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

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| Complete List of Authors: | Musavi, Talie; Max-Planck-Institute for Biogeochemistry Jena, Biogeochemical Integration  
Migliavacca, Mirco; Max-Planck-Institute for Biogeochemistry Jena, Biogeochemical Integration  
vande 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, Ecophysioleologie Forestierës  
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)  
Kalhorn, 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
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.

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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 CO₂ 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 \( GPP_{\text{sat}} \)). 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. \( GPP_{\text{sat}} \)). CV is calculated by dividing the standard deviation of annual EFP estimates (\( GPP_{\text{sat}} \)) by the mean of the annual EFP estimates at the sites. For example if the \( GPP_{\text{sat}} \) of AT-Neu is 39.43, 33.08, 36.64, 40.45 and 38.99 \( \mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1} \) 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 \( GPP_{\text{sat}} \) (i.e. 90th percentile of \( GPP_{\text{sat}} \) daily time series). The CV was subsequently computed as the standard deviation of annual \( GPP_{\text{sat}} \) of all years available, divided by the mean annual \( GPP_{\text{sat}} \) for all years available at the respective site (CV \( GPP_{\text{sat}} \)).”

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 \( A_{\text{max}}=20 \) and site B has \( A_{\text{max}}=5 \), because they will both have \( A_{\text{min}}=0 \) in the winter, then CVs will be higher site A, simply because it has a higher \( A_{\text{max}} \). 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 \( GPP_{\text{sat}} \) 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 \( GPP_{\text{sat}} \) 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


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 Fig.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).”

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10. Overall I was surprised on how well TRY traits worked to predict fluxes ($\text{R}^2=0.27$ 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 GPPsat 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 $\text{R}^2$ of the fit, respectively.
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

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 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 Fig.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.

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“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).”

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.:


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 surprised 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).


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 $A_{\text{max}}$. Parea to $P_{\text{area}}$. Narea to $N_{\text{area}}$. Pmass to $P_{\text{mass}}$.

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 Musavi1*, Mirco Migliavacca1, Martine Janet van de Weg2, Jens Kattge1, 3, Georg Wohlfahrt4, Peter M. van Bodegom5, Markus Reichstein1, 3, Michael Bahn4, Arnaud Carrara6, Tomas F. Domingues7, Michael Gavazzi8, Damiano Gianelle9,10, Cristina Gimeno6, André Granier11, Carsten Gruening12, Kateřina Havránková13, Mathias Herbst14, Charmaine Hrynkiw15, Aram Kalhori16, Thomas Kaminski17, Katja Klumpp18, Pasi Kolari19, Bernard Longdoz11, Stefano Minerbi20, Leonardo Montagnani20,21, Eddy Moors22, Walter C. Oechel16,23, Peter B. Reich24,25, Shani Rohatyn26,27, Alessandra Rossi16, Eyal Rotenberg27, Andrej Varlagin28, Matthew Wilkinson29, Christian Wirth1,3,30, Miguel D. Mahecha1, 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 Forestières, 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
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).
covariance (EC) measurements of carbon dioxide (CO₂), 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

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 straightforward 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 ($V_{c_{max}}$), 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 CO₂ fluxes and plant traits and the associated uncertainties have been systematically investigated for spatio-temporal variation and the
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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 100 gram leaf dry mass- N%), leaf nitrogen content per leaf area (Narea, g m\(^{-2}\)), leaf phosphorus content per leaf dry mass (Pmass, mg g\(^{-1}\)) and per leaf area (Parea, 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, ThermoQuest 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 ($\delta^{13}$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):

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

where \( \alpha \) is the initial slope of the light response curve, \( \theta \) 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 \texttt{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 $A_{\text{max}}$ 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 $R_g$ 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) $A_{\text{max}}$ : parameter of the Eq. 1; 2) $A_{\text{max structure}}$ : parameter of Eq. 1 but with APAR as driving radiation to account for canopy structure; 3) $GPP_{\text{sat}}$ : GPP at light saturation using PAR as driving radiation 4) $GPP_{\text{sat structure}}$ : as $GPP_{\text{sat}}$ but with APAR as radiance variable; 5) $GPP_{\text{cum}}$ : integral of the fitted light response until light saturation and 6) $GPP_{\text{cum structure}}$ : as $GPP_{\text{sat}}$ but using APAR as radiation until light saturation (Fig. 1a, Table 1).

A time series of daily values of $A_{\text{max}}, A_{\text{max structure}}, GPP_{\text{sat}}, GPP_{\text{sat structure}}, GPP_{\text{cum}},$ and $GPP_{\text{cum structure}}$ was then derived for each year. In Fig. 1b $GPP_{\text{sat}}$ 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 $R^2$ 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 ($90^{\text{th}}$ to $60^{\text{th}}$) 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 each 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, δ^{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\textsubscript{cum} and GPP\textsubscript{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\textsubscript{cum} is related to the whole growing season, GPP\textsubscript{sat} is related mostly to the peak of growing season. However, GPP\textsubscript{cum} and GPP\textsubscript{sat} are strongly correlated (Table S1). GPP\textsubscript{cum,structure} and GPP\textsubscript{sat,structure}, accounting for canopy structure, show slightly higher IAV than GPP\textsubscript{cum} and GPP\textsubscript{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$_{\text{sat}}$ are not strongly linked to climate variables (Fig. S8).

We conclude that the 90$^{\text{th}}$ percentile of GPP$_{\text{cum}}$ or GPP$_{\text{sat}}$ 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$_{\text{sat}}$ (20$\%$ of GPP$_{\text{sat,structure}}$) (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$_{\text{sat}}$, and GPP$_{\text{sat,structure}}$ 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$_{\text{sat}}$ and GPP$_{\text{sat,structure}}$ were replaced by GPP$_{\text{sat}}$ and GPP$_{\text{sat,structure}}$ 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$_{\text{sat}}$ and from 0.47 to 0.63 for GPP$_{\text{sat,structure}}$, 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$_{\text{sat}}$ (significantly different in slope and intercept, $p < 0.01$) or
GPP\textsubscript{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\textsubscript{sat} and GPP\textsubscript{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\textsubscript{sat} and GPP\textsubscript{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\textsubscript{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\textsubscript{sat} and GPP\textsubscript{sat,structure} between sites is best explained by leaf C/N ratio and \( P_{\text{area}} \)\textsuperscript{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 $A_{\text{max}}$ (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 $A_{\text{max}}$ 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$_{\text{sat}}$ or GPP$_{\text{cum}}$ showed much smaller IAV and therefore we suggest the use GPP$_{\text{sat}}$ or GPP$_{\text{cum}}$ 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 $A_{\text{max}}$. 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$_{\text{sat}}$ 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$_{\text{sat-structure}}$. 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.

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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.

<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>Photosynthetic Capacity</th>
<th>Radiation</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPP$_{sat}$</td>
<td></td>
<td>PAR</td>
<td>GPP at light saturation using PAR as driving radiation and 2110 µmol m$^{-2}$ s$^{-1}$ as saturating light</td>
</tr>
<tr>
<td>GPP$_{sat,structure}$</td>
<td></td>
<td>APAR</td>
<td>GPP at light saturation using APAR as driving radiation and 2000 µmol m$^{-2}$ s$^{-1}$ as saturating light</td>
</tr>
<tr>
<td>$A_{max}$</td>
<td></td>
<td>PAR</td>
<td>Light saturated GPP - parameter of Eq. 1 with PAR as driving radiation</td>
</tr>
<tr>
<td>$A_{max,structure}$</td>
<td></td>
<td>APAR</td>
<td>Light saturated GPP - parameter of Eq. 1 but with APAR as driving radiation</td>
</tr>
</tbody>
</table>
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$_{\text{sat}}$ for one year. Higher values of GPP$_{\text{sat}}$ occur during the growing season (usually around mid-spring to end-summer). For this
study we use the 90\textsuperscript{th} percentile as the maximum GPP\textsubscript{sat} of each year, which is indicated with the dashed line. For comparison the 60\textsuperscript{th} percentile of GPP\textsubscript{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 GPP_{sat, structure} extracted from La Thuile and N\% from TRY, b) GPP_{sat} and GPP_{sat, structure} from La Thuile and N\% in-situ, c) GPP_{sat} and GPP_{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 GPP_{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 (GPP_{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 those without 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.

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

<table>
<thead>
<tr>
<th>Variable</th>
<th>Model</th>
<th>Distance-Correlation R^2</th>
<th>adj. R^2</th>
<th>Intercept ± s.e.</th>
<th>Slope ± s.e.</th>
<th>p</th>
<th>df</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>LAI</td>
<td>N%</td>
<td>0.70</td>
<td>0.48</td>
<td>0.34 ± 0.38</td>
<td>0.71 ± 0.18</td>
<td>0.001</td>
<td>1 + 17</td>
<td>44</td>
</tr>
<tr>
<td>GPP_{sat}</td>
<td>LAI</td>
<td>0.57</td>
<td>0.28</td>
<td>0.24 ± 4.03</td>
<td>5.43 ± 2.09</td>
<td>0.01</td>
<td>1 + 17</td>
<td>138</td>
</tr>
<tr>
<td>GPP_{sat}</td>
<td>N%</td>
<td>0.73</td>
<td>0.50</td>
<td>0.47 ± 3.79</td>
<td>7.41 ± 1.81</td>
<td>0.0008</td>
<td>1 + 17</td>
<td>132</td>
</tr>
<tr>
<td>GPP_{sat}</td>
<td>LAI + N%</td>
<td>0.71</td>
<td>0.50</td>
<td>0.44 ± 3.98</td>
<td>N% 6.78 ± 2.58</td>
<td>0.004</td>
<td>2 + 16</td>
<td>134</td>
</tr>
<tr>
<td>GPP_{sat}</td>
<td>N% + LAI + LAI:N%</td>
<td>0.64</td>
<td>0.56</td>
<td>0.74 ± 6.94</td>
<td>N% 15.22 ± 4.22</td>
<td>0.001</td>
<td>3 + 15</td>
<td>129</td>
</tr>
</tbody>
</table>

Note: N%:LAI 4.71 ± 1.98
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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Model</th>
<th>Distance-Correlation</th>
<th>R$^2$</th>
<th>adj. R$^2$</th>
<th>Intercept ± s.e.</th>
<th>Slope ± s.e.</th>
<th>p</th>
<th>df</th>
<th>AIC</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPP$_{sat}$</td>
<td>C/N + P$_{area}^2$</td>
<td>0.67</td>
<td>0.61</td>
<td>0.55</td>
<td>41.62 ± 3.01</td>
<td>C/N -0.39 ± 0.08</td>
<td>0.0009</td>
<td>2 + 15</td>
<td>119</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>P$_{area}^2$ 23.94 ± 16.20</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPP$_{sat.structure}$</td>
<td>C/N + P$_{area}^2$</td>
<td>0.65</td>
<td>0.54</td>
<td>0.48</td>
<td>49.02 ± 4.07</td>
<td>C/N -0.48 ± 0.12</td>
<td>0.004</td>
<td>2 + 14</td>
<td>123</td>
<td>-0.28</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>P$_{area}^2$ 38.89 ± 22.22</td>
<td></td>
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</table>
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SUPPORTING MATERIAL

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

<table>
<thead>
<tr>
<th></th>
<th>GPP&lt;sub&gt;sat&lt;/sub&gt;</th>
<th>GPP&lt;sub&gt;sat.structure&lt;/sub&gt;</th>
<th>A&lt;sub&gt;max&lt;/sub&gt;</th>
<th>A&lt;sub&gt;max.structure&lt;/sub&gt;</th>
<th>GPP&lt;sub&gt;cum&lt;/sub&gt;</th>
<th>GPP&lt;sub&gt;cum.structure&lt;/sub&gt;</th>
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<tr>
<td>GPP&lt;sub&gt;sat&lt;/sub&gt;</td>
<td>1</td>
<td>0.93</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GPP&lt;sub&gt;sat.structure&lt;/sub&gt;</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A&lt;sub&gt;max&lt;/sub&gt;</td>
<td>0.82</td>
<td>0.90</td>
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<td>A&lt;sub&gt;max.structure&lt;/sub&gt;</td>
<td></td>
<td>0.84</td>
<td>0.95</td>
<td>0.94</td>
<td>1</td>
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<tr>
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<td>0.85</td>
<td>0.71</td>
<td>0.73</td>
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<tr>
<td>GPP&lt;sub&gt;cum.structure&lt;/sub&gt;</td>
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<td>0.95</td>
<td>0.86</td>
<td>0.86</td>
<td>0.90</td>
<td>1</td>
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</table>

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<sub>sat</sub> (or GPP<sub>sat.structure</sub>) of the sites, we sampled randomly (with replacement) for each site the annual GPP<sub>sat</sub> (also GPP<sub>sat.structure</sub>) 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<sup>2</sup> and p-value. In none of the cases the fit was better than the one in Fig. 4c when GPP<sub>sat</sub> was used (time and space matched data). Using GPP<sub>sat.structure</sub> only 1% of the random site-year combination had an R<sup>2</sup> higher than the one in Fig. 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.

<table>
<thead>
<tr>
<th>EFP estimate</th>
<th>R&lt;sup&gt;2&lt;/sup&gt;</th>
<th>p.value</th>
</tr>
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<tbody>
<tr>
<td>GPP&lt;sub&gt;sat&lt;/sub&gt;</td>
<td>0.2683</td>
<td>0.002288</td>
</tr>
<tr>
<td>1&lt;sup&gt;st&lt;/sup&gt; Qu.</td>
<td>0.2845</td>
<td>0.004134</td>
</tr>
<tr>
<td>Median</td>
<td>0.3315</td>
<td>0.007891</td>
</tr>
<tr>
<td>Mean</td>
<td>0.3309</td>
<td>0.009602</td>
</tr>
<tr>
<td>3&lt;sup&gt;rd&lt;/sup&gt; Qu.</td>
<td>0.3745</td>
<td>0.015435</td>
</tr>
<tr>
<td>Max.</td>
<td>0.4118</td>
<td>0.019314</td>
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<tr>
<td>GPP&lt;sub&gt;sat.structure&lt;/sub&gt;</td>
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<td>0.002061</td>
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<td>1&lt;sup&gt;st&lt;/sup&gt; Qu.</td>
<td>0.2967</td>
<td>0.007480</td>
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<tr>
<td>Median</td>
<td>0.3345</td>
<td>0.007891</td>
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<td>Mean</td>
<td>0.3309</td>
<td>0.009602</td>
</tr>
<tr>
<td>3&lt;sup&gt;rd&lt;/sup&gt; Qu.</td>
<td>0.3514</td>
<td>0.015927</td>
</tr>
<tr>
<td>Max.</td>
<td>0.4369</td>
<td>0.019853</td>
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</table>
Figure S1 Time series of daily GPP_{sat}. Data filtering using the $R^2$ of the model fit shows that only GPP_{sat} 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.
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% \textit{in-situ}. GPP_{sat} and GPP_{sat,structure} derived from the same year of the trait sampling and N% \textit{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 shrubland and cropland as the plant functional types of the sites, respectively.
Figure S7 From left to right Relationship between GPP$_{\text{sat}}$ and GPP$_{\text{sat,structure}}$ extracted from La Thuile and N% from TRY. GPP$_{\text{sat}}$ and GPP$_{\text{sat,structure}}$ from La Thuile and N% in-situ. GPP$_{\text{sat}}$ and GPP$_{\text{sat,structure}}$ derived from the same year of the trait sampling and N% in-situ. The Macro accent on the EFP indicates that the GPP$_{\text{sat}}$ and GPP$_{\text{sat,structure}}$ 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$_{\text{sat}}$ as the EFP estimate. Non-bold R$^2$ and round points are for the relationship with GPP$_{\text{sat,structure}}$ 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 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:


SUPPLEMENTARY DATA-TABLES

InSitu_Traits

Table provides the species sampled at 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.