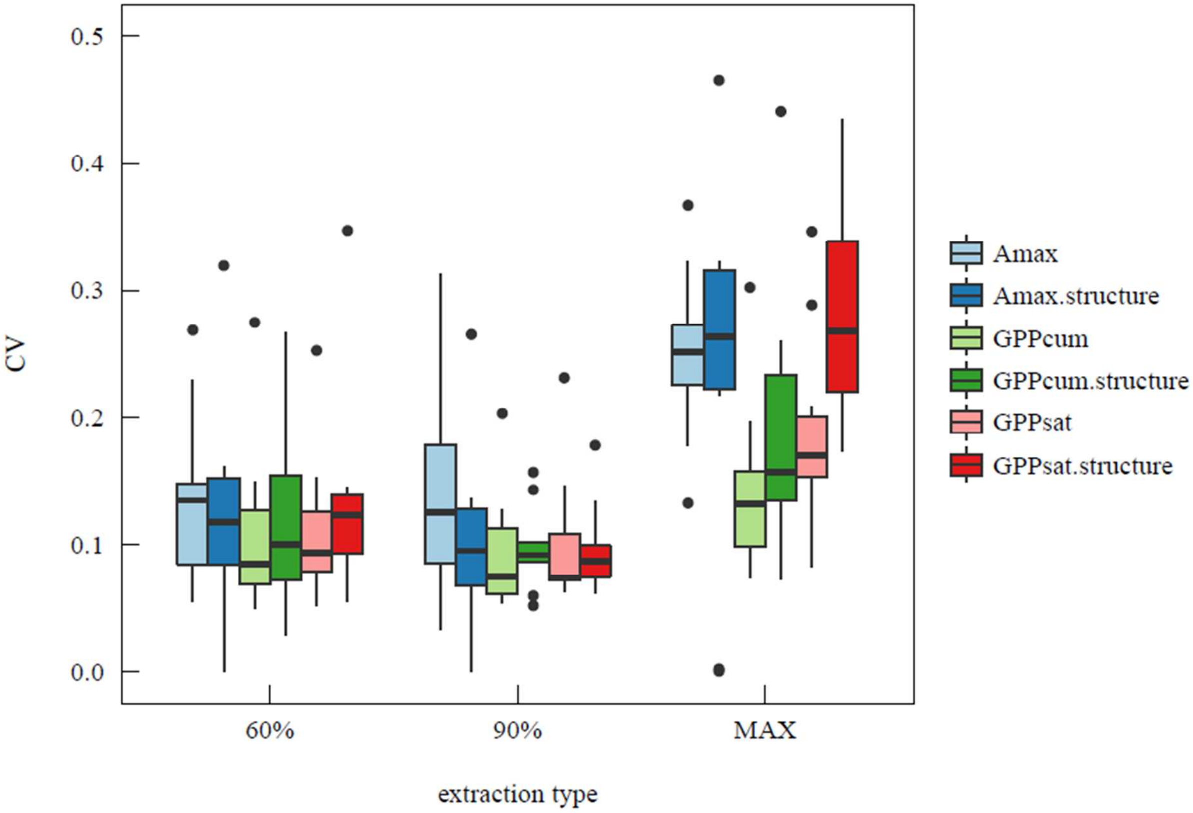


Figure 2 Comparison of mean and ranges of the different estimates of ecosystem photosynthetic capacity and different annual extractions. CV denotes the coefficient of variation (standard deviation/mean), which was calculated for every site. The results are based on sites with at least 5 years of available estimates (AT-Neu, DE-Hai, FI-Hyy, FR-Hes, IL-Yat, IT-MBo, IT-Ren, IT-SRo, NL-Loo, RU-Fyo). The lines across the box indicate the mean CV values and lower and upper boxes show the 25th and 75th percentiles. The lines on the ending of the boxes range from the maximum to minimum values. CV can be used to quantify the interannual variability of the estimates (small range and low average denotes low interannual variability). For explanations of the ecosystem photosynthetic capacity estimates described in the legend see Table 1.

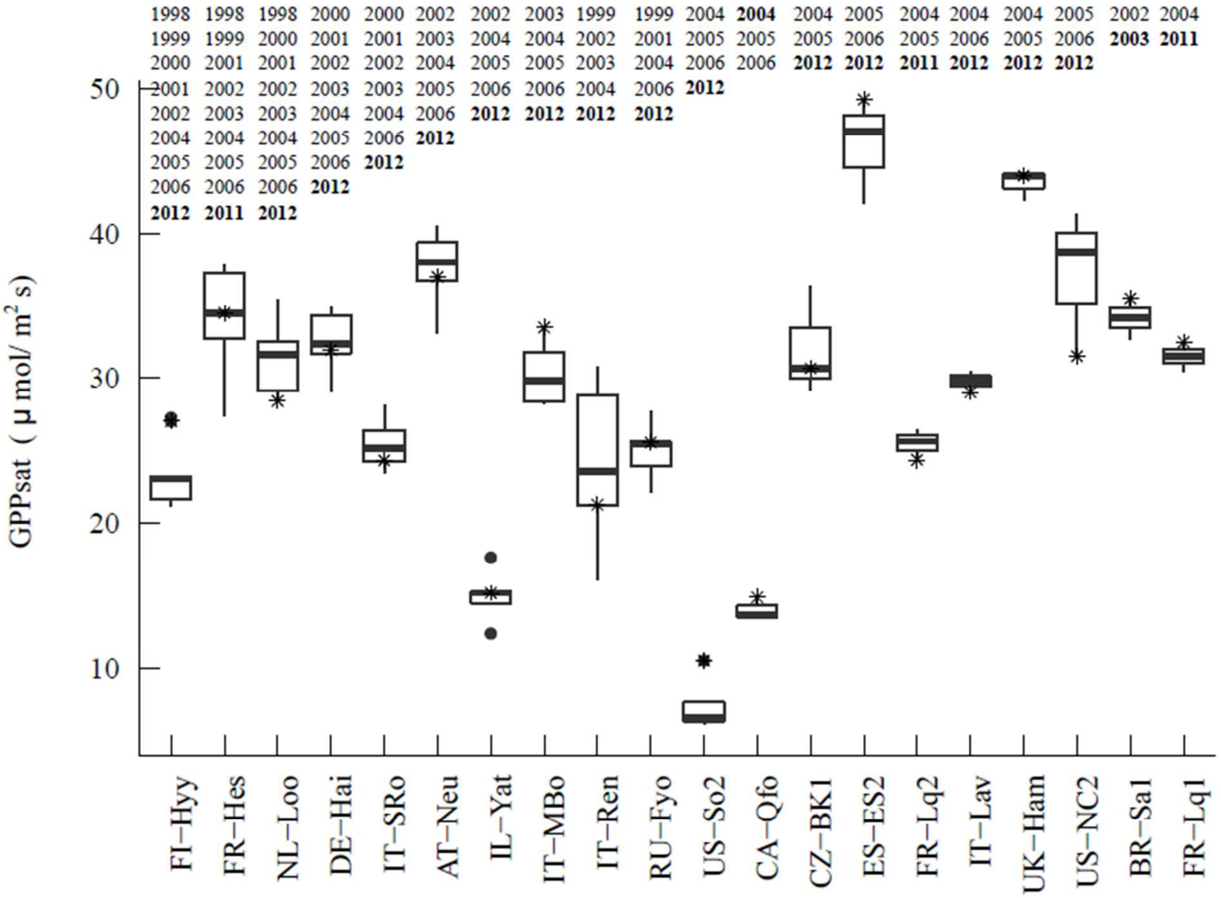


Figure 3 Boxplots of annual GPP$_{sat}$ values derived from the La Thuile database for each FLUXNET site. The line across the boxplot shows the mean GPP$_{sat}$ for each site and the lower and upper boxes show the 25th and 75th percentiles of GPP$_{sat}$. The stars denote GPP$_{sat}$ values of the respective sites in the year of *in-situ* plant trait measurements (bold years).

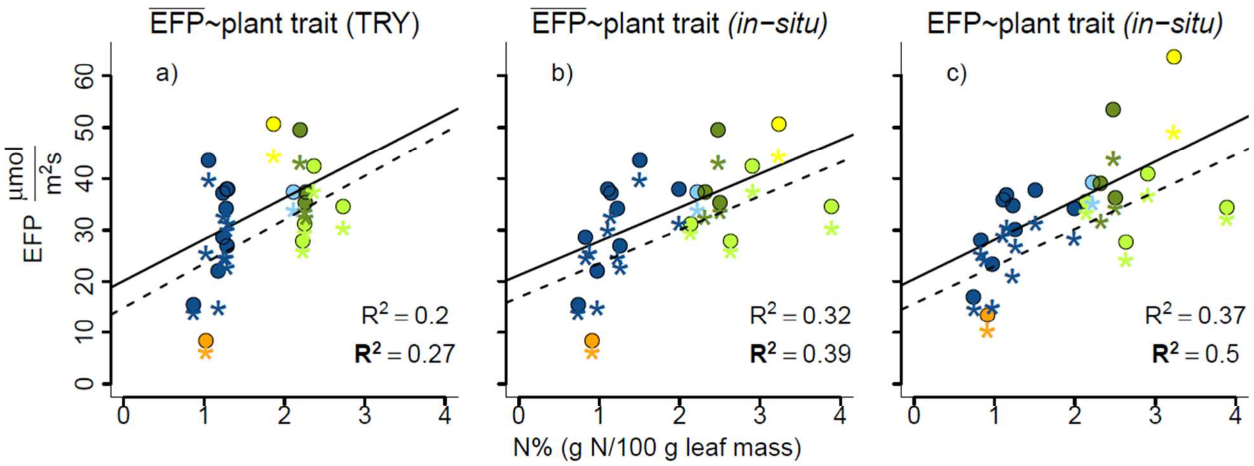


Figure 4 Relationship between a) GPP_{sat} and $\text{GPP}_{\text{sat.structure}}$ extracted from La Thuile and N% from TRY, b) GPP_{sat} and $\text{GPP}_{\text{sat.structure}}$ from La Thuile and N% *in-situ*, c) GPP_{sat} and $\text{GPP}_{\text{sat.structure}}$ derived from the same year of the trait sampling and N% *in-situ*. Y axes are ecosystem photosynthetic capacity as an example of an EFP and x axes are community weighted N%. The Macro accent on the EFP indicates that the GPP_{sat} and $\text{GPP}_{\text{sat.structure}}$ are the multi-year averages for each site. The gray color indicates ecosystem photosynthetic capacity estimates using APAR and black color stands for estimates using PAR. Bold R2 and star symbols are for the relationships with ecosystem photosynthetic capacity estimates using PAR (GPP_{sat}). Non-bold R2 and round points are for the relationship with ecosystem photosynthetic capacity estimates using APAR ($\text{GPP}_{\text{sat.structure}}$). The colors dark blue, light blue, dark green, light green, orange and yellow represent evergreen needle leaf forest, evergreen broad leaf forest, deciduous broad leaf forest, grassland, closed shrub-land and cropland as the plant functional types of the sites, respectively.

Table 2 Statistics of the relationships shown in Fig. 4. Ecosystem photosynthetic capacity estimates with macron accent are averaged over several years at each site and thosewithout macron accent are from the year of leaf sampling. RRMSE and EF are estimated in a cross-validation with leave-one-out mode and represents, relative root mean square error and model efficiency, respectively. The number of FLUXNET sites that are used with GPP_{sat} are 20, but 19 of the sites have $GPP_{sat.structure}$ available.

Ecosystem photosynthetic capacity	Model	Distance-Correlation	R^2	adj. R^2	Intercept ± s.e.	Slope ± s.e.	*p*	RRMSE	EF	df
GPP_{sat}	N%	0.73	0.50	0.47	15.67 ± 3.51	7.25 ± 1.71	0.0005	26.2	0.31	1 + 18
$\overline{GPPsat}$	N%	0.67	0.39	0.36	16.89 ± 3.95	6.57 ± 1.93	0.003	29.09	0.18	1 + 18
$\overline{GPPsat}$	$N\%^{TRY}$	0.56	0.27	0.23	14.88 ± 5.74	8.55 ± 3.28	0.018	30.65	0.09	1 + 18
$GPP_{sat.structure}$	N%	0.63	0.37	0.34	20.45 ± 5	7.62 ± 2.39	0.005	30	0.10	1 + 17
$\overline{GPPsat.structure}$	N%	0.58	0.32	0.28	21.18 ± 4.87	6.59 ± 2.33	0.01	25.5	-0.15	1 + 17
$\overline{GPPsat.structure}$	$N\%^{TRY}$	0.47	0.20	0.15	20.08 ± 7.01	8.07 ± 3.94	0.06	26.1	-0.20	1 + 17

Table 3 Relationships between N%, LAI, and GPP_{sat} tested. The GPP_{sat} is derived from the year at which the sampling of leaf N% was done. N% here is measured from *in-situ* samples. LAI is the 90th percentile of the bi-monthly LAI values retrieved from remote sensing and corresponds to the LAI of the sampling year as well (available for 19 sites).

Variable	Model	Distance-Correlation	R^2	adj. R^2	Intercept ± s.e.	Slope ± s.e.	*p*	df	AIC
LAI	N%	0.70	0.48	0.45	0.34 ± 0.38	0.71 ± 0.18	0.001	1 + 17	44
GPP_{sat}	LAI	0.57	0.28	0.24	20.10 ± 4.03	5.43 ± 2.09	0.01	1 + 17	138
GPP_{sat}	N%	0.73	0.50	0.47	15.25 ± 3.79	7.41 ± 1.81	0.0008	1 + 17	132
GPP_{sat}	LAI + N%	0.71	0.50	0.44	14.96 ± 3.98	N% 6.78 ± 2.58 LAI 0.87 ± 2.51	0.004	2 + 16	134
GPP_{sat}	N% + LAI + LAI:N%	-	0.64	0.56	0.74 ± 6.94	N% 15.22 ± 4.22 LAI 10.33 ± 4.55 N%:LAI -4.71 ± 1.98	0.001	3 + 15	129

Table 4 Results of the variable selection analyses conducted with a stepwise regression. The selected explanatory variables for GPP_{sat} are $C/N + P_{area}^2$. The same variables are tested for $GPP_{sat.structure}$ as well. Subsets of sites are used because only 18 sites had these two traits available and only 17 have the two traits and LAI measurements.

Variable	Model	Distance-Correlation	R^2	adj. R^2	Intercept ± s.e.	Slope ± s.e.	*p*	df	AIC	EF
GPP_{sat}	$C/N + P_{area}^2$	0.67	0.61	0.55	41.62 ± 3.01	C/N -0.39 ± 0.08 P_{area}^2 23.94 ± 16.20	0.0009	2 + 15	119	0.18
$GPP_{sat.structure}$	$C/N + P_{area}^2$	0.65	0.54	0.48	49.02 ± 4.07	C/N -0.48 ± 0.12 P_{area}^2 38.89 ± 22.22	0.004	2 + 14	123	-0.28

REFERENCES:

Albert CH, Grassein F, Schurr FM, Vieilledent G, Violle C (2011) When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology Evolution and Systematics*, **13**, 217-225.

Alton PB (2011) How useful are plant functional types in global simulations of the carbon, water, and energy cycles? *Journal of Geophysical Research-Biogeosciences,* **116**.

Asner GP, Martin RE (2015) Spectroscopic Remote Sensing of Non-Structural Carbohydrates in Forest Canopies. *Remote Sensing,* **7**, 3526-3547.

Asner GP, Martin RE, Anderson CB, Knapp DE (2015) Quantifying forest canopy traits: Imaging spectroscopy versus field survey. *Remote Sensing of Environment,* **158**, 15-27.

Atkin OK, Westbeek MHM, Cambridge ML, Lambers H, Pons TL (1997) Leaf respiration in light and darkness - A comparison of slow- and fast-growing Poa species. *Plant Physiology,* **113**, 961-965.

Bahn M, Wohlfahrt G, Haubner E *et al.* (1999) Leaf photosynthesis, nitrogen contents and specific leaf area of 30 grassland species in differently managed mountain ecosystems in the Eastern Alps. In: *Land-use changes in European mountain ecosystems. ECOMONT-Concept and Results.* . (eds Cernusca A, Tappeiner U, Bayfield N) pp Page, Blackwell Wissenschaft, Berlin.

Baldocchi D (2008) Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany,* **56**, 1-26.

Baldocchi D, Falge E, Gu LH *et al.* (2001) FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bulletin of the American Meteorological Society,* **82**, 2415-2434.

Baldocchi D, Meyers T (1998) On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and trace gas fluxes over vegetation: a perspective. *Agricultural and Forest Meteorology,* **90**, 1-25.

Becknell JM, Powers JS (2014) Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* **44**, 604-613.

Bonan GB (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science,* **320**, 1444-1449.

Britton CM, Dodd JD (1976) Relationships of Photosynthetically Active Radiation and Shortwave Irradiance. *Agricultural Meteorology,* **17**, 1-7.

Byrd RH, Lu PH, Nocedal J, Zhu CY (1995) A Limited Memory Algorithm for Bound Constrained Optimization. Siam Journal on Scientific Computing, **16**, 1190-1208.

Campbell C, Atkinson L, Zaragoza-Castells J, Lundmark M, Atkin O, Hurry V (2007) Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. *New Phytologist,* **176**, 375-389.

Cavender-Bares J, Keen A, Miles B (2006) Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology,* **87**, S109-S122.

Cescatti A, Marcolla B, Vannan SKS *et al.* (2012) Intercomparison of MODIS albedo retrievals and in situ measurements across the global FLUXNET network. *Remote Sensing of Environment,* **121**, 323-334.

Coomes DA, Heathcote S, Godfrey ER, Shepherd JJ, Sack L (2008) Scaling of xylem vessels and veins within the leaves of oak species. *Biology Letters,* **4**, 302-306.

Cornelissen JHC (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *Journal of Ecology,* **84**, 573-582.

Cornelissen JHC, Cerabolini B, Castro-Diez P *et al.* (2003a) Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? *Journal of Vegetation Science,* **14**, 311-322.

Cornelissen JHC, Diez PC, Hunt R (1996) Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology,* **84**, 755-765.

Cornelissen JHC, Quested HM, Gwynn-Jones D *et al.* (2004) Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology,* **18**, 779-786.

Cornwell WK, Cornelissen JHC, Amatangelo K *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters,* **11**, 1065-1071.

Craine JM, Elmore AJ, Aidar MPM *et al.* (2009) Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New Phytologist,* **183**, 980-992.

Craine JM, Lee WG, Bond WJ, Williams RJ, Johnson LC (2005) Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology,* **86**, 12-19.

De Dios VR, Goulden ML, Ogle K et al. (2012) Endogenous circadian regulation of carbon dioxide exchange in terrestrial ecosystems. *Global Change Biology*, **18**, 1956-1970.

Diaz S, Hodgson JG, Thompson K *et al.* (2004) The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science,* **15**, 295-304.

Elser JJ, O'brien WJ, Dobberfuhl DR, Dowling TE (2000) The evolution of ecosystem processes: growth rate and elemental stoichiometry of a key herbivore in temperate and arctic habitats. *Journal of Evolutionary Biology*, **13**, 845-853.

Evans J (1989) Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia,* **78**, 9-19.

Everitt B (1998) *The Cambridge Dictionary of Statistics,* Cambridge, UK New York, Cambridge University Press.

Falge E, Baldocchi D, Olson R *et al.* (2001) Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agricultural and Forest Meteorology,* **107**, 43-69.

Field C, Mooney HA (1986) The photosynthesis - nitrogen relationship in wild plants. In: *On the economy of plant form and function.* (ed Givnish TJ) pp Page. Cambridge, Cambridge University Press.

Filippa G, Cremonese E, Migliavacca M et al. (2016) Phenopix: A R package for image-based vegetation phenology. Agricultural and Forest Meteorology, **220**, 141-150.

Freschet GT, Cornelissen JHC, Van Logtestijn RSP, Aerts R (2010) Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology,* **98**, 362-373.

Fyllas NM, Patino S, Baker TR *et al.* (2009) Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences,* **6**, 2677-2708.

Garnier E, Cortez J, Billes G *et al.* (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology,* **85**, 2630-2637.

Garnier E, Lavorel S, Ansquer P *et al.* (2007) Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. *Annals of Botany,* **99**, 967-985.

Gilmanov TG, Verma SB, Sims PL, Meyers TP, Bradford JA, Burba GG, Suyker AE (2003) Gross primary production and light response parameters of four Southern Plains ecosystems estimated using long-term CO2-flux tower measurements. *Global Biogeochemical Cycles,* **17**.

Goll DS, Brovkin V, Parida BR *et al.* (2012) Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling. *Biogeosciences,* **9**, 3547-3569.

Golub T (2010) Counterpoint: Data first. *Nature*, **464**, 679-679.

Grassi G, Vicinelli E, Ponti F, Cantoni L, Magnani F (2005) Seasonal and interannual variability of photosynthetic capacity in relation to leaf nitrogen in a deciduous forest plantation in northern Italy. *Tree Physiology,* **25**, 349-360.

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902-910.

Groenendijk M, Dolman AJ, Van Der Molen MK *et al.* (2011) Assessing parameter variability in a photosynthesis model within and between plant functional types using global Fluxnet eddy covariance data. *Agricultural and Forest Meteorology,* **151**, 22-38.

Han WX, Fang JY, Guo DL, Zhang Y (2005) Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytologist,* **168**, 377-385.

Hessen DO, Jensen TC, Kyle M, Elser JJ (2007) RNA responses to N- and P-limitation; reciprocal regulation of stoichiometry and growth rate in Brachionus. *Functional Ecology*, **21**, 956-962.

Hickler T (1999) Plant functional types and community characteristics along environmental gradients on Öland's Great Alvar (Sweden). University of Lund, Sweden.

Hollinger DY, Aber J, Dail B *et al.* (2004) Spatial and temporal variability in forest-atmosphere CO2 exchange. *Global Change Biology,* **10**, 1689-1706.

Homolova L, Maenovsky Z, Clevers JGPW, Garcia-Santos G, Schaeprnan ME (2013) Review of optical-based remote sensing for plant trait mapping. *Ecological Complexity,* **15**, 1-16.

Houborg R, Cescatti A, Migliavacca M, Kustas WP (2013) Satellite retrievals of leaf chlorophyll and photosynthetic capacity for improved modeling of GPP. *Agricultural and Forest Meteorology,* **177**, 10-23.

Jacobs CMJ, Jacobs AFG, Bosveld FC *et al.* (2007) Variability of annual CO2 exchange from Dutch grasslands. *Biogeosciences,* **4**, 803-816.

Jayasekera R, Schleser GH (1991) Seasonal-Changes in Organic-Carbon Content of Leaves of Deciduous Trees. *Journal of Plant Physiology,* **138**, 507-510.

Jung M, Verstraete M, Gobron N *et al.* (2008) Diagnostic assessment of European gross primary production. *Global Change Biology,* **14**, 2349-2364.

Kandasamy S, Baret F, Verger A, Neveux P, Weiss M (2013) A comparison of methods for smoothing and gap filling time series of remote sensing observations - application to MODIS LAI products. *Biogeosciences,* **10**, 4055-4071.

Kattge J, Diaz S, Lavorel S *et al.* (2011) TRY - a global database of plant traits. *Global Change Biology,* **17**, 2905-2935.

Kattge J, Knorr W, Raddatz T, Wirth C (2009) Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology,* **15**, 976-991.

Kazakou E, Vile D, Shipley B, Gallet C, Garnier E (2006) Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology,* **20**, 21-30.

Kazakou E, Violle C, Roumet C, Navas ML, Vile D, Kattge J, Garnier E (2014) Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science*, **25**, 235-247.

Kergoat L, Lafont S, Arneth A, Le Dantec V, Saugier B (2008) Nitrogen controls plant canopy light-use efficiency in temperate and boreal ecosystems. *Journal of Geophysical Research-Biogeosciences,* **113**.

Kerkhoff AJ, Fagan WF, Elser JJ, Enquist BJ (2006) Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *American Naturalist,* **168**, E103-E122.

Kleyer M, Bekker RM, Knevel IC *et al.* (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology,* **96**, 1266-1274.

Kutsch WL, Wirth C, Kattge J, Nollert S, Herbst M, Kappen L (2009) Ecophysiological Characteristics of Mature Trees and Stands - Consequences for Old-Growth Forest Productivity. *Old-Growth Forests: Function, Fate and Value,* **207**, 57-79.

Lasslop G, Reichstein M, Papale D *et al.* (2010) Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: critical issues and global evaluation. *Global Change Biology,* **16**, 187-208.

Laughlin DC, Leppert JJ, Moore MM, Sieg CH (2010) A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology,* **24**, 493-501.

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology,* **16**, 545-556.

Lavorel S, Mcintyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution,* **12**, 474-478.

Law BE, Arkebauer T, Campbell J *et al.* (2008) Terrestrial Carbon Observations: Protocols for Vegetation Sampling and Data Submission. pp Page, Rome, Italy, Terrestrial Carbon Observations Panel of the Global Terrestrial Observing System.

Loague K, Green RE (1991) Statistical and graphical methods for evaluating solute transport models: Overview and application. *Journal of Contaminant Hydrology,* **7**, 51-73.

Louault F, Pillar VD, Aufrere J, Garnier E, Soussana JF (2005) Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. *Journal of Vegetation Science,* **16**, 151-160.

Loveys BR, Atkinson LJ, Sherlock DJ, Roberts RL, Fitter AH, Atkin OK (2003) Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species. *Global Change Biology,* **9**, 895-910.

Ma SY, Baldocchi DD, Mambelli S, Dawson TE (2010) Are temporal variations of leaf traits responsible for seasonal and inter-annual variability in ecosystem CO2 exchange? *Functional Ecology,* **25**, 258-270.

Mcmurtrie RE, Norby RJ, Medlyn BE, Dewar RC, Pepper DA, Reich PB, Barton CVM (2008) Why is plant-growth response to elevated CO2 amplified when water is limiting, but reduced when nitrogen is limiting? A growth-optimisation hypothesis. *Functional Plant Biology,* **35**, 521-534.

Medlyn BE, Badeck FW, De Pury DGG *et al.* (1999) Effects of elevated [CO2] on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant Cell and Environment,* **22**, 1475-1495.

Meng TT, Wang H, Harrison SP, Prentice IC, Ni J, Wang G (2015) Responses of leaf traits to climatic gradients: adaptive variation versus compositional shifts. *Biogeosciences,* **12**, 5339-5352.

Mercado LM, Patino S, Domingues TF *et al.* (2011) Variations in Amazon forest productivity correlated with foliar nutrients and modelled rates of photosynthetic carbon supply. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **366**, 3316-3329.

Messier J, Mcgill BJ, Lechowicz MJ (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters,* **13**, 838-848.

Meziane D, Shipley B (1999) Interacting determinants of specific leaf area in 22 herbaceous species: effects of irradiance and nutrient availability. *Plant Cell and Environment,* **22**, 447-459.

Mickelbart MV (2010) Variation in Leaf Nutrient Concentrations of Freeman Maple Resulting from Canopy Position, Leaf Age, and Petiole Inclusion. *Hortscience,* **45**, 428-431.

Migliavacca M, Galvagno M, Cremonese E *et al.* (2011) Using digital repeat photography and eddy covariance data to model grassland phenology and photosynthetic CO2 uptake. *Agricultural and Forest Meteorology,* **151**, 1325-1337.

Monteith JL (1972) Solar-Radiation and Productivity in Tropical Ecosystems. *Journal of Applied Ecology,* **9**, 747-766.

Musavi T, Mahecha MD, Migliavacca M *et al.* (2015) The imprint of plants on ecosystem functioning: A data-driven approach. *International Journal of Applied Earth Observation and Geoinformation,* **43**, 119-131.

Niinemets U (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology,* **82**, 453-469.

Ogaya R, Penuelas J (2003) Comparative field study of Quercus ilex and Phillyrea latifolia: photosynthetic response to experimental drought conditions. *Environmental and Experimental Botany,* **50**, 137-148.

Ollinger SV, Richardson AD, Martin ME *et al.* (2008) Canopy nitrogen, carbon assimilation, and albedo in temperate and boreal forests: Functional relations and potential climate feedbacks. *Proceedings of the National Academy of Sciences of the United States of America,* **105**, 19336-19341.

Onoda Y, Westoby M, Adler PB *et al.* (2011) Global patterns of leaf mechanical properties. *Ecology Letters,* **14**, 301-312.

Ordonez JC, Van Bodegom PM, Witte JPM, Bartholomeus RP, Van Hal JR, Aerts R (2010) Plant Strategies in Relation to Resource Supply in Mesic to Wet Environments: Does Theory Mirror Nature? *American Naturalist,* **175**, 225-239.

Pappas C, Fatichi S, Burlando P (2016) Modeling terrestrial carbon and water dynamics across climatic gradients: does plant trait diversity matter? *New Phytologist*, **209**, 137-151.

Pereira HM, Ferrier S, Walters M *et al.* (2013) Essential Biodiversity Variables. *Science,* **339**, 277-278.

Perez-Priego O, Guan J, Rossini M *et al.* (2015) Sun-induced Chlorophyll fluorescence and PRI improve remote sensing GPP estimates under varying nutrient availability in a typical Mediterranean savanna ecosystem. *Biogeosciences Discuss.,* **12**, 11891-11934.

Pinty B, Andredakis I, Clerici M et al. (2011a) Exploiting the MODIS albedos with the Two-stream Inversion Package (JRC-TIP): 1. Effective leaf area index, vegetation, and soil properties. Journal of Geophysical Research-Atmospheres, 116.

Pinty B, Clerici M, Andredakis I et al. (2011b) Exploiting the MODIS albedos with the Two-stream Inversion Package (JRC-TIP): 2. Fractions of transmitted and absorbed fluxes in the vegetation and soil layers. Journal of Geophysical Research-Atmospheres, 116.

Pinty B, Lavergne T, Vossbeck M et al. (2007) Retrieving surface parameters for climate models from Moderate Resolution Imaging Spectroradiometer (MODIS)-Multiangle Imaging Spectroradiometer (MISR) albedo products. Journal of Geophysical Research-Atmospheres, 112.

Poorter H, Niinemets U, Poorter L, Wright IJ, Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis (vol 182, pg 565, 2009). *New Phytologist,* **183**, 1222-1222.

Poschlod P, Kleyer M, Jackel AK, Dannemann A, Tackenberg O (2003) BIOPOP - a database of plant traits and Internet application for nature conservation. *Folia Geobotanica,* **38**, 263-271.

Quested HM, Cornelissen JHC, Press MC *et al.* (2003) Decomposition of sub-arctic plants with differing nitrogen economies: A functional role for hemiparasites. *Ecology,* **84**, 3209-3221.

Reich PB (2012) Key canopy traits drive forest productivity. *Proceedings of the Royal Society B-Biological Sciences,* **279**, 2128-2134.

Reich PB, Oleksyn J, Wright IJ (2009) Leaf phosphorus influences the photosynthesis-nitrogen relation: a cross-biome analysis of 314 species. *Oecologia,* **160**, 207-212.

Reich PB, Tjoelker MG, Pregitzer KS, Wright IJ, Oleksyn J, Machado JL (2008) Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecology Letters,* **11**, 793-801.

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America,* **94**, 13730-13734.

Reichstein M, Bahn M, Mahecha MD, Kattge J, Baldocchi DD (2014) Linking plant and ecosystem functional biogeography. *Proc Natl Acad Sci U S A,* **111**, 13697-13702.

Reichstein M, Falge E, Baldocchi D et al. (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, **11**, 1424-1439.

Richardson AD, Aubinet M, Barr AG, Hollinger DY, Ibrom A, Lasslop G, Reichstein M (2012) Uncertainty Quantification. In: *Eddy Covariance. A Practical Guide to Measurement and Data Analysis.* (ed Papale D) pp Page., Springer.

Richardson AD, Hollinger DY, Aber JD, Ollinger SV, Braswell BH (2007) Environmental variation is directly responsible for short- but not long-term variation in forest-atmosphere carbon exchange. *Global Change Biology,* **13**, 788-803.

Roman MO, Schaaf CB, Woodcock CE *et al.* (2009) The MODIS (Collection V005) BRDF/albedo product: Assessment of spatial representativeness over forested landscapes. *Remote Sensing of Environment,* **113**, 2476-2498.

Rong QQ, Liu JT, Cai YP, Lu ZH, Zhao ZZ, Yue WC, Xia JB (2015) Leaf carbon, nitrogen and phosphorus stoichiometry of Tamarix chinensis Lour. in the Laizhou Bay coastal wetland, China. *Ecological Engineering,* **76**, 57-65.

Ruimy A, Jarvis PG, Baldocchi DD, Saugier B (1995) CO2 fluxes over plant canopy and solar radiation: A review. *Advances in Ecological Research,* **26**.

Sack L, Cowan PD, Jaikumar N, Holbrook NM (2003) The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. *Plant Cell and Environment,* **26**, 1343-1356.

Sack L, Melcher PJ, Liu WH, Middleton E, Pardee T (2006) How strong is intracanopy leaf plasticity in temperate deciduous trees? *Am J Bot,* **93**, 829-839.

Sardans J, Penuelas J (2012) The Role of Plants in the Effects of Global Change on Nutrient Availability and Stoichiometry in the Plant-Soil System. *Plant Physiology,* **160**, 1741-1761.

Sardans J, Penuelas J (2013) Tree growth changes with climate and forest type are associated with relative allocation of nutrients, especially phosphorus, to leaves and wood. *Global Ecology and Biogeography,* **22**, 494-507.

Schaaf CB, Gao F, Strahler AH et al. (2002) First operational BRDF, albedo nadir reflectance products from MODIS. Remote Sensing of Environment, **83**, 135-148.

Schrodt F, Kattge J, Shan HH et al. (2015) BHPMF-a hierarchical Bayesian approach to gap-filling and trait prediction for macroecology and functional biogeography. Global Ecology and Biogeography, **24**, 1510-1521.

Shipley B (1995) Structured Interspecific Determinants of Specific Leaf-Area in 34 Species of Herbaceous Angiosperms. *Functional Ecology,* **9**, 312-319.

Shipley B (2002) Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance. *Functional Ecology,* **16**, 682-689.

Shipley B, Vu TT (2002) Dry matter content as a measure of dry matter concentration in plants and their parts. *New Phytologist,* **153**, 359-364.

Sterner, R.W., & Elser, J. J. (2002). *Ecological stoichiometry*. Princeton, NJ USA: Princeton University Press.

Stoy PC, Richardson AD, Baldocchi DD *et al.* (2009) Biosphere-atmosphere exchange of CO2 in relation to climate: a cross-biome analysis across multiple time scales. *Biogeosciences,* **6**, 2297-2312.

Szekely GJ, Rizzo ML, Bakirov NK (2007) Measuring and testing dependence by correlation of distances. 2769-2794.

Urbanski S, Barford C, Wofsy S *et al.* (2007) Factors controlling CO2 exchange on timescales from hourly to decadal at Harvard Forest. *Journal of Geophysical Research-Biogeosciences,* **112**.

V. Buttlar J, Zscheischler J, Mahecha MD (2014) An extended approach for spatiotemporal gapfilling: dealing with large and systematic gaps in geoscientific datasets. *Nonlin. Processes Geophys.,* **21**, 203-215.

Van Bodegom PM, Douma JC, Witte JPM, Ordonez JC, Bartholomeus RP, Aerts R (2012) Going beyond limitations of plant functional types when predicting global ecosystem-atmosphere fluxes: exploring the merits of traits-based approaches. *Global Ecology and Biogeography,* **21**, 625-636.

Van Dijk AIJM, Dolman AJ, Schulze ED (2005) Radiation, temperature, and leaf area explain ecosystem carbon fluxes in boreal and temperate European forests. *Global Biogeochemical Cycles,* **19**.

Verheijen LM, Aerts R, Bonisch G, Kattge J, Van Bodegom PM (2015) Variation in trait trade-offs allows differentiation among predefined plant functional types: implications for predictive ecology. *New Phytol*.

Vile D (2005) Signifcations fonctionnelle et ecologique des traits des especes vegetales: exemple dans une succession post-cultural mediterraneenne et generalisations.

Vile D, Shipley B, Garnier E (2006) Ecosystem productivity can be predicted from potential relative growth rate and species abundance. *Ecology Letters*, **9**, 1061-1067.

Walker AP, Beckerman AP, Gu LH *et al.* (2014) The relationship of leaf photosynthetic traits - V-cmax and J(max) - to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. *Ecology and Evolution,* **4**, 3218-3235.

Wang YP, Jarvis PG (1990) Influence of Crown Structural-Properties on Par Absorption, Photosynthesis, and Transpiration in Sitka Spruce - Application of a Model (Maestro). *Tree Physiology,* **7**, 297-316.

White MA, Thornton PE, Running SW, Nemani RR (2000) Parameterization and Sensitivity Analysis of the BIOME–BGC Terrestrial Ecosystem Model: Net Primary Production Controls. *Earth Interactions,* **4**, 1-85.

Willis CG, Halina M, Lehman C, Reich PB, Keen A, Mccarthy S, Cavender-Bares J (2010) Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. *Ecography,* **33**, 565-577.

Wong CYS, Gamon JA (2015) Three causes of variation in the photochemical reflectance index (PRI) in evergreen conifers. *New Phytologist,* **206**, 187-195.

Wright IJ, Ackerly DD, Bongers F *et al.* (2007) Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany,* **99**, 1003-1015.

Wright IJ, Reich PB, Westoby M *et al.* (2004) The worldwide leaf economics spectrum. *Nature,* **428**, 821-827.

Wright SJ, Kitajima K, Kraft NJB *et al.* (2010) Functional traits and the growth-mortality trade-off in tropical trees. *Ecology,* **91**, 3664-3674.

Yamashita T, Yamashita K, Kamimura R (2007) A stepwise AIC method for variable selection in linear regression. *Communications in Statistics-Theory and Methods,* **36**, 2395-2403.

Yang X, Thornton PE, Ricciuto DM, Post WM (2014) The role of phosphorus dynamics in tropical forests – a modeling study using CLM-CNP. *Biogeosciences,* **11**, 1667-1681.

SUPPORTING MATERIAL

Table S1 Summary of Pearson correlation coefficient between the different estimates of ecosystem photosynthetic capacity.

	GPP$_{sat}$	GPP$_{sat.structure}$	A$_{max}$	A$_{max.structure}$	GPP$_{cum}$	GPP$_{cum.structure}$
GPP$_{sat}$	1					
GPP$_{sat.structure}$	0.93	1				
A$_{max}$	0.82	0.90	1			
A$_{max.structure}$	0.84	0.95	0.94	1		
GPP$_{cum}$	0.97	0.85	0.71	0.73	1	
GPP$_{cum.structure}$	0.95	0.95	0.86	0.86	0.90	1

Table S2 In order to compare Fig. 4b with Fig. 4c in respect to random effects (whether the relationship in Fig. 4c is just by chance better that Fig. 4b), we performed a bootstrapping test. For the relationship in Fig. 4b prior to estimating the mean GPP$_{sat}$ (or GPP$_{sat.structure}$) of the sites, we sampled randomly (with replacement) for each site the annual GPP$_{sat}$ (also GPP$_{sat.structure}$) and then estimated the mean over the years. This was done 100 times and at each step the linear regression of the model was tested for R^2 and *p-value*. In none of the cases the fit was better than the one in Fig. 4c when GPP$_{sat}$ was used (time and space matched data). Using GPP$_{sat.structure}$ only 1% of the random site-year combination had an R^2 higher than the one in Fg.4c (0.37) with a *p-value* < 0.05 and a positive slope. Below are the summary of the results from the 100 random fit of Fig. 4b.

	R^2	*p.value*	EFP estimate
Min.	0.2683	0.002288	**GPP$_{sat}$**
1st Qu.	0.2845	0.004134	
Median	0.3315	0.007891	
Mean	0.3309	0.009602	
3rd Qu.	0.3745	0.015435	
Max.	0.4118	0.019314	
Min.	0.2799	0.002061	**GPP$_{sat.structure}$**
1st Qu.	0.2967	0.007480	
Median	0.3345	0.009494	
Mean	0.3320	0.011045	
3rd Qu.	0.3514	0.015927	
Max.	0.4369	0.019853	

Figure S1 Time series of daily GPP_{sat}. Data filtering using the R^2 of the model fit shows that only GPPsat during growing season will be selected (colored in dark green). The related model fit R^2 of the filtered data is shown in red stars. The example is made for two sites with two different plant functional types. ENF is ever green needle leaved forest and DBF is for deciduous broad leaved forest.

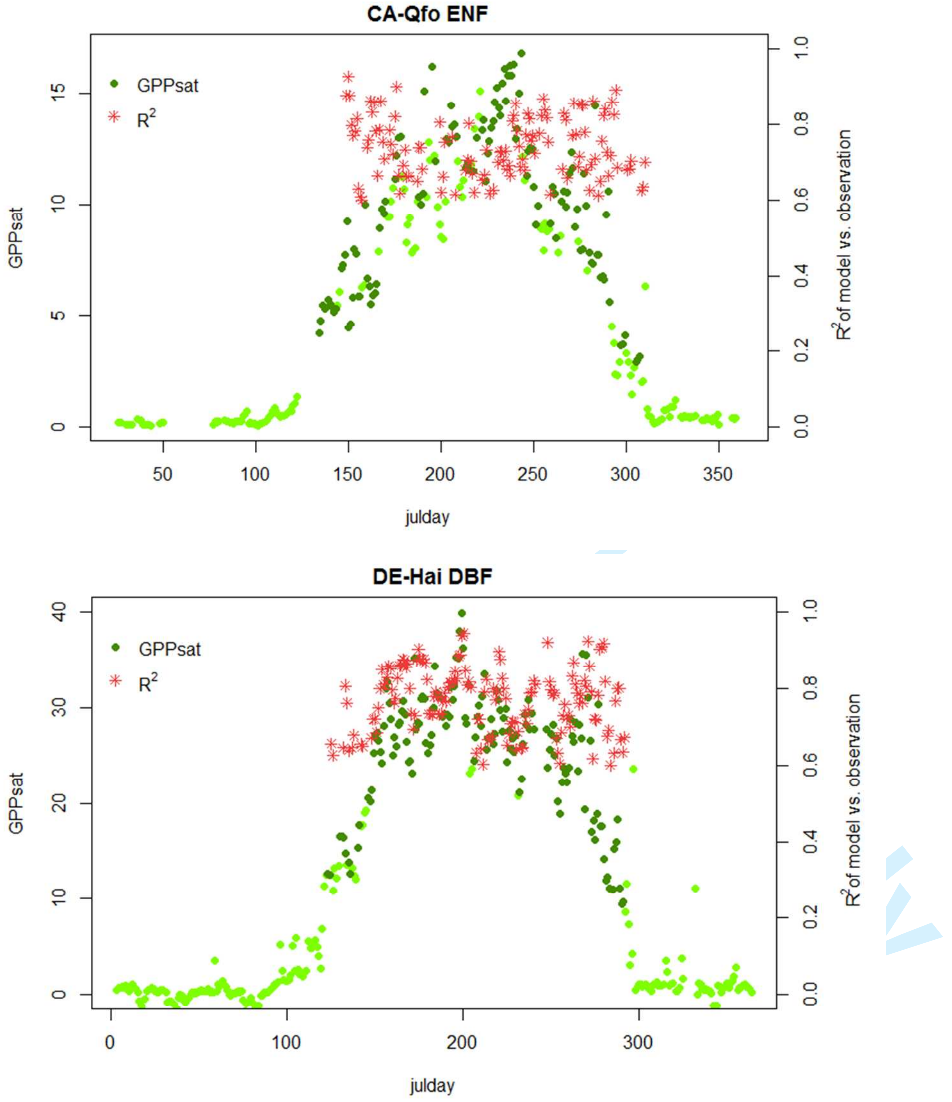
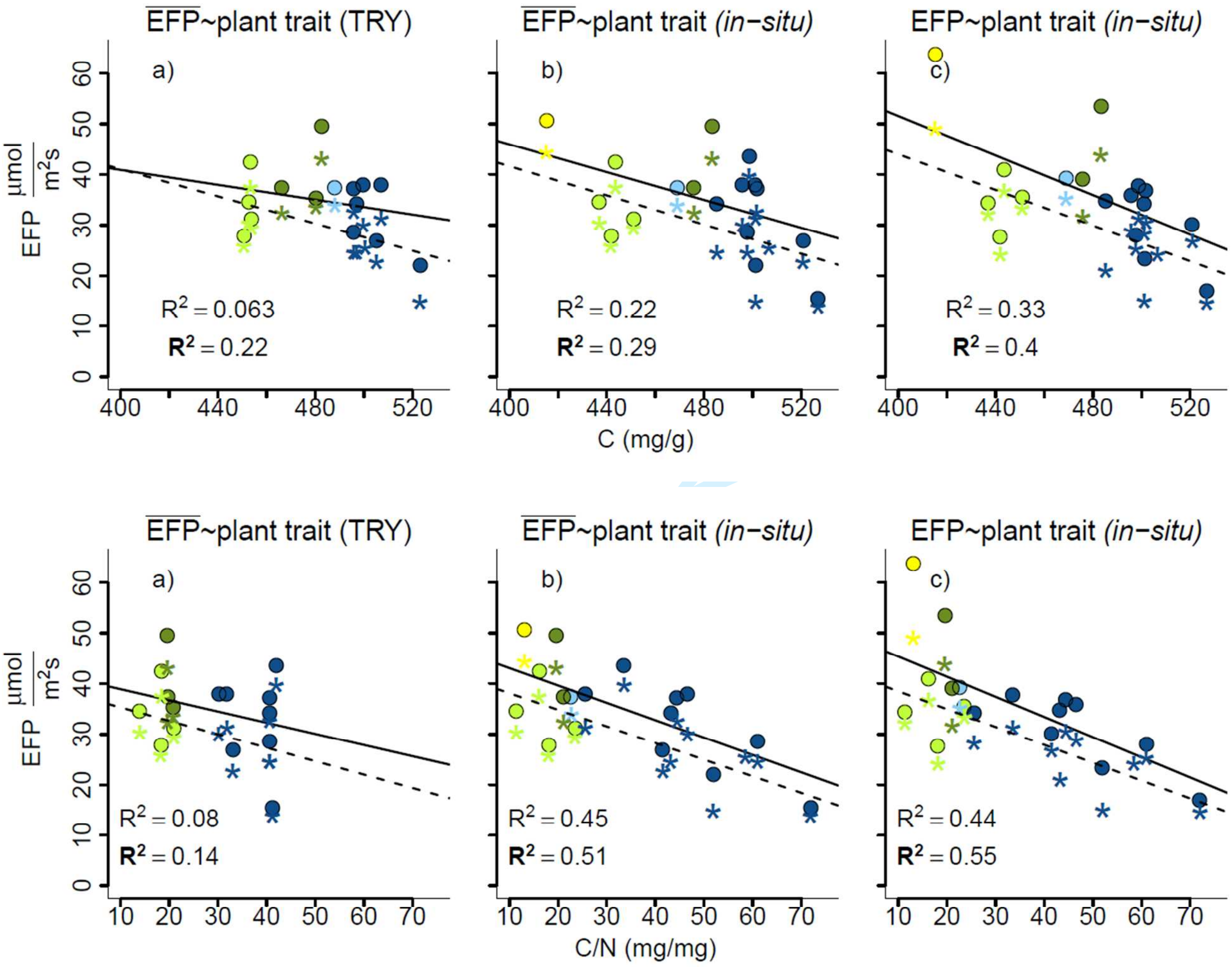
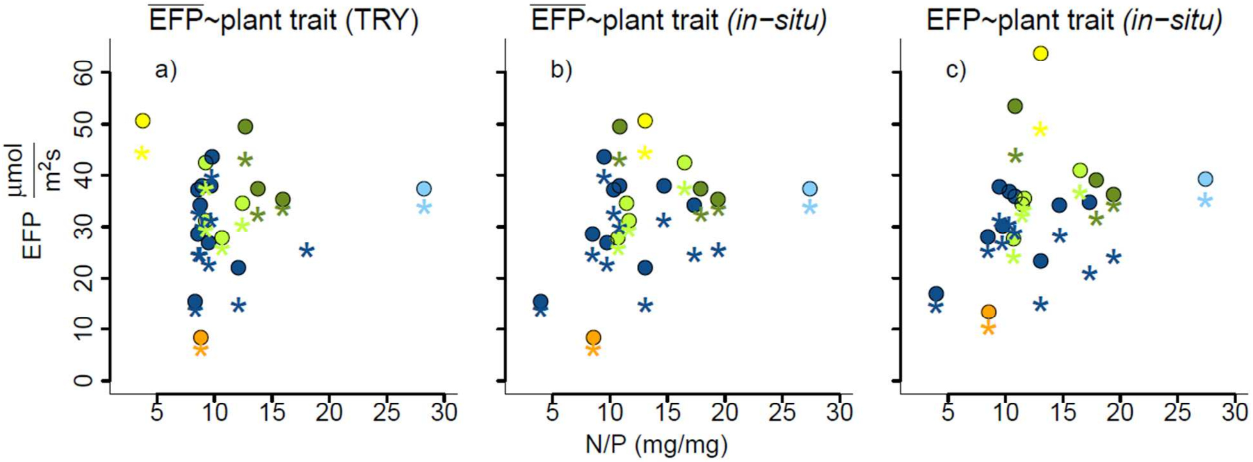
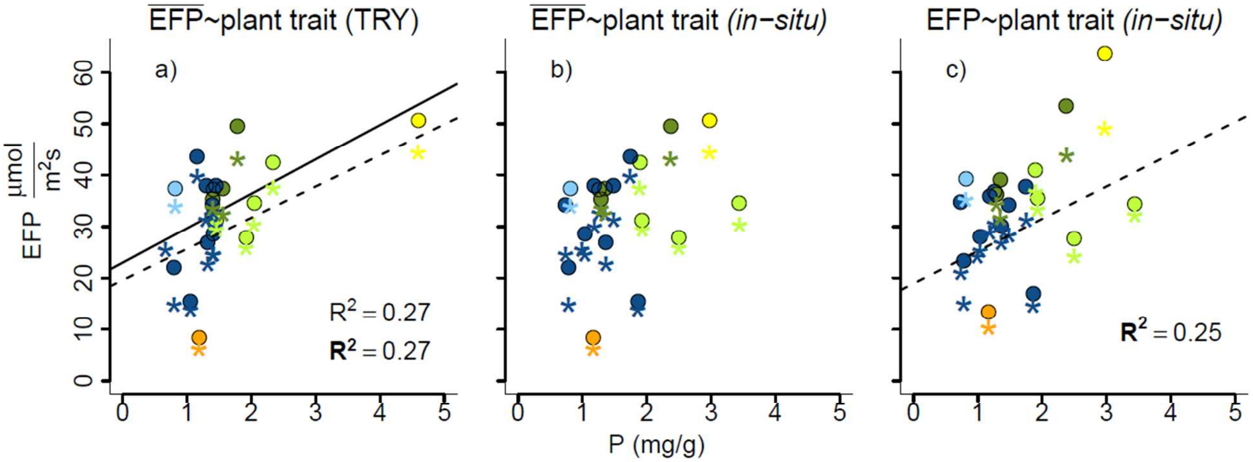


Figure S2 a) Relationship between GPP_{sat} and $GPP_{sat.structure}$ extracted from La Thuile and the trait from TRY. b) GPP_{sat} and $GPP_{sat.structure}$ from La Thuile and the trait from *in-situ* measurements. c) GPP_{sat} and $GPP_{sat.structure}$ derived from the same year of the trait sampling and the trait from *in-situ* measurements. The Macro accent on the EFP indicates that the GPP_{sat} and $GPP_{sat.structure}$ are the multi-year averages for each site. The traits are all community weighted averaged. The adjusted R^2 of the relationship is shown in the figures in case there was a significant relationship (0.05>p-value). Bold R^2 and star symbols are for the relationships with GPP_{sat} as the EFP estimate. Non-bold R^2 and round points are for the relationship with $GPP_{sat.structure}$ as the EFP estimate. The colors dark blue, light blue, dark green, light green, orange and yellow represent evergreen needle leaf forest, evergreen broad leaf forest, deciduous broad leaf forest, grassland, closed shrub-land and cropland as the plant functional types of the sites, respectively.




$\overline{\text{EFP}}$~plant trait (TRY)
$\overline{\text{EFP}}$~plant trait (*in−situ)*
EFP~plant trait *(in−situ)*
a)
b)
c)
EFP $\frac{\mu mol}{m^2 s}$
0
10
20
30
40
50
60
5
10
15
20
25
30
N/P (mg/mg)


$\overline{\text{EFP}}$~plant trait (TRY)
$\overline{\text{EFP}}$~plant trait (*in−situ)*
EFP~plant trait *(in−situ)*
a)
b)
c)
EFP $\frac{\mu mol}{m^2 s}$
0
10
20
30
40
50
60
0
1
2
3
4
5
$R^2 = 0.27$
R^2 $= 0.27$
R^2 $= 0.25$
P (mg/g)

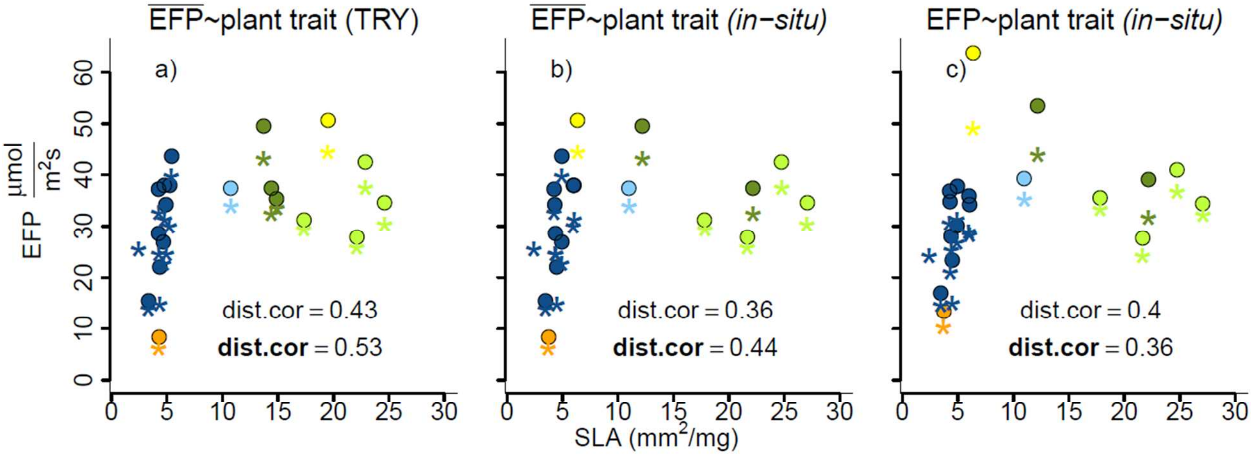

$\overline{\text{EFP}}$~plant trait (TRY)
$\overline{\text{EFP}}$~plant trait (*in−situ)*
EFP~plant trait *(in−situ)*
a)
b)
c)
EFP $\frac{\mu mol}{m^2 s}$
0
10
20
30
40
50
60
0
5
10
15
20
25
30
dist.cor = 0.43
dist.cor = 0.53
dist.cor = 0.36
dist.cor = 0.44
dist.cor = 0.4
dist.cor = 0.36
SLA (mm^2/mg)

Figure S3 Boxplots of annual GPPsat values derived from the La Thuile database for each FLUXNET site. The red point denotes GPPsat values of the 2003 year were a heat wave happened in Europe. For some European sites that year 2003 is removed already due to prepossessing of data GPPsat estimates.

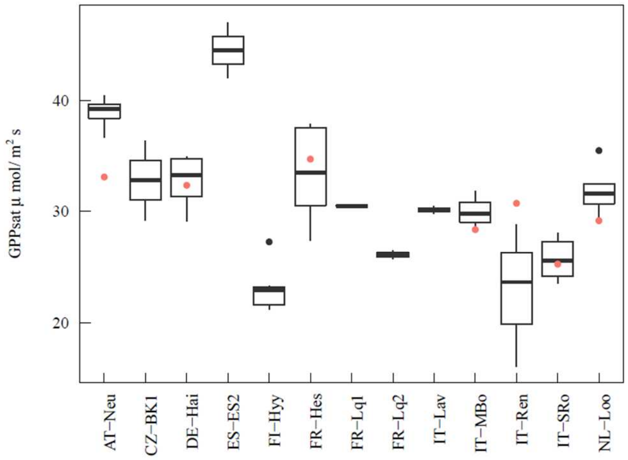


Figure S4 Relationship between a) GPPsat and GPPsat.structure extracted from La Thuile and N% from TRY, b) GPPsat and GPPsat.structure from La Thuile and N% *in-situ*. The Macro accent on the EFP indicates that the GPPsat and GPPsat.structure are the multi-year averages for each site. Here the 2003 year related to the heat wave was removed for European sites before using the averages.

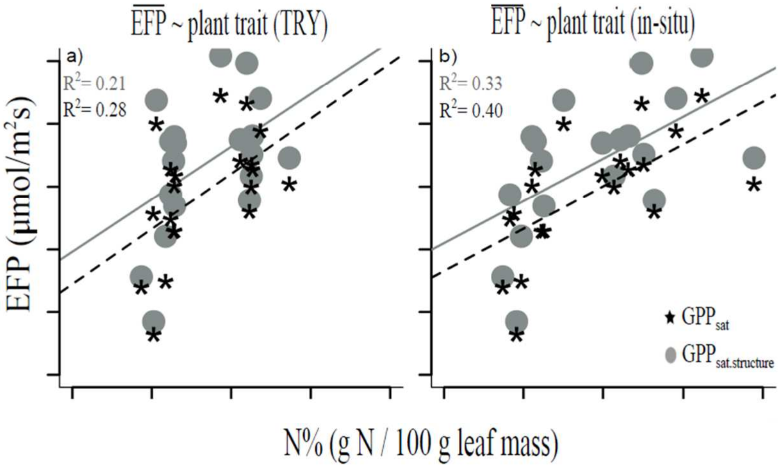


Figure S5 Summary of the fit between the *in-situ* measured and database derived community weighted mean of the plant traits. X-axes are plant traits from TRY and Y-axes are *in-situ* plant traits. The numbers on the left upper corner are the Pearson correlation coefficients between the two sources of plant traits.

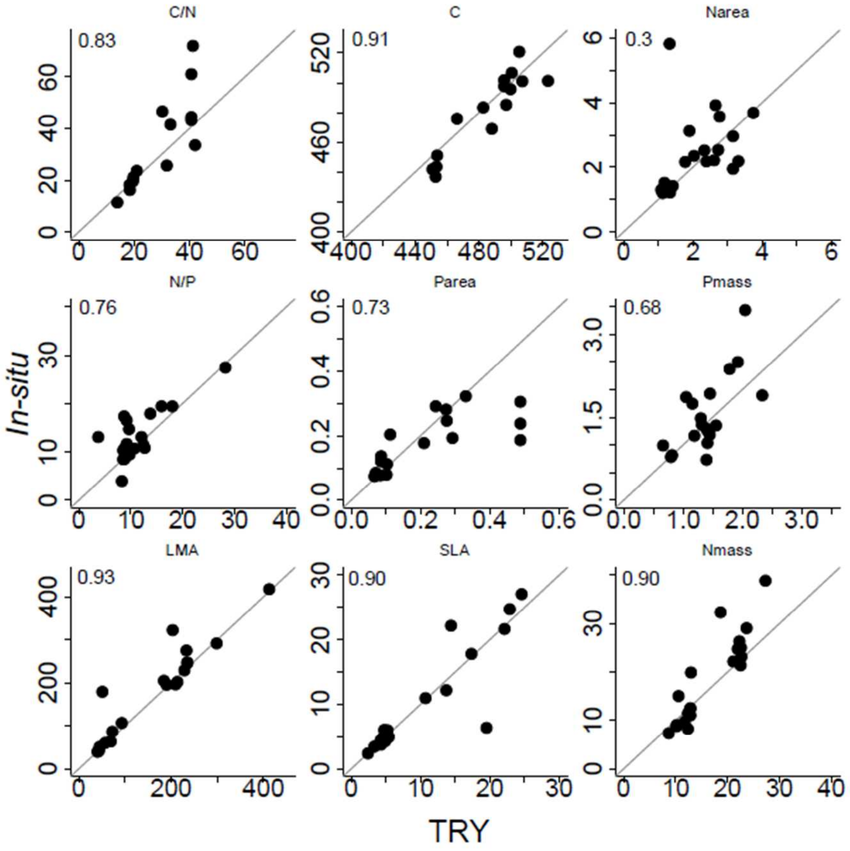


Figure S6 From left to right relationship between GPP$_{sat}$ and GPP$_{sat.structure}$ extracted from La Thuile and N% from TRY. GPP$_{sat}$ and GPP$_{sat.structure}$ from La Thuile and N% *in-situ*. GPP$_{sat}$ and GPP$_{sat.structure}$ derived from the same year of the trait sampling and N% *in-situ*. The Macro accent on the EFP indicates that the GPP$_{sat}$ and GPP$_{sat.structure}$ are the multi-year averages for each site._N% is the abundance weighted gram nitrogen per 100 gram leaf mass. The adjusted R^2 of the relationship is shown in the figures. Bold R^2 and star symbols are for the relationships with GPP$_{sat}$ as the EFP estimate. Non-bold R^2 and round points are for the relationship with GPP$_{sat.structure}$ as the EFP estimate. The colors dark blue, light blue, dark green, light green, orange and yellow represent evergreen needle leaf forest, evergreen broad leaf forest, deciduous broad leaf forest, grassland, closed shrub-land and cropland as the plant functional types of the sites, respectively.

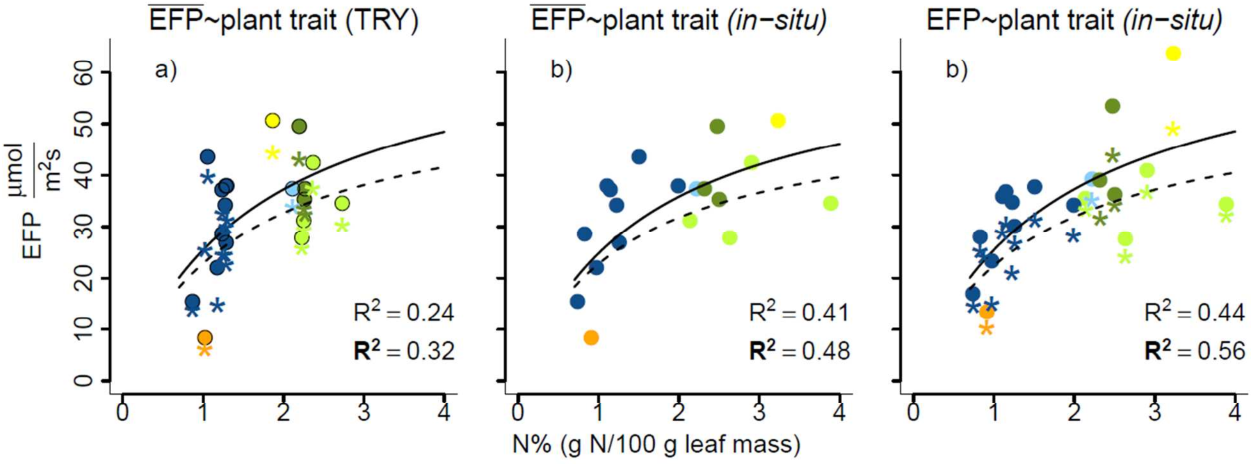
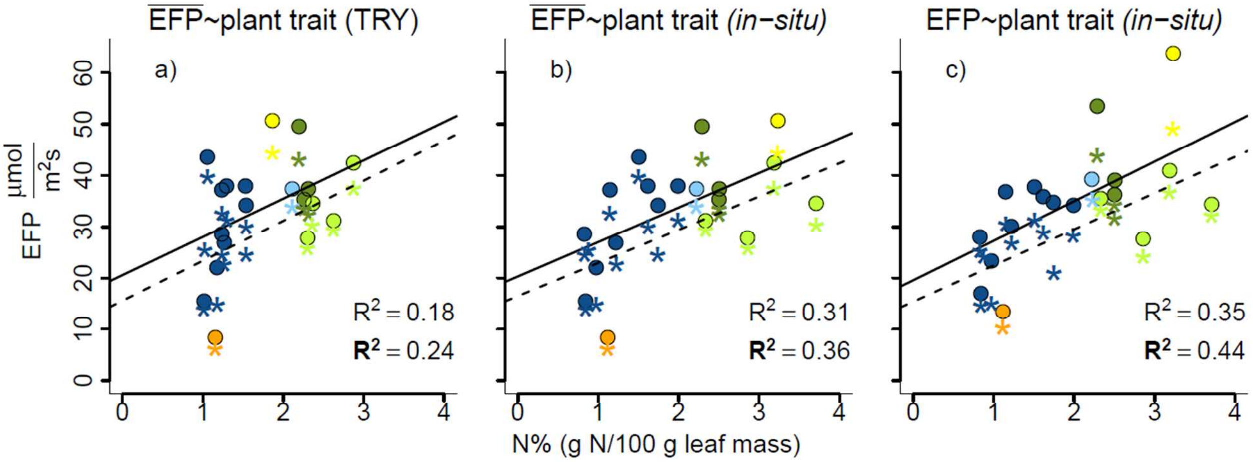


Figure S7 From left to right Relationship between GPP$_{sat}$ and GPP$_{sat.structure}$ extracted from La Thuile and N% from TRY. GPP$_{sat}$ and GPP$_{sat.structure}$ from La Thuile and N% *in-situ*. GPP$_{sat}$ and GPP$_{sat.structure}$ derived from the same year of the trait sampling and N% *in-situ*. The Macro accent on the EFP indicates that the GPP$_{sat}$ and GPP$_{sat.structure}$ are the multi-year averages for each site. N% is the average of species N% at each site. The adjusted R^2 of the relationship is shown in the figures in case there was a significant relationship (0.05>p-value). Bold R^2 and star symbols are for the relationships with GPP$_{sat}$ as the EFP estimate. Non-bold R^2 and round points are for the relationship with GPP$_{sat.structure}$ as the EFP estimate. The colors dark blue, light blue, dark green, light green, orange and yellow represent evergreen needle leaf forest, evergreen broad leaf forest, deciduous broad leaf forest, grassland, closed shrub-land and cropland as the plant functional types of the sites, respectively.



$\overline{\text{EFP}}$~plant trait (TRY)

$\overline{\text{EFP}}$~plant trait (*in−situ*)

EFP~plant trait (*in−situ*)

Figure S8 The extraction of GPP_{sat} considers the optimal conditions and thereby less correlated to climate variables. The fact that GPP_{sat} is the potential GPP at light saturation overcomes the direct effects of climate as well. The two figures below indicate that the difference between sites for GPP_{sat} is not related to the mean precipitation and only slightly related to air temperature of the sites. Both climate variables were estimated during the growing season. In a and b the link between the annual average air temperature and cumulative precipitation is shown with annual GPP_{sat}. In c and d the link between mean annual temperature (MAT) and mean annual precipitation (MAP) with the site averaged GPP_{sat} is shown.

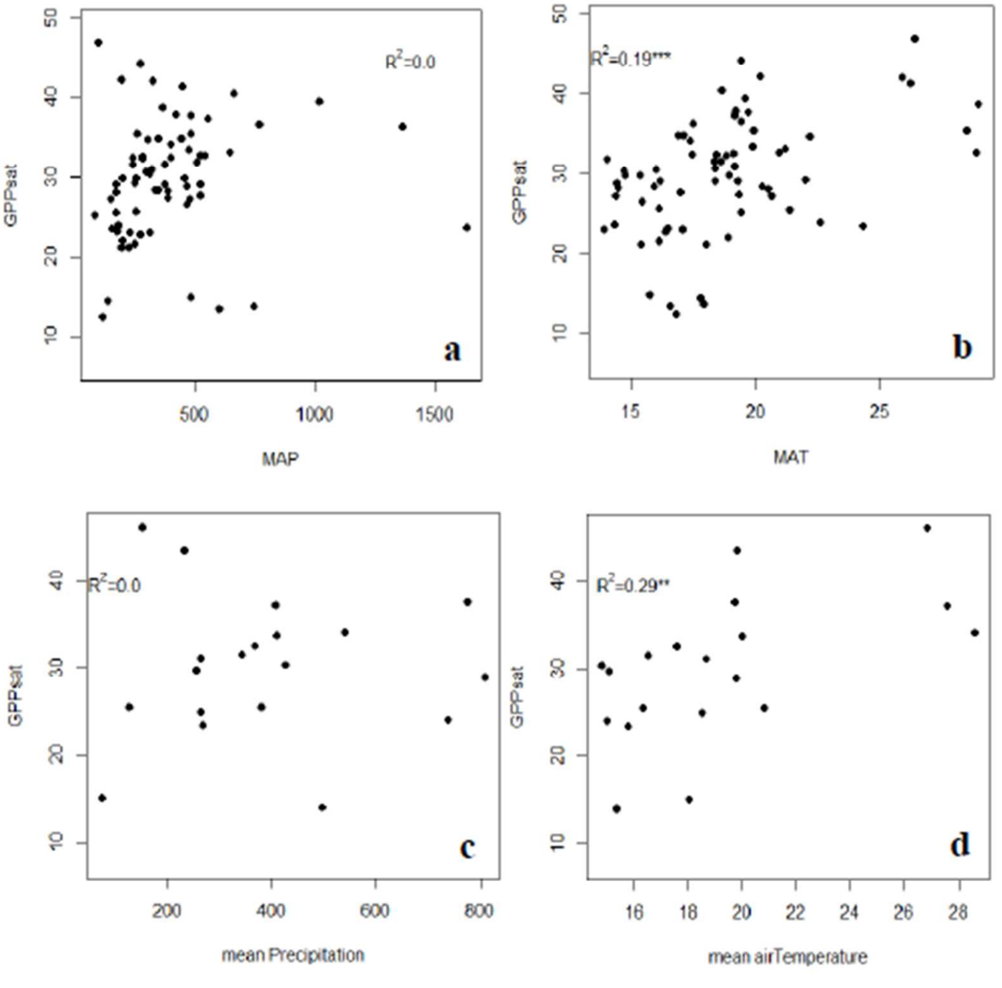
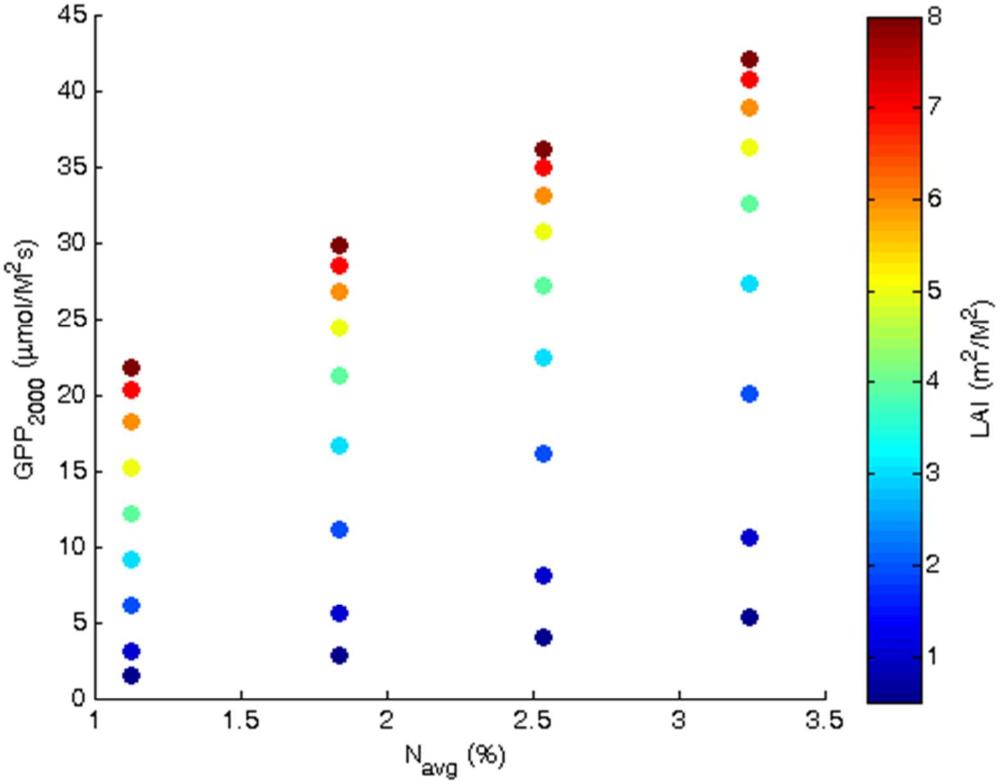


Figure S9 Relationship between N% (here total canopy nitrogen content divided by LAI) and photosynthetic capacity Simulations of GPP2000 were done using De Pury & Farquhar (1997) model, based on the combination of Farquhar photosynthesis model (Farquhar *et al.,* 1980) with the two-leaf big-leaf presentation of the canopy radiative transfer. Simulations were done with a given leaf temperature, prescribed Ci (25 Pa), a diffuse fraction of 20% and a solar angle of 65° and turning off daytime mitochondrial respiration. Vcmax at 25°C in the model depends on leaf nitrogen content (N%) – forbs parameterisation from Wohlfahrt *et al.,* (1999; Fig. 3a) were used. LAI simulations vary from 0.5-8 m2/m2 and N% of the uppermost leaves varying from 1.5-4.5%.



REFERENCES:

De Pury DGG, Farquhar GD (1997) Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell and Environment, 20, 537-557.

Farquhar GD, Caemmerer SV, Berry JA (1980) A Biochemical-Model of Photosynthetic Co2 Assimilation in Leaves of C-3 Species. Planta, 149, 78-90.

Wohlfahrt G, Bahn M, Haubner E et al. (1999) Inter-specific variation of the biochemical limitation to photosynthesis and related leaf traits of 30 species from mountain grassland ecosystems under different land use. Plant Cell and Environment, 22, 1281-1296.

SUPPLEMENTARY DATA-TABLES

InSitu_Traits

Table provides the species sampled at the each site with the measured traits. Mean.trait is the averaged trait value, whereas Inv.No is the number of individuals that were sampled used to estimate the average trait value and the standard deviation of the trait values (SD.trait). DOY is the day of the year when the sampling was done. For more information please contact Martine Janet van de Weg (marjan@marjanvandeweg.com).

CWMtraits_EFPs

Community weighted traits and ecosystem photosynthetic capacity estimates for the 20 sites (used in the analyses of the link between plant functional traits and ecosystem photosynthetic capacity). CWM at the beginning of the column names means that the values are community weighted means of in-situ data and CWMT is for community weighted means of traits from TRY database.

SpeciesComposition

Species names and abundance of the FLUXNET sites. Only for BR-Sa1 we did not have access to the species abundance and therefore equal abundances for the species are considered.