The imprint of plants on ecosystem functioning

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Synopsis

This is a cumulative dissertation comprised of three original studies (three published papers) expanding the idea of ecosystem functional properties (EFP) that are abstractions of ecosystem behavior and should indicate intrinsic properties of the ecosystems embedding the response of ecosystem to climate variability. I show that specific plant traits can explain spatial variability of potential photosynthetic capacity. Whilst assessing the potential of using trait information from big integrated databases like TRY in this regard, I demonstrate the importance of initiating continuous measurement of plant traits at FLUXNET sites. What is more, I show the strong control of stand age and species richness on the stability of potential photosynthetic capacity. The three papers forming this dissertation add novel information on the important role that plants play in mediating ecosystem functioning, specifically ecosystem photosynthetic capacity.

[*] Duplicated references from different studies are counted

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PREFACE

The aim of this dissertation was to improve our understanding on the role that plants play in mediating functions in the ecosystems. It is of high importance especially now that we are facing the consequences of our huge influence on climate change. Any progress in understanding the ecosystem processes and functions and their feedback to climate can support better decisions for our future. Motivated to do so, in this thesis I expand the idea of ecosystem functional properties (EFP) that are abstraction of our macroscopic view on the ecosystem behavior and should indicate ecosystem intrinsic properties. As a case study, I examine the link between potential photosynthetic capacity and different plant traits also considering the opportunities that big integrated trait databases like TRY (a data platform that puts together different databases to make one common database, Kattge *et al.*, 2011) can offer. Furthermore, for the first time using 50 different forest sites I show the strong control of stand age and species richness on the stability of these EFPs. The three papers forming this dissertation add novel information on the important role that plants play in mediating ecosystem functioning, specifically ecosystem photosynthetic capacity. In the general introduction I provide background on the main topic and show the connection of the different papers and how they fit into my research topic. In the general method section I present detailed and complementary information that was not all included in the papers. In the general discussion I review general results from the different papers and show how each paper was driven by the questions in the previous one.

SUMMARY

The state and composition of the Earths atmosphere is partly controlled by its interactions with ecosystems at the surface. These interactions are manifested in the exchange of energy and matter at the interfaces of land and oceans with the atmosphere and are a key to global biogeochemical cycles. In particular the terrestrial biosphere plays a prominent role in mediating these interactions by activating biogeochemical cycles e.g. through assimilating, storing and releasing carbon, nitrogen, phosphorus and other key elements. A steadily growing body of knowledge suggests that the vegetation plays a key role in these processes, and hence, it is increasingly acknowledged that various aspects of biodiversity are essential for the functioning of the Earth system as a whole.

However, despite of the huge scientific progress over the past decades in this scientific field, we still face large knowledge gaps. In particular, we have only a very limited understanding of the global role of biotic acclimation, adaptation and plant functional diversity in the biosphere-atmosphere processes. In this context we have to consider community assembly processes amongst other aspects. Environmental filtering determines plant community structure in dependency of climate condition and acts in tandem with evolutionary processes on long time scales and competitive interactions on shorter time scales. In other words, climate variability or in general environmental changes on different time scales will result in changes of species composition and alterations in plant characteristics, all ultimately affecting ecosystem functioning. Based on these insights, the basic hypothesis of this thesis is that it is the combination of plant community structure and plant characteristics that jointly determine the imprint of vegetation on ecosystem functioning. Studying plant traits – plant characteristics that can be quantified at the individual organism or even organ level – together with community structure in relation to ecosystem functioning should therefore be a promising avenue to unravel the impact of plants on ecosystem functioning.

To address this grand question, this thesis profits from an unprecedented breadth of *in-situ* observations from most ecosystems of the world. Baldocchi (2014) states that: “Flux information can be viewed as the currency by which we study ecosystem–atmosphere interactions”. And today ecosystem-atmosphere exchanges of energy and matter (the exchange fluxes of CO_2, H_2O) can be estimated using eddy covariance methods. Using these flux observations we can

characterize ecosystem physiological processes and functions and study them in relation to vegetation effects. This data are collected in the FLUXNET database (www.fluxdata.org) and are available for many sites covering a wide range of different ecosystem types, with a consistent data treatment and high temporal resolution.

Unlike the fluxes plant traits and information on the vegetation has only been collected at some of the FLUXNET sites. However, the global database of plant traits – TRY– started to bring together plant trait databases and now by 2018 it contains nearly 7 million trait records for 1800 traits (www.try-db.org). This database can be used to parameterize the traits from the plant species present at the FLUXNET sites.

The fluxes and processes estimated from them like photosynthesis are under strong influence of environmental factors (e.g. temperature and radiation) and can vary within seconds unlike most of plant traits that vary on a slower paste. Using modeling approaches and theories coming from leaf physiology we can quantify the response of fluxes at ecosystem scale to environmental changes. For instance using a light response curve we can quantify the response of the ecosystem photosynthesis flux to increase in light density and thereby estimate ecosystems photosynthetic capacity analog to leaf level light-saturated photosynthesis known as A_{max}. This way we overcome the direct and instantaneous ecosystem response to environmental variability and look more into the ecosystems adaptive response that embeds plants response strategies. Properties as such are defined as ‘ecosystem functional property’ (EFP): intrinsic properties of the ecosystems that inherently include the influence of plant traits and their local heterogeneity. EFPs change rather slowly, at annual or seasonal time scales and are suitable to be linked to plant traits.

In the context of the first paper contributing to this thesis, I expand the idea of EFPs and their link to plant community structure and traits. I provide extensive examples of EFPs that can be estimated by fluxes or retrieved from remote sensing information. In the second paper I evaluate the usefulness of species mean trait values to characterize the link between spatial variability of ecosystem photosynthetic capacity and plant traits. Finally, in the third paper, I assess the controlling factors on the stability of ecosystem photosynthetic capacity.

Paper 1: The imprint of plants on ecosystem functioning: A data-driven approach

In this conceptual paper I highlight opportunities that the consolidated information on plant species traits (*in-situ* and remotely sensed) and ecosystem fluxes at local to global scale offer to study the link between plants and ecosystem functioning. I extend the definition of ecosystem functional properties (EFPs) and introduce its relationship with plant traits as a complementary strategy to previous concepts on the link between plants and ecosystem functions. Since the approach is interdisciplinary, I hope to bring the two scientific communities that monitor fluxes - geo-ecologists and micro-meteorologists – and plant biologists together. Here, I demonstrate the opportunities that plant trait databases like TRY can offer. In order to have measures of plant traits representative of the whole ecosystem, I introduce top-down and bottom-up scaling approaches to match the temporal and spatial scales of plant traits and EFPs. Finally, I discuss remote sensing advances that can be profitably used to link EFPs and biotic factors related to them.

Paper 2: Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits

The relationship between different plant traits (e.g. foliar nitrogen concentration) and the EFP ecosystem photosynthetic capacity (GPPsat) is tested in this paper. GPPsat is the amount of gross primary productivity (GPP flux) at light saturation using a light response curve. A three step approach is used to understand the link of plant traits to spatial variation of ecosystem photosynthetic capacity and to evaluate potential and limitation of using data from plant trait databases (here TRY) to characterize plant species at the sites (ergo ignoring intra-specific trait variability). In this way plant traits from *in-situ* measurements and plant traits from TRY are compared. To identify plant traits with the highest explanatory capacity of ecosystem photosynthetic capacity variation, a stepwise multiple regression for variable selection based on the Akaike's information criterion (AIC) is used. Plant traits used in this context include foliar nitrogen, phosphorous and carbon concentration, stable carbon isotope ratio $\delta^{13}C$, and specific leaf area. In addition to the traits leaf area index (LAI) – amount of leaf area seen from top of canopy per ground area - as a community measure was also considered.

I found that the relationships are tighter when both of the measurements are synchronized in space and time (i.e. both *in-situ* and from the same year). While using plant traits from TRY to characterize plant species occurring at the sites provided the pattern of the relationships, but it was always showing a weak correlation. Using plant traits measured *in-situ*, improved the relationship only marginally. Only when the ecosystem photosynthetic capacity estimates were corresponding to the year of *in-situ* leaf sampling tighter relationships emerged. This was associated to the substantial inter-annual variability of ecosystem photosynthetic capacity, even though, years with known disturbances had been removed from the data beforehand.

Using a stepwise regression model considering multiple plant traits and LAI simultaneously as predictors (also accounting for nonlinear relationships and interactions between variables), I show that the combination of leaf carbon to nitrogen ratio with leaf phosphorus content explains the variance of GPPsat between sites best (adjusted $R^2 = 0.55$).

Paper 3: Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity

In this study I explore the influence of plant traits and vegetation structure on the inter-annual variability of GPPsat. For 50 forest sites, between site differences of inter-annual variability magnitude of GPPsat was investigated. Inter-annual variability magnitude of GPPsat (cvGPPsat) is estimated as the coefficient of variation (cv) that is the standard deviation of GPPsat divided by the mean GPPsat within sites. The subject of the paper is based on the hypothesis that forest vegetation properties are main factors contributing the stability of the ecosystems. While considering forest age (here: stand age, which is the average tree age of the stand or age of the stand since the last major disturbance with stand replacement) and species richness, other factors related to climate, environment and forest structure that might have direct or indirect effects on ecosystem photosynthetic capacity are also studied.

The year to year variability of GPPsat shows a close link to annual variation in air temperature and the water availability index (WAI) of the soil. However, the coefficient of variation of air temperature or WAI is not related to cvGPPsat. When I use a stepwise regression algorithm considering the different biotic and abiotic variables, stand age and species richness are chosen to be the most important factors explaining the between site differences of cvGPPsat. Together the two variables could explain more than 50 percent (R^2= 0.55, $P< 0.0001$) of the between sites variability of cvGPPsat. Stand age and species richness are negatively correlated to cvGPPsat and their relationship holds across different forest types (i.e. evergreen needle-leaved forest and deciduous broad-leaved and mixed forests). This means that the inter-annual variability of GPPsat is greatest in young forest with one or two dominant species, and is lowest in older and more species rich forests. Using a relative importance method (quantification of the contribution of individual regressors to a multiple regression model), shows the most important predictor between the two variables is the stand age, which contributes about 75% to the explained variance of cvGPPsat by both variables. In sum, older and more diverse forests seem to dampen the effect of climate variability on GPPsat irrespective of forest type.

Conclusion

To improve the predictive capacity of biosphere-atmosphere models, an independent quantitative evaluation of the imprint of plants on ecosystem function and ecosystem functional properties like photosynthetic capacity is needed. EFPs can be estimated in a comparable manner from fluxes at all FLUXNET sites and provide the response of ecosystems to climate embedded. They could be suitable means for empirically analyzing plants controls on ecosystem functioning. As shown in the second paper, between site differences of GPPsat was strongly linked to community weighted mean of different plant traits and strongest when both data were space and time synchronized. Considering the developmental stages of plants, their phenology and also acclimation of plants towards their environment, it seems necessary to measure plant traits *in-situ* and in parallel to ecosystem fluxes. Since, space and time synchronized measurements of plant traits and ecosystem fluxes seem to be most informative, I highly recommend making continuous observations of species composition and plant traits several time during the growing season at the FLUXNET sites. In this regard, remote sensing retrievals of ecosystem scale plant traits and EFPs can be a potential avenue in the future to circumvent the mismatch between flux and trait data and in addition will potentially provide means to study temporal and spatial variability of plant traits in synchrony with EFPs.

In addition to the variability in plant traits, EFPs (in my study ecosystem photosynthetic capacity-GPPsat) can be also far from stable. Although GPPsat can be stable in old and species rich forests, it shows a high inter-annual variability in younger, species poor sites. When forests age, species diversity increases, and forest structure (e.g. canopy surface) becomes more diverse or complex. Both of these facets of diversity can help the forest to buffer unfavorable conditions.

It remains to be understood whether other EFPs characterizing efficiency in using water, radiation, nitrogen and carbon could explain the stability of photosynthetic capacity of the forests. Also, to understand whether it is plant functional diversity rather than species richness that can provide buffer for the ecosystems.

ZUSAMMENFASSUNG

Zustand und Zusammensetzung der Atmosphäre der Erde werden teilweise durch Interaktion mit den Ökosystemen kontrolliert. Die Interaktionen manifestieren sich im Austausch von Energie und Materie an den Grenzen von Landoberfläche und Ozean zur Atmosphäre und sind von grundlegender Bedeutung für die globalen biogeochemischen Kreisläufe. Insbesondere die terrestrische Biosphäre hat hierbei eine zentrale Bedeutung, da sie die biogeochemischen Kreisläufe durch Photosynthese, Aufnahme und Abgabe von Kohlenstoff, Stickstoff, Phosphor und anderen Elemente antreibt. Der terrestrischen Vegetation kommt in diesen Prozessen eine Schlüsselrolle zu und es wird zunehmend akzeptiert, dass verschiedene Aspekte der Biodiversität für das Funktionieren des Systems Erde als Ganzes ausschlaggebend sind.

Trotz großer Fortschritte in diesem Bereich der Wissenschaft, gibt es allerdings noch große Wissenslücken. Insbesondere haben wir nur ein sehr begrenztes Wissen über die Bedeutung von Akklimatisation, Adaptation und funktioneller Biodiversität für die Austauschprozesse zwischen Biosphäre und Atmosphäre. Unter anderem muss dabei die Zusammensetzung der Pflanzengemeinschaften beachtet werden. In Kombination mit den Umweltbedingungen bestimmen auf langen Zeitskalen evolutionäre Prozessen und auf kurzen Zeitskalen Konkurrenz zwischen Arten die Zusammensetzung der Artgemeinschaften. Mit anderen Worten, Klimaänderungen oder generell Veränderungen der Umwelt auf verschiedenen Zeitskalen resultiert in einer Änderung der Zusammensetzung der Pflanzengemeinschaft und in Änderungen der Eigenschaften der einzelnen Pflanzen(arten), die zusammen wiederum die Funktionen der Ökosysteme beeinflussen. Basierend auf diesen Ergebnissen, ist die grundlegende Hypothese dieser Arbeit, dass die Kombination aus Struktur der Pflanzengemeinschaft und Eigenschaften der Pflanzen zusammen die Bedeutung der Vegetation für die Funktion der Ökosysteme prägen. Auf dieser Grundlage sollte die Analyse von quantifizierbaren Pflanzenmerkmalen – Eigenschaften die an einzelnen Pflanzen oder ihren Organen gemessen werden können – in Kombination mit der Zusammensetzung der Pflanzengemeinschaft ein vielversprechender Ansatz sein, um den Einfluss der Pflanzen auf die Funktion der Ökosysteme zu studieren.

Um diese Fragen zu beantworten kann sich die Arbeit auf einen beispiellosen Datensatz aus Beobachtungen aus den meisten Ökosystemen der Welt stützen. Baldocchi (2014) schreibt, dass der Austausch von Energie und Materien eine einheitliche Währung darstellt in der die Interaktion von Ökosystemen mit der Atmosphäre gemessen werden kann. Der Austausch von Wasser und Materie (die Flüsse von CO_2 und H_2O) kann heutzutage mit Hilfe der Eddy-Kovarianz Methode bestimmt werden. Auf der Basis dieser Beobachtungen können wir physiologische Prozesse und Funktionen der Ökosysteme charakterisieren und sie in Relation zu Attributen der Vegetation analysieren. Diese Flüsse werden im

Rahmen der FLUXNET Initiative (www.fluxdata.org) an Standorten in einem großen Teil der Ökosysteme weltweit gemessen und in einheitlicher Form mit hoher zeitlicher Auflösung zur Verfügung gestellt.

Im Gegensatz zu den Flüssen werden Daten zu Pflanzenmerkmalen und zu Vegetationseigenschaften nur an wenigen Standorten des FLUXNET Netzwerkes erhoben. Daten zu Pflanzenmerkmalen werden weltweit im Rahmen der TRY Datenbank (www.try-db.org) zusammengefasst. Die TRY Datenbank enthält, Stand 2018, annähernd 7 Millionen Messungen für 1800 Pflanzenmerkmale. Diese Datenbank kann verwendet werden um die Eigenschaften der Pflanzenarten an FLUXNET Standorten zu parametrisieren.

Flüsse und Prozesse die auf Basis von Eddy Kovarianz Messungen bestimmt werden, z.B. Photosynthese, zeigen einen starken Einfluss von Umweltfaktoren (z.B. Temperatur und Strahlung) und können sich binnen Sekunden ändern. Demgegenüber schwanken Pflanzenmerkmale wesentlich langsamer. Mit Hilfe von Modellierungstechniken und Theorien aus der Ökophysiology kann die Reaktion der Ökosystemflüsse auf Umweltänderungen bestimmt werden. Zum Beispiel kann die Photosynthese-Kapazität von Ökosystemen auf der Basis von Lichtsättigungskurven bestimmt werden. Auf diese Weise werden direkte Reaktionen der Ökosystemflüsse auf kurzfristige Schwankungen der Umweltbedingungen umgangen und Anpassungen von Ökosystemen an langfristige Umweltbedingungen können betrachtet werden. Diese Eigenschaften werden als funktionale Ökosystemeigenschaften (Ecosystem Functional Properties, EFPs) bezeichnet: intrinsische Eigenschaften der Ökosysteme die den Einfluss der Pflanzen und lokale Heterogenität enthalten. Diese Ökosystemeigenschaften schwanken eher langsam, auf saisonaler bis jährlicher Basis, und können daher gut mit Pflanzenmerkmalen korreliert werden.

Im Rahmen des ersten Artikels, der zu dieser Arbeit beiträgt, vertiefe ich die Idee der funktionalen Ökosystemeigenschaften, insbesondere ihre Verbindung zu Pflanzenmerkmalen, und stelle eine Reihe von EFPs vor. Im zweiten Artikel untersuche ich in wie weit mittlere Pflanzenmerkmale pro Art geeignet sind um die Korrelation von funktionalen Pflanzenmerkmalen und EFPs zur charakterisieren. Im dritten Artikel untersuche ich schließlich welche Faktoren die Stabilität von EFPs unter variablen Umweltbedingungen bestimmen.

Artikel 1: The imprint of plants on ecosystem functioning: A data-driven approach (Die Bedeutung der Pflanzen für Ökosystemfunktionen: ein empirischer Ansatz)

In diesem ersten, eher konzeptionellen Artikel, beschreibe ich die Möglichkeiten die die Kombination weltweit konsolidierter Daten von Ökosystemflüssen und Pflanzenmerkmalen bieten. Zunächst vertiefe ich dabei die Definition von EFPs und ihrer Verbindung zu Pflanzenmerkmalen als empirische Alternative zu prozess-orientierten Ansätzen. Da der Ansatz interdisziplinär ist, hoffe ich, dass er dazu beiträgt, die wissenschaftlichen Gemeinschaften von Geoökologen und Mikrometeorologen auf der einen Seite mit Pflanzenökologen auf der anderen Seite zusammenzubringen. Außerdem zeige ich das Potential auf, das eine globale Datenbank zu Pflanzenmerkmalen in diesem Zusammenhang hat. Um Pflanzenmerkmale repräsentativ für Ökosysteme zu berechnen führe ich eine Top-Down / Bottom-up Skalierung ein. Schließlich diskutiere ich den potentiellen Beitrag von satellitengestützter Fernerkundung zur Analyse der Beziehung von EFPs und Pflanzenmerkmalen.

Artikel 2: Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits (Zur Eignung von Pflanzenmerkmalen für die Charakterisierung der Photosynthese Kapazität von Ökosystemen: Potential und Grenzen)

In diesem Artikel werden die Korrelation verschiedener Pflanzenmerkmale (z.B. Blatt Stickstoff Konzentration) mit der Photosynthese Kapazität von Ökosystemen (GPP_{sat}) getestet. GPP_{sat} ist definiert als maximale Photosynthese des Ökosystems bei Lichtsättigung und ist ein Beispiel für funktionale Ökosystemeigenschaften (EFPs).

Znächst analysiere ich in wie weit mittlere Pflanzenmerkmale der Arten (ohne Berücksichtigung der intraspezifischen Variabilität) und Mittelwerte von GPP_{sat} (ohne Berücksichtigung der interannuellen Variation), geeignet sind um die räumliche Variation von GPP_{sat} zwischen den FLUXNET Standorten durch Pflanzenmerkmale zu erklären. Hierbei werden mittlere EFPs und Pflanzenmerkmale schrittweise durch räumlich-zeitlich synchronisierte Messungen ersetzt. Die Korrelationen der Pflanzenmerkmale mit GPP_{sat} werden enger, je besser die Messungen der Ökosystemflüsse und der Pflanzenmerkmale räumlich und zeitlich synchronisiert waren. Auf der Basis der mittleren Pflanzenmerkmale und GPP_{sat} werden Richtung und Steigung der Korrelationen erkannt, aber mit geringen Korrelationskoeffizienten. Eine räumliche Synchronisation durch vor Ort gemessene Pflanzenmerkmale verbesserte die Korrelationskoeffizienten nur marginal. Erst die räumliche und zeitliche Synchronisation von Pflanzenmerkmalen und Ökosystemflussmessungen verbesserte die Korrelationskoeffizienten deutlich. Dies führe ich darauf zurück, dass GPPsat zumindest an einigen FLUXNET Satndorten eine erhebliche interannuelle Variation zeigt, die offensichtlich mit einer Variation der Pflanzenmerkmale korreliert ist.

Daneben identifiziere ich die Kombination der Pflanzenmerkmale, die die räumliche Variation von GPPsat zwischen FLUXNET Standorten am besten erklärt. Neben den Pflanzenmerkmalen Blatt Stickstoff, Phosphor, Kohlenstoff und C^{13} Konzentration, dem C/N Verhältnis und der spezifischen

Blattfläche, berücksichtige ich hierbei den Blattflächenindex (Blattfläche pro Grundfläche) als strukturelles Merkmal der Vegetation. Ich verwende multiple Regression zur schrittweise Variablen Selektion auf der Basis des Akaike Kriteriums. Der Regression Algorithmus berücksichtigt auch nichtlineare Relationen und Interaktionen zwischen den Variablen. Die Kombination aus C/N Verhältnis und Phosphorkonzentration in den Blättern erklärt die Variabilität von GPP_{sat} zwischen den FLUXNET Standorten am besten (adjustiertes R^2=0.55). Dies unterstreicht die globale Bedeutung von Stickstoff- und Phosphorkreislauf für den Kohlenstoffhaushalt der Ökosysteme.

Artikel 3: Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity (Bestandesalter und Artenzahl dämpfen die interannuelle Variation der Photosynthesekapazität von Ökosystemen)

In dieser Studie untersuche ich den Einfluss von Pflanzenmerkmalen und Vegetationsstruktur auf die interannuelle Variation von GPPsat, da sich im vorhergehenden Artikel zeigt, dass die interannuelle Variation von GPPsat zwischen FLUXNET Standorten sehr schwankt und einige Standorte eine erhebliche Variation aufweisen. Die Studie basiert auf der Annahme, dass bestimmte Pflanzenmerkmale und Aspekte der Vegetationsstruktur zur Stabilität von Ökosystemen beitragen. Die Studie bezieht sich nur auf Wälder. Neben den oben genannten Pflanzenmerkmalen berücksichtige ich das Bestandesalter (das mittlere Alter der Bäume oder der Zeitraum seit der letzten starken Störung), Anzahl der Baumarten und andere Faktoren, wie z.B. Klima, die einen direkten oder indirekten Einfluss auf die Variabilität von GPPsat haben könnten. Die interanuelle Variation von GPPsat wird als Variationskoeffizient berechnet (cvGPPsat, Standardabweichung dividiert durch den Mittelwert, relativ) und die relevanten Faktoren werden wieder über multiple Regression mit schrittweiser Variablen Selektion bestimmt.

Während die Jahr zu Jahr Variation von GPPsat eine deutliche Verbindung zur Variation der Lufttemperatur und der Wasserverfügbarkeit aufweist, sind ihre Variationskoeffizienten nicht mit cvGPPsat korreliert. Die Anzahl der Baumarten pro Standort und das Bestandesalter werden als die Faktoren selektiert, die die Variation von cvGPPsat zwischen den FLUXNET Standorten am besten erklären. Zusammen erklären beide Faktoren mehr als 50% der Variabilität von cvGPPsat (R^2= 0.55, $P<$ 0.0001). 75% der erklärten Varianz enfallen hierbei auf das Bestandesalter. Beide Faktoren sind negativ mit cvGPPsat korreliert. Dies gilt auch für die verschiedenen Waldtypen (Nadelwald, Laubwald, Mischwald). Dies bedeutet, dass die relativen interannuellen Schwankungen von GPPsat in jungen Beständen mit ein oder zwei dominanten Baumarten am größten ist und am geringsten in artenreichen Altbeständen. Dies bedeutet dass artenreiche Altbestände, unabhängig von Waldtyp, deutlich besser in der Lage sind Klimaschwankungen abzupuffern als artenarme Jungbestände.

Fazit

Um die Vorhersagekraft von Ökosystemmodellen zu verbessern, ist eine unabhängige empirische Evaluation des Einflusses der Pflanzen auf Ökosystemfunktionen und funktionale Ökosystemeigenschaften notwendig. Am Beispiel der Photosynthesekapazität von Ökosystemen (GPPsat) zeige ich, wie EFPs in vergleichbarer Weise für alle FLUXNET Standorte aus den standardmäßig gemessenen Ökosystemflüssen berechnet werden können und Unterschiede der Ökosysteme charakterisieren. EFPs sind daher ein vielversprechender Ansatz um den Einfluss der Pflanzen auf Eigenschaften der Ökosysteme empirisch zu bestimmen. Im zweiten Artikel zeigt sich, dass Pflanzenmerkmale die Photosynthesekapazität der Ökosysteme am besten erklären, wenn die Messungen zeitlich und räumlich synchronisiert sind. Dies deutet auf eine sehr enge Beziehung von Pflanzenmerkmalen und Ökosystemfunktionen hin. Unter Berücksichtigung der verschiedenen Entwicklungsstadien von Pflanzen, ihrer Phänologie, und der Anpassung ihrer Eigenschaften an Umweltbedingungen, scheint es daher in diesem Zusammenhang ratsam, Pflanzmerkmale vor Ort und zeitlich synchronisiert mit den entsprechenden Ökosystemflüssen zu messen. Da diese räumlich-zeitlich synchronisierten Messungen den höchsten Informationsgehalt haben, wäre es sehr empfehlenswert an FLUXNET Standorten zusätzlich regelmäßige Messungen zur Zusammensetzung der Arten, inklusive Abundanz, und ihrer Merkmale in das Standard Messprotokoll aufzunehmen. Satellitengestützte Fernerkundung kann dabei in Zukunft helfen, wird aber wohl bis auf weiteres durch limitiertes Auflösungsvermögen nicht in der Lage sein den Einfluss der Biodiversität an den Standorten zu charakterisieren.

Viele FLUXNET Standorte zeigen eine deutliche interannuelle Variation der Photosynthesekapazität, die auf Klimaschwankungen zurückzuführen ist. Für Wälder haben dabei Bestandesalter und Artenvielfalt eine dämpfende Wirkung. Mit zunehmendem Alter und höheren Artenvielfalt weisen verschiedene Bestandesstrukturen (z.B. die Oberfläche der Krone) zunehmend komplexe Muster auf. Diese Komplexität, ein wesentlicher Aspekt der Biodiversität, scheint den Beständen zu helfen unvorteilhafte Bedingungen gut zu überstehen - eine weitere Bestätigung des Absicherungseffektes der Biodiversität.

Da ich in meiner Arbeit die nur Photosynthesekapazität als Beispiel für eine funktionale Ökosystemeigenschaft betrachtet habe, bleibt zu untersuchen, ob und wie sich die hier gewonnenen Erkenntnisse auf andere EFPs übertragen lassen, und ob und wie verschiedene EFPs miteinander korrelieren und somit eventuell die Stabilität der Photosynthesekapazität beeinflussen. Die dritte Studie wirft die Frage auf, ob ein ähnliches Muster auch für nicht-Wald Ökosysteme, z.B. Grassland, zu beobachten ist. Generell wirft das Ergebnis des dritten Artikels die Frage auf, inwieweit mess- und quantifizierbare Merkmale funktionaler Diversität (z.B. funktionale Pflanzenmerkmale, Zusammensetzung des Bestandes) hinreichend in der Lage sind relevante Aspekte der Biodiversität, die hier offensichtlich in Artenzahl und Bestandesalter enthalten sind, widerzuspiegeln.

1. GENERAL INTRODUCTION

1.1 Motivation

The earth system emerges from the interaction of its different spheres. The interaction of the biosphere and atmosphere is one of them. Ecosystems vegetation plays an essential role in this important interaction (Heimann & Reichstein, 2008). Plants cover about 70 percent of the earths land surface, and are one of the major adaptive parts of the earth system (WWF, 2016). They can exchange large quantities of carbon and water with the atmosphere and thus have a big impact on the biogeochemical cycles. Annually, plants absorb 123 Pg C through gross photosynthesis and release 118 PgC by respiration (Ciais *et al.*, 2013). Globally, ecosystems can return 39 ± 10% of incident precipitation back to the atmosphere by transpiration (Schlesinger & Jasechko, 2014). The ecosystems are subject to the conditions in their local climate, which creates different feedback pathways between ecosystem and climate (Heimann & Reichstein, 2008). These feedbacks might dampen or magnify the effect of climate change on the ecosystems (Heimann & Reichstein, 2008). One of the sources of uncertainties in current earth system models is the poor understanding of the feedback, adaptation and acclimation processes in the ecosystems involving the phytosphere, i.e. plants.

The ecosystems feedback to the climate is dominated by the interaction between organismal and physical properties at the ecosystem level and is manifested in the exchange of energy and matter between biosphere and atmosphere and cycling of chemical compounds (Bonan, 2008). In most experimental analyses and terrestrial biosphere models a grouping system based on functional similarity of plant types – plant functional type (PFT) – is used to represent characteristics of vegetation (Lavorel *et al.*, 1997). The abundance of plant species and their traits are assumed to determine the characteristics of the vegetation and the variation within (Garnier *et al.*, 2004, Lavorel & Garnier, 2002, Violle *et al.*, 2012). Therefore, plant traits and related vegetation model parameters can be highly variable within PFTs (Alton, 2011, Groenendijk *et al.*, 2011, Kattge *et al.*, 2011, Reichstein *et al.*, 2014). Plant traits are also highly variable within species (Siefert *et al.*, 2014). Consequently, both modeling (Pappas *et al.*, 2016, Van Bodegom *et al.*, 2012, Verheijen *et al.*, 2015) and observational efforts (Meng *et al.*, 2015) aim to account for the variation of plant traits within and between PFTs, in order to better understand the relationship between vegetation characteristics and ecosystem functioning. The models have parameterized a few specific plant traits and assume a clear process-based impact of these parameter values on modeled characteristics at the ecosystem level such as gross photosynthesis and respiration. However, empirical analyses are needed to back up these assumptions, especially with respect to carbon fluxes related to photosynthesis and respiration. Model uncertainties in these fluxes can lead to projection of land carbon fluxes in the future that can show the land as source or sink (Friedlingstein *et al.*, 2014, Heimann & Reichstein, 2008). Empirical analyses on the relationship between plant traits and ecosystem functions can help have a better grasp on the adaptation and feedback of plants to climate.

Presently there is a growing amount of data on plant traits (Kattge *et al.*, 2011) that can offer opportunities for introducing more detailed information and parameterization on plants in global terrestrial biosphere models (Brovkin *et al.*, 2012, Pavlick *et al.*, 2013, Sakschewski *et al.*, 2016, Sakschewski *et al.*, 2015, Van Bodegom *et al.*, 2012, Verheijen *et al.*, 2013, Wang *et al.*, 2012). Despite of the huge scientific progress over the past decades in the field, we still face large knowledge gaps (Chapin *et al.*, 2000, Grime, 1979, Lavorel & Garnier, 2002, Southwood *et al.*, 1988). In particular, we have only a very limited understanding of the global role of biotic acclimation, adaptation and plant functional diversity in biosphere-atmosphere processes. Many studies have focused on specific regions or sites (e.g. Ma *et al.*, 2010, Ollinger *et al.*, 2008) and only few cover a wide range of ecosystems, but, if so then they are constrained in the number of traits (e.g. Kergoat *et al.*, 2008).

Today, we have access to unprecedented information on ecosystem-atmosphere exchanges of energy and matter from which we can estimate different ecosystem functions (Chu *et al.*, 2017). This data are collected in the FLUXNET (www.fluxdata.org) database and are available for many sites covering a wide range of different ecosystems, with a consistent data treatment and high temporal resolution (Pastorello *et al.*, 2017). Unlike the fluxes, plant traits and information on the vegetation has only been collected at some of these sites. However, the global database of plant traits – TRY (Kattge *et al.*, 2011)– started to bring together plant trait databases and now by 2017 it contains nearly 7 million trait records for 1800 traits (www.try-db.org). This database can be used to parameterize the traits from the plant species present at the FLUXNET sites. While these data are not explicitly collected at the sites, they could potentially give us a first glimpse which traits are important for which ecosystem functions. Using these two global databases together could help to identify key plant traits that influence ecosystem functions, which might not have been considered yet.

Motivated by the importance of plants in mediating ecosystem functions, this study is geared toward a better understanding of the role of plants in the ecosystems. More specifically this thesis aims to present a conceptual framework to bring together knowledge from different communities of research. It presents the idea of estimating and understanding the ecosystem functions and its variability via the combination of ecosystem fluxes with plant characteristics. In addition, the thesis evaluates the link between plant traits and ecosystem functions benefiting from new opportunities that accessible big databases of fluxes and plant traits bring.

In the introduction I will first provide background on ecosystems, ecosystem functions and the description of state of the art on how we can derive ecosystem functions globally (section 1.3). I will then give a short introduction on the role of plant traits and forest structure in mediating ecosystem functions (section 1.3, 1.4, and 1.5). After that, I will present the main objectives and structure of the thesis with a short overview of the three peer-reviewed scientific articles that will be discussed in the thesis (section 1.6):

1. Musavi, T., et al., (2015) The imprint of plants on ecosystem functioning: A data-driven approach. International Journal of Applied Earth Observation and Geoinformation, 43 119-131.
2. Musavi, T., et al., (2016) Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits. Ecology and Evolution, 00: 1-15.
3. Musavi, T., et al., (2017) Stand age and species richness dampen inter-annual variation of ecosystem-level photosynthetic capacity. Nature Ecology and Evolution, 1, 0048.

After this section I will describe the dataset used in the thesis (section 2). Here, I will describe also the methodology used in the study with particular focus on plant traits data collection, eddy covariance data, and satellite data used in the analysis, and finally I will describe the methodology used to analyze the data and the relationship between the derived ecosystem functions and plant traits.

1.2 Background

An ecosystem is a group of different types of living organisms together with the abiotic environment (physical and chemical) that they interact with as a functional unit (Chapin *et al.*, 2002). One of the first times that the word ‘ecosystem’ was mentioned was in a publication by Tansley (1935). Ecosystems have no defined size and thus could be referred to at the scale of the earth system or, as we discuss it in this thesis, as small as a needle-leaved forest or a grassland (Chapin *et al.*, 2002). The concept has been very useful for studying and understanding natural systems considering interactions within (Willis, 1997). The interaction between the biotic and abiotic components of the ecosystem is realized by the exchange of matter and energy. Estimating the “magnitude and dynamics of ecosystem processes” one can quantify ecosystem functioning (Naeem *et al.*, 1999). Ecosystem processes and functioning are influenced by external factors like climate variability and disturbances but are mediated by the feedback of the abiotic and biotic compartments to these factors (Reichstein *et al.*, 2014). Advancing in understanding ecosystem processes and functioning can help improving ecosystem models and their predictions. Understanding them can help to discover how the interactions between the biotic and abiotic compartments of the ecosystem can be influenced by climate fluctuations and to what degree they can alter the earth system as a whole. Ecosystem processes and functioning are the outcome of interactions within different biota levels with each other and with their environment and it is not always possible to separate these different contributions (Naeem *et al.*, 1999). For example forest productivity is the total production of all individual trees and is the result of the interaction between individual trees in terms of how the energy of sun light is distributed between the canopies and how they interact with their environment.

1.3 Ecosystem fluxes and functions – with focus on carbon cycle

1.3.1 Global Carbon Cycle

The uncertainties in the carbon cycle predictions of earth system models are much higher than other cycles (e.g. water). Plants release a lot more carbon (C) to the atmosphere compared to anthropogenic activities. The plants role in a future with increasing atmospheric CO_2 concentration and temperatures is unknown (e.g. whether it will be sink or source). The global carbon (C) cycle is represented in the scheme in Figure 1, adapted from the recent AR5 IPCC Report (Ciais *et al.*, 2013).

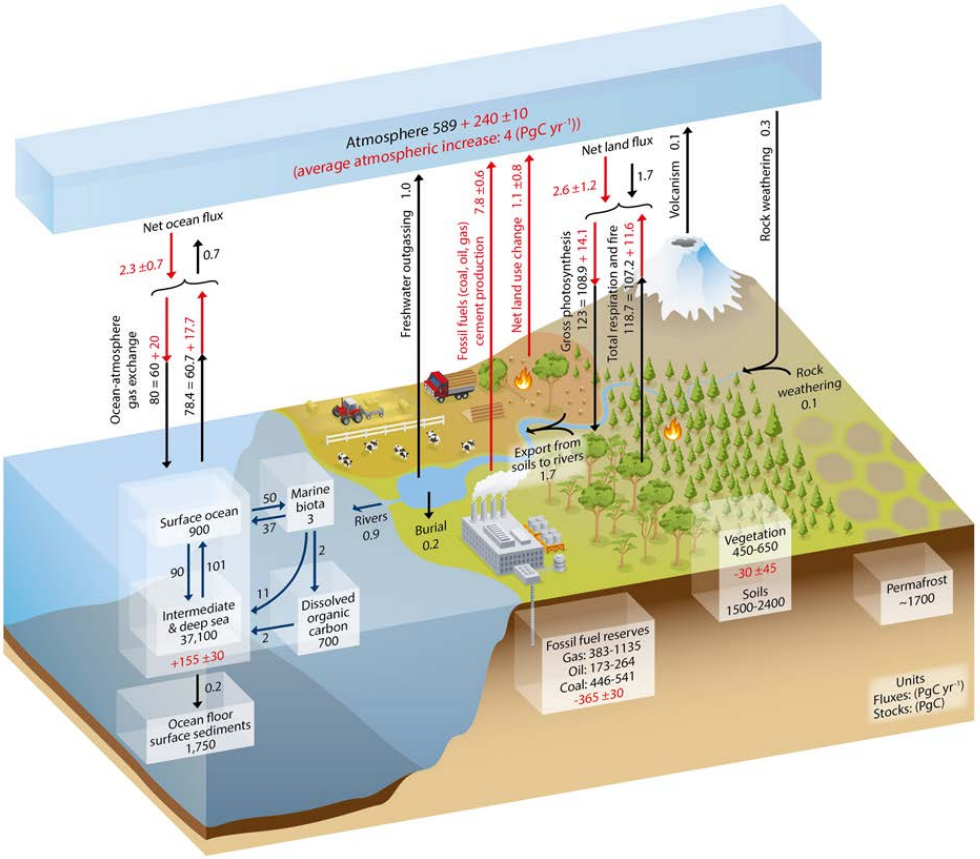

Figure 1: Scheme of the global carbon cycle (cf Fig 6.1 of IPCC report 2006 – section 6). The numbers are represented in PgC for carbon stocks (1PgC = 10^{15} gC) and in PgC yr^{-1} for annual carbon exchange fluxes. This figure shows how carbon moves between atmosphere, land and oceans. Red fluxes are human contributions while the others are the natural fluxes. Boxes indicate the stored carbon. Positive fluxes are inputs to the atmosphere (emissions) and negative fluxes are losses from atmosphere (sinks).

C is removed from the atmosphere through the photosynthesis of plants - Gross Primary Production (GPP), which is estimated as 123 PgC yr^{-1} (Ciais *et al.*, 2013). The C fixed into plants is then converted in plant tissues, and cycled through litter and soil carbon pools. C is released back to the atmosphere by respiratory processes (Total Ecosystem Respiration, TER) and disturbances (e.g. fires). TER is composed by two main processes: autotrophic (plant) and heterotrophic (soil microbial and animal) respiration. TER and fires together is quantified to be about 118.7 PgC yr^{-1} (Ciais *et al.*, 2013).

GPP and TER are by far the largest carbon fluxes between the atmosphere and biosphere, and the net carbon uptake of an ecosystem (Net Ecosystem Productivity, NEP, or Net Ecosystem Exchange, NEE), is in most ecosystems dominated by these two components as defined by Chapin *et al.* (2006):

NEE = TER-GPP = -NEP

C losses from the ecosystem could be also from non-respiratory processes like C emissions from fire or volatile organic compounds or by lateral transport. The net balance considering these C losses is defined as Net Ecosystem Carbon Balance – NECB (Chapin *et al.*, 2006) and as Net Biome Productivity – NBP for larger scales (Schulze, 2006).

Ciais *et al.* (2013) report a global terrestrial NBP of 2.6 ± 1.2 PgC yr^{-1}. This value represents the amount of C that the terrestrial land surface assimilates from the atmosphere and therefore it is called “sink” for atmospheric CO_2.

It has been shown that C storage has increased in the terrestrial ecosystems (Le Quéré *et al.*, 2009). According to Ciais et al. (2013) the increased C storage is not affected by land use change and is likely to be caused by enhanced GPP due to higher CO_2 concentrations in the atmosphere and nitrogen deposition, and changes in climate favoring greening of the Northern Hemisphere that enhance the C sinks by lengthening growing seasons in mid-to-high latitudes (Piao *et al.*, 2006).

The contribution of terrestrial ecosystems not affected by land use change is the so called “residuals land sink” and shows a pronounced inter-annual variability (IAV) (Le Quéré *et al.*, 2009). The main contributors to this IAV are considered to be the tropical rainforests – because of its’ sensitivity to non-CO_2 atmospheric warming (Cox *et al.*, 2013) and the semi-arid ecosystems (Poulter *et al.*, 2014). Extreme events are also largely contributing to the IAV of the C cycle (Reichstein *et al.*, 2014), such as the effect of El Niño on the photosynthesis of tropical forest (Cavaleri *et al.*, 2017).

1.3.2 Monitoring high temporal resolution carbon fluxes in a variety of ecosystem types

Micrometeorological techniques can provided a convenient option to estimate ecosystem physiological properties. It is possible to quantify the exchange of carbon dioxide (CO_2) between the ecosystem and atmosphere using the eddy covariance method (Aubinet *et al.*, 2000, Baldocchi & Meyers, 1998, Baldocchi & Bowling, 2003).

The eddy covariance technique measures the covariance between vertical wind velocity and gas mixing ratio within the atmospheric boundary layer – the air layer near the ground with rapid fluctuations of temperature, moisture, etc. that has a strong vertical mixing– and allows the assessment of mass and energy exchanges across the biosphere-atmosphere interface (Aubinet *et al.*, 2000). In the last three decades it has been widely used in micrometeorology as well as ecosystem ecology to determine exchange rates of trace gases over natural ecosystems and agricultural fields, and to quantify gas emission rates of CO_2, water, methane among others and latent and sensible heat fluxes between the ecosystem and the atmosphere.

Eddy covariance technique can provide flux measurements at the ecosystem scale (from few hundred meters to one km around the flux tower, depending on the height of the instrumentation and the wind speed); it provides continuous measurements at a half-hourly resolution. In addition, it is possible to look at the variability of fluxes at a variety of temporal scales (Campioli *et al.*, 2016, Stoy *et al.*, 2009). Therefore this technique has become widely distributed over the last three decades in a way that now more than 500 research sites exist that are located across a variety of biomes and climatic regions, which collect the data and contribute them to regional and global networks (Baldocchi, 2008, Pastorello *et al.*, 2017). The number of sites is still growing. The result was the establishment of a worldwide network of micrometeorological eddy covariance stations (FLUXNET, http://www.fluxdata.org) (Baldocchi *et al.*, 2001) with the goal to evaluate carbon exchange (water vapor and energy) dynamics in different ecosystems and to create an integrated database for synthesis and modeling. In addition, scientists are continuously working on improving techniques and instruments at the micrometeorological tower sites.

The FLUXNET database was developed using standardized data treatment described in Papale *et al.* (2006) and Pastorello *et al.* (2017), which facilitates the data comparison over different sites.

The map of the sites in the FLUXNET database is reported in Figure 2. Long-term measurements of CO_2 and greenhouse gas fluxes obtained using the eddy covariance technique are a useful tool for elucidating the carbon balance of terrestrial ecosystems, the causes of its IAV and for improving the understanding of the interaction between carbon, water, energy fluxes and climate. Moreover, data from eddy covariance sites are also used to test and evaluate a variety of terrestrial biosphere models.

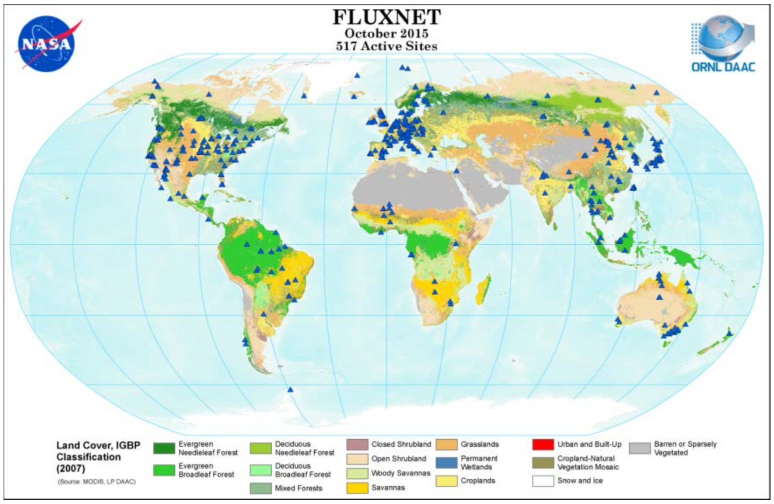

Figure 2: Location of FLUXNET sites over the globe.

With the typical set up, this technique provides accurate and continuous measurements of NEE, resulting from the balance between the assimilatory (i.e. photosynthesis) and respiratory (i.e. autotrophic and heterotrophic respiration) processes. From the NEE measurements, other flux components of the carbon cycle, ecosystem processes of GPP and TER can be derived. This is typically achieved using modeling approaches known as partitioning methods (Lasslop *et al.*, 2010, Reichstein *et al.*, 2005).

The flux partitioning method used in this work relies on the method proposed by Reichstein *et al.* (2005), which is currently implemented into the R package REddyProc (Wutzler et al., 2018 submitted). The method uses only high quality measured data (typically 40% of the time series, Falge *et al.* (2001)) to derive the constituent flux TER from the relation between air temperature and nigh-time NEE, which represent the respiratory process. In this procedure a respiration model (Lloyd & Taylor, 1994) is fitted to night-time NEE data (data below the global radiation threshold of 20 Wm−2). First the sensitivity to temperature (E0) is estimated using a moving window approach (Reichstein *et al.*, 2005). Then an annual E0 is estimated and kept fixed for the second step, which is the estimation of all the other model parameters using a moving window approach. Then the model is applied to daytime data to compute TER, and the GPP is calculated as the difference between TER and NEE (Reichstein *et al.*, 2005).

One of the possibilities offered by eddy covariance data and the high temporal resolution meteorological measurements collected alongside is to extract parameters related to ecosystem functioning using modeling approaches and theories coming from leaf physiology. For instance, the light response curve, typically used at leaf level to evaluate the response of photosynthesis to increase in photon flux density (PPFD), could be used and tested at ecosystem scale. The light-response curve can be used to derive parameters such as the potential photosynthetic capacity (i.e. GPP at saturating light) from the relationship between GPP and PPFD, or the apparent quantum yield (slope of the relationship GPP vs PPFD at low radiation level). These parameters can then be used to analyze temporal and across sites variations of ecosystem functioning and can be related to site and vegetation characteristics. These parameters defined as ecosystem functional properties (Reichstein *et al.* (2014), EFPs) can quantify the response of ecosystem processes to the environment and can be directly linked to vegetation properties.

The fluxes and processes estimated are under strong influence of environmental factors (e.g. temperature and radiation). Global synthesis analyses of the FLUXNET dataset have shown that much of the observed spatial and temporal variability of ecosystem fluxes and functional properties can be explained when ancillary information on soils, climate and vegetation structure is taken into consideration (Marcolla *et al.*, 2011, Richardson *et al.*, 2007).

Climate has a direct control on short-term variability (i.e. hourly and daily) of fluxes like GPP and TER (Richardson *et al.*, 2007, Stoy *et al.*, 2009). Stoy *et al.* (2009) show that across ecosystem types and specifically in short time scales, the variability of C fluxes is strongly linked to climate drivers. However, the authors argue that understanding the flux variability on longer time scales needs the information on how the ecosystems adapt to climate change instead of the direct ecosystem response to climate variability (Stoy *et al.*, 2009).

The climate influence is also evident when looking at the seasonal variability of fluxes by controlling plant phenology (Richardson *et al.*, 2013). The phenology of plants in boreal and temperate ecosystems is controlled by climatical factors such as temperature, radiation and day length (photoperiod) and in water limited regions by water availability (Forkel *et al.*, 2015). Therefore, short-term variation of fluxes can be explained by climatic variables, but the long term variations (inter-annual or longer) can only be understood accounting for the properties of the vegetation at the sites.

Using the link between fluxes and environmental variables the fluxes can be up-scaled to continental and global level to estimate for example regional carbon uptake (Beer *et al.*, 2010, Jung *et al.*, 2010, Jung *et al.*, 2011, Jung *et al.*, 2017, Papale & Valentini, 2003). One of the first times the upscaling was done, was for CO_2 fluxes and only few environmental variables were used (air temperature, air relative humidity and photosynthetic active radiation) (Papale & Valentini, 2003). Nevertheless, it is important to account for changes in vegetation variability, characteristics and biodiversity when we want to understand the long term dynamics and responses of fluxes to climate drivers (Richardson *et al.*, 2013, Stoy *et al.*, 2009).

Later, for advancing up-scaling practices of ecosystem processes of evapotranspiration and fluxes of CO_2, vegetation structure (using the remotely sensed fraction of absorbed photosynthetic radiation), and vegetation types (e.g. PFTs) were also considered as model input (Beer *et al.*, 2010, Jung *et al.*, 2010, Jung *et al.*, 2011). Still these studies did not take the spatial and temporal variability of plant characteristics within the PFTs in to account. This is because climate is not only changing the phenology of the vegetation as mentioned before but also the average values of traits (will be discussed later in section 1.4.).

1.4 Plants and plant traits

As introduced above, plants are fundamental for the functioning of the terrestrial ecosystem. They capture sunlight and CO_2 from the atmosphere and release oxygen. They turn the light energy into chemical energy while producing carbohydrates by combining CO_2 and water. The fixed carbon along with some other elements in the plant tissue is then further transferred to the soil by the formation of humus and to other organisms in the ecosystem through herbivores and carnivores who feed on herbivores. By acquiring and transforming resources they create cycles of different matters like carbon or nitrogen and link different organism and physical reactions together. These cycles depend on the interaction of all the elements in the earth's system. Further, plants have also substantial indirect effects on ecosystem processes through shading, thermal insulation, tissue-quality effects on decomposition, etc. (Chapin *et al.*, 2002).

Plants can change their functioning in order to optimize their ecological performance in response to a changing environment – in other words to survive and enhance their fitness. This is called acclimation and could happen during the life-time of a plant individual. Acclimation changes the phenotype of individuals, i.e. their properties, e.g. amount of nitrogen they allocate in leaves or roots. But these changes are limited to ranges determined by the genotype. This ability helps the plants to function during their life cycle while being faced with various changes in their surroundings and not being able to move away when it is unfavorable for them. Therefore, characteristics of plants have been seen to change in relation to environmental drivers. On longer time scales adaptation helps plants adapting to their environment by changes in the genotype pool.

In the evolutionary process plant species evolve with gradual genetic – and in consequence phenotypic - shifts and are comprised of distinct traits or properties characterized by a specific range of possible values. Plant traits are properties (e.g. morphological, physiological) that can be quantified at the individual organism or even organ level (Violle *et al.*, 2007) and it has received attention of ecologists decades ago (Keddy, 1992).

Plant traits reflect the outcome of evolutionary adaptation and short term acclimation processes as response to abiotic and biotic environmental constraints (Diaz *et al.*, 2004, Valladares *et al.*, 2007, Westoby *et al.*, 2002). Thus plant traits are dynamic, so the impacts and relative importance of their influence can also change over the growing season and with plant age (Eviner & Chapin, 2003). Information on plant traits may therefore be a more objective predictor of ecosystem dynamics and functioning than for instance species identity or functional group classification (McGill *et al.*, 2006).

When plant individuals change functional traits for fitness in their environment, their population should be able to influence dynamics in their community and so also the functioning of the ecosystem they form. A range of different species can have different responses to environmental perturbations and this functional diversity can increase the stability of an ecosystem in terms of process and functioning in response to disturbance and variation in abiotic conditions (Hooper *et al.*, 2005). The combination of plant species can be complementary in the use of resources and can thus improve productivity and nutrient retention (Hooper *et al.*, 2005). Plant species composition and diversity are known to affect ecosystem processes and function (Hooper *et al.*, 2005). In summary, ecosystem responses to climate variability or in general environmental changes will manifest in changes in species composition or trait alterations and ultimately alterations in ecosystem functioning (Mori *et al.*, 2013, Tomimatsu *et al.*, 2013).

While I mentioned that short-term variations in fluxes are linked to environmental variables, plant traits vary with environmental variables at longer time scales. Leaf traits such as leaf nitrogen content, leaf lifespan, specific leaf area (SLA) change with temperature and precipitation at inter – to multi-year scales (Wright *et al.*, 2004). Leaf area, SLA, seed mass, wood density and plant height are related to solar radiation (Ackerly & Cornwell, 2007, Ackerly *et al.*, 2002). There are many more studies showing the link between plant traits and environment (Cingolani *et al.*, 2007, Díaz *et al.*, 1998, Grime, 1974, Grime, 2007, Ozinga *et al.*, 2004) and some also on the link between traits with each other and their traid-offs (Díaz *et al.*, 2004, Díaz *et al.*, 2016, Wright *et al.*, 2004). Plant traits variation in accordance to their environment creates spatial variation in the traits along environmental gradients (Martinez-Vilalta *et al.*, 2009, Vila-Cabrera *et al.*, 2015). In addition to the spatial variation plant traits vary in the course of the growing season as well. Some like nitrogen concentration of the leaves vary more compared to the others such as leaf carbon concentration or leaf mass per leaf area ratio (Ma *et al.*, 2010, Migita *et al.*, 2007).

Plant species effects on ecosystem processes can be better explained by considering multiple plant traits than a single trait (Eviner & Chapin, 2003, Mack & D'Antonio, 2003). Single plant traits or a combination of plant traits can be involved in the control of multiple ecosystem processes (de Bello *et al.*, 2010, Diaz *et al.*, 2006, Eviner & Chapin, 2003, Lavorel & Garnier, 2002). For example leaf area and leaf nitrogen concentration are related to NPP (total photosynthetic gain of the vegetation per unit area of soil surface and per unit time after subtracting the quantity of respired carbon) (Gross *et al.*, 2008). Generally, traits linked to the leaf economic spectrum (Wright *et al.*, 2004) are mostly linked to photosynthesis, productivity or litter decomposition processes while root traits are more linked to respiration and water related processes. This links could be at different levels, such as leaf, species, community and ecosystem. Studying the links at higher levels such as the ecosystem level, could be more difficult since various factors can be interacting together to influence certain processes.

Functional diversity is the variety in plant functional traits of a plant community with respect to their value, the range of the value and relative abundance (Chapin *et al.*, 2000, Diaz & Cabido, 2001), which is more relevant to local-scale ecosystem functioning than taxonomic diversity (Chapin *et al.*, 2000, Diaz & Cabido, 2001, Grime, 1998b, Hooper *et al.*, 2005). Abiotic and biotic changes and disturbance in the environment affects the functional diversity of plant communities in the direction that they can lead to the selection of species that sustain certain traits (Diaz *et al.*, 1999). For example high nitrogen availability in soils favors fast growing species over slow growing species (Thompson, 1994). This in turn can change the ecosystem processes and functions. Therefore changes in environmental drivers (e.g. climate or disturbance) will affect the functional diversity and will favor species exhibiting certain traits. This in turn will change the ecosystem functioning and the altered ecosystem processes and functions will influence change climate via the atmosphere-biosphere feedback (Diaz *et al.*, 2007).

Still, it is not clear how these trait syndromes – patterns of trait correlations indicating different ecological strategies (Nock *et al.*, 2016) – respond to changes in climate and how these can be translated into ecosystem functioning related to nutrient and carbon cycles and also ecosystem resilience to environmental changes. In simple words, how are the long-term variations in fluxes of carbon, water and energy that are not well explained by environmental drivers determined by the properties of the plants?

1.4.1 Plant traits at FLUXNET sites

Studying ecosystem processes and functions derived from fluxes in relation to species richness and diversity is not always feasible due to a lack of information on the biodiversity at the sites. It is even harder to include plant traits is these studies because measurements of traits are not done in most of the sites or are done but only once and are then rarely repeated in time. While there are general protocols on how to measure plant traits with some description of the sampling methods (Cornelissen *et al.*, 2003, Perez-Harguindeguy *et al.*, 2013), there are no "standard" ways of sampling methods, selection of individuals and species at the footprint of the FLUXNET sites.

The sampling at the sites is important because it should be in a way that the traits and species are representative of the part of the vegetation that has the most significant contribution to the fluxes ("footprint"). In addition, the seasonal distribution of environmental conditions such as temperature or light is essential for the adaptation of plants to their environment (Grime, 1997, Lechowicz, 2002) and plant traits are different the way they change throughout the phenological cycle. Moreover, some traits appear to be more plastic in response to their environment like specific leaf area (SLA) and plant height to variation in light availability, while this is not the case for seed mass (Garnier *et al.*, 2015). Thus at which phenological stages and how many times the sampling should be done is also important and not yet described extensively for different traits and at the FLUXNET sites it is mostly done at the peak of the phenological state.

Only in recent years attention has been given to this matter and scientists started to work on common protocols on sampling and measuring plant traits at the FLUXNET sites (ICOS - https://www.icos-ri.eu/ and NEON - http://www.neoninc.org/). Yet information on what type of traits would be important for the fluxes to be measured are insufficient and most of the efforts are limited to a handful of traits like SLA, leaf nitrogen and phosphorous concentration. Hence meta-analysis using data from FLUXNET and plant trait databases can be a good step to bring insight in to which plant traits are better linked to which fluxes or processes in order to necessitate their collection at field campaigns (discussed in section 1.6 and extensively in section 2). Using plant trait databases means that one should generalize the trait values for a given species i.e. using average values. However, it is not investigated whether it is acceptable to ignore intra-specific variability of traits for the analyses of plant imprint on ecosystem functions like GPP, TER or NPP. This will be further discussed in section 2.

1.4.2 Plant trait database

The plant trait database TRY used in this thesis is a data platform, which has put together different databases to make one common curated database (Kattge *et al.*, 2011). The underlying mission is: “TRY is a network of vegetation scientists headed by Future Earth and the Max Planck Institute for Biogeochemistry, providing a global archive of curated plant traits. The TRY database is a research platform of iDiv.” (https://www.try-db.org/TryWeb/Home.php)

In the past scientist who collected data either published it alongside their study or the data was lost and forgotten. Some datasets were deposited in archives like DRYAD but not curated. The idea behind TRY was to make one big database providing plant trait records standardized to be fit for purpose that could be used free of charge while still acknowledging the people who collected and shared the data. In this way it is easier for people in other disciplines to access plant trait data even though plant traits might be not their field of expertise or they might not know all the small and local databases that have the data they need. It also facilitates the understanding in which area data collection is missing so that new studies could focus on them.

Since they are many different formats for different databases, like the way meta data are reported or the units of the traits or the way the traits are measured or named, every time a database is added to TRY, it is first verified, reformatted and integrated with previous information in TRY and only afterwards it is published on the web to be available for everyone. Harmonizing all the different databases, TRY made it easy to find data on specific traits with specific condition.

Now TRY is highly disseminated and used. The data describes plant traits from throughout the globe and includes 1,800 traits. It has now 6.9 million trait records for 148,000 plant taxa (mostly species).

1.5. Objectives and structure

The overall aim of this thesis is to better understand the link between ecosystem functioning and plant traits. The introduction continues with the description of the research topics that are the focus of this thesis and are presented in three peer-reviewed papers in sections 2, 3 and 4. After the introduction, section 2 follows with a general description of the methods applied throughout the thesis. The main conclusions of the thesis as a whole are summarized with respect to the research topics in section 3.1, 3.2, and 3.3. Figure 3 shows how the papers are linked together. In addition it demonstrates how each was a consequence of the previous one regarding the questions that were arising in every step and tested in the subsequent one.

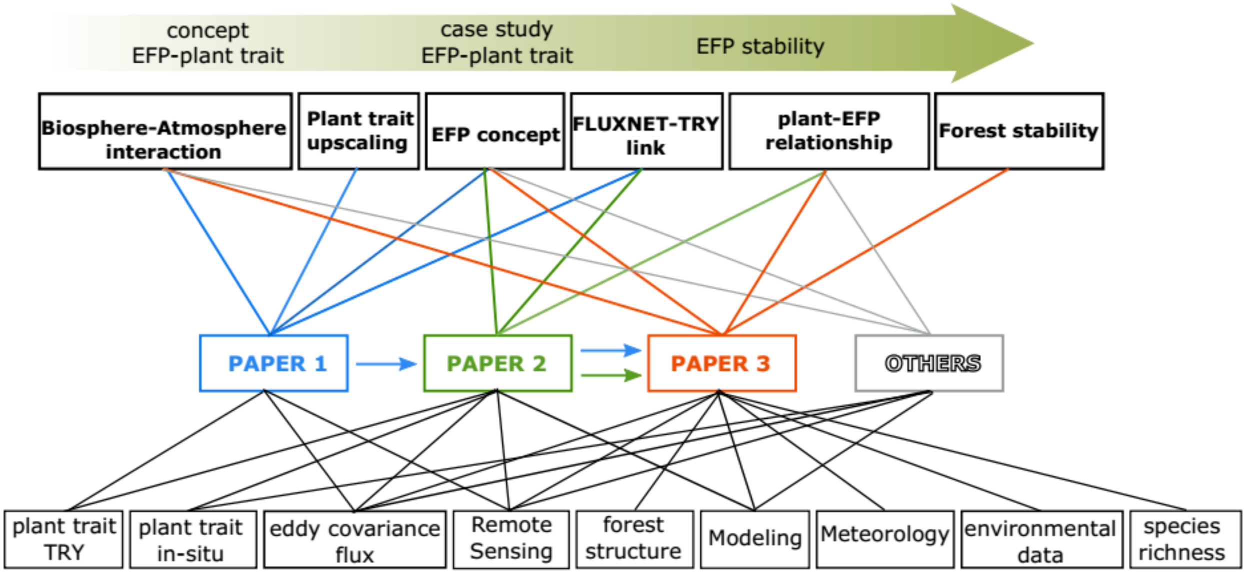

Figure 3: Framework demonstrating the link between the articles resulting from this dissertation. Upper black and bold boxes show the different topics and links studied in this dissertation. Colored boxes in the middle indicate articles included in this dissertation (i.e. Paper 1 – Musavi et al., 2015, International Journal of Applied Earth Observation and Geoinformation; Paper 2 – Musavi et al., 2016, Ecology and Evolution; Paper 3 – Musavi et al., 2017, Nature Ecology and Evolution). Black boxes in the bottom row indicate different data types and methodologies applied in the different papers. The lines show the different topics, data and methodological applications that were used in each paper. Arrows between the middle boxes, indicate the influence of each paper on the next one. Others presents the topic related articles that I co-authored; Migliavacca et al., 2017, New Phytologist (contributed data analysis, edited and discussed paper), Thonike et al., in preparation (contributed in writing and editing paper) and Mahecha et al., in preparation (contributed data, discussed and edited paper). EFP: ecosystem functional property, TRY: plant trait database, FLUXNET: micrometeorological database network.

At first in Paper 1, which is a conceptual article, I formally introduce the role of plant traits in the context of ecosystem functional properties and discuss concepts of using the two global data-base FLUXNET and TRY in order to understand the effects of plant traits on ecosystem functional properties. In Paper 2 I analyzed the relevance of spatial and temporal synchronization of flux and trait measurements. I executed a study using plant traits from TRY and plant traits from leaf samples at the FLUXNET sites and compare them in relation to GPPsat derived from FLUXNET eddy covariance data. Paper 3 is then further examining the IAV of GPPsat which was shown to be a significant part of the GPPsat property in relation to plant traits. Please see Figure 3 for an abstract introduction of the link between the papers.

1.5.1. Paper 1 - Plant traits in the context of ecosystem functional properties (EFPs)

In the past, many attempts were made to identify plant traits that could have strong effects on ecosystem functioning, e.g. classifying them by traits that control the acquisition and use of resources, those that are important for structuring the food web and the ones that have an influence on how disturbances (e.g. fire) can affect the ecosystems (Chapin *et al.*, 1997) or classifying them into effect and response traits (Lavorel & Garnier, 2002, Suding *et al.*, 2008). These studies mostly focus on the plant traits and do state links to ecosystem properties are only in qualitative term, which is in contrary to flux studies that mostly focus on fluxes, environmental variables and vegetation structural properties as a proxy for biotic influences. In this Paper I integrate traits-based research into the concept of ecosystem functional properties to establish a framework how empirically analyze the impact of plants on ecosystem functioning. I aim bring to the attention of both communities that fluxes and functional biodiversity need to be studied in concert. In this paper I aim to highlight opportunities – so far not fully explored in ecology – realized by consolidated information on plant species characteristics (*in-situ* and remotely) and ecosystem fluxes at local to global scale. Although many studies exist on the link between ecosystem processes and functions with environmental factors the role of the vegetation is still not fully understood. This is due to the fact that monitoring fluxes is done mostly by geo-ecologists and micro-meteorologists, while studies on biodiversity and plants are done by biologists, ecologists, community ecologist etc. and the subjects needs a more interdisciplinary approach. In addition, sampling of plants at the flux sites in order to have a representative measure of the whole ecosystem has also its complications. Most of the research done on the link between plants and fluxes or function and processes derived from them were on limited number of sites. (See Figure 4)

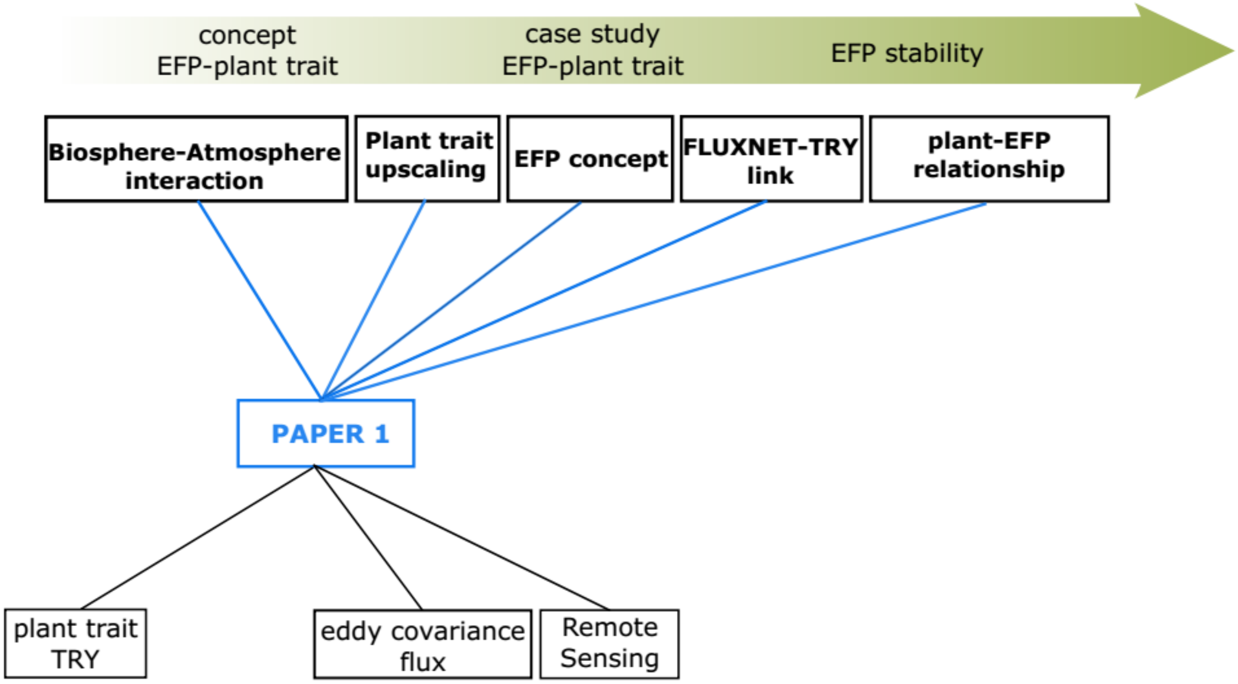

Figure 4: Framework demonstrating topics covered and data sources employed in the conception of paper 1 of this dissertation (Musavi *et al.* (2015), International Journal of Applied Earth Observation and Geoinformation).

Measurements of plant traits with biweekly frequency at two sites for several years have shown a strong association between seasonal and inter-annual variability (IAV) in ecosystem photosynthesis with the dynamics of leaf traits (Ma *et al.*, 2010). Another study conducted at 12 sites confirms the known relationship between leaf photosynthesis and leaf nitrogen concentration at forest canopy scale (Ollinger *et al.*, 2008). Also, ecosystem level light use efficiency which is the ratio between photosynthesis and light capture has been shown to be strongly linked to the leaf nitrogen concentration of the dominant species at the sites (Kergoat *et al.*, 2008).

In all studies in this direction either the study was done on a few sites with many plant traits or on many sites but one or two plant traits. One of the first times that the link between plants and ecosystem functions derived from fluxes is formally recommended is in Reichstein *et al.* (2014). They introduce Ecosystem Functional Properties (EFP) “as quantities that characterize ecosystem processes and responses in an integrated and comparable manner” and as comparable to ecophysiological leaf-level characteristics. In Paper I, I expand the definition of EFPs and provide two extensive tables with examples on EFPs derived using eddy covariance fluxes or retrieved from remote sensing.

Next, I introduce top-down and bottom-up scaling approaches to match the temporal and spatial scales of plant traits and EFPs. In addition, I discuss how recent advances in remote sensing information can be used in linking EFPs and biotic factors related to them. Here, I also discuss how recent efforts in collecting plant trait data has created a global database of plant traits that can be used to take a first glimpse of what plant traits are important for ecosystem functioning and, in this way, overcome the limited trait information that are present at the sites. By this means it is possible to also identify the plant traits important for different EFPs and to provide suggestions for plant sampling protocols at the sites. Especially that more than 100 plant traits are collected in TRY and we might identify significant links between EFPs and plant traits that were never considered to be important in the EFP-plant relationship. Overall, I propose a way to empirically explore the intrinsic biotic controls of terrestrial ecosystems on ecosystem functioning. These new pathways can potentially increase our understanding of which plant traits or plant trait combinations control spatio-temporal variations of functions occurring at the ecosystem scale, in interaction with climate and environmental factors.

1.5.2. Paper 2 - Spatial and temporal synchronization of plant trait and EFP measurements

Following paper 1, here I conduct a case study realizing the idea to use species averaged plant trait data from TRY to identify important plant traits explaining between-site variations of EFPs (See Figure 5). One of the constrains for testing the links between plant traits and EFPs is that on the one hand measurements of plant functional traits have not yet been carried out systematically at FLUXNET sites. On the other hand where measurements of plant traits were systematically done, fluxes and EFPs were not sufficiently estimated. Therefore, studies linking EFPs and plant traits across a wide range of ecosystems are rare (e.g. Kergoat *et al.*, 2008). In the previous paper I suggested using the global database of plant traits - TRY (Kattge *et al.*, 2011) to facilitate the identification of different traits for plant species present at FLUXNET sites to overcome the limited plant trait information that exists at FLUXNET sites. However, it is possible for trait values of particular site to deviate from those reported in broad scale databases. Therefore, here I test the potentials and limitations of using plant functional traits derived from a global database (e.g. TRY) versus traits obtained directly from the FLUXNET sites. In this paper I systematically explore the uncertainties introduced to the relationship between EFPs and plant functional traits that are related to the spatial and temporal dynamics of both ecosystem functioning and traits and the relevance of synchronized observations. Using ecosystem photosynthetic capacity as an example, I first provide an objective approach to derive robust estimates of the EFP ecosystem potential photosynthetic capacity (GPPsat) from gross primary productivity (GPP) obtained from eddy covariance flux measurements. Thereafter, I evaluate the EFP-plant trait relationship by investigating the impact of synchronizing EFPs and plant functional traits in time and space. I use this analysis to understand to which extent we can benefit from global plant trait databases to explain the variability of ecosystem GPPsat and to obtain a first indication which plant traits can be important to provide this link. In addition, using the *in-situ* plant traits and a pure data driven approach I identify a set of plant functional traits that control ecosystem GPPsat at the selected sites.

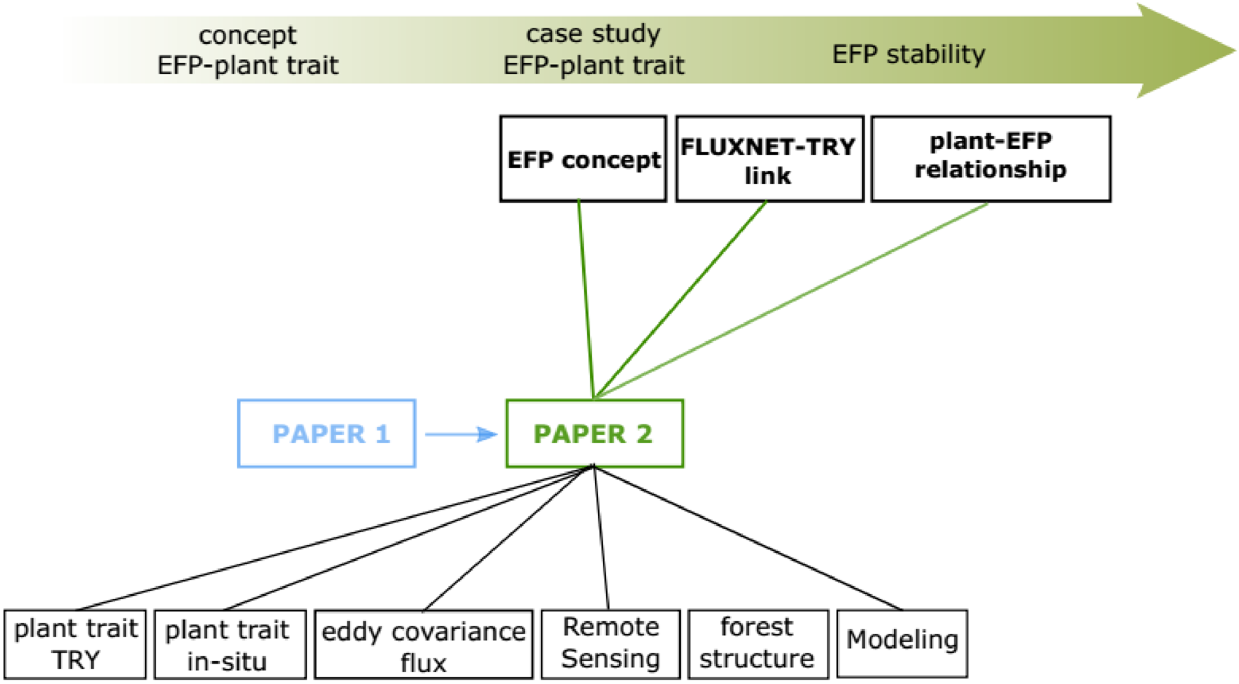

Figure 5: Framework demonstrating topics covered, data sources, methodological approaches and previous study (Paper 1) employed in the development of paper 2 of this dissertation (Musavi (2016), Ecology and Evolution).

1.5.3. Paper 3 - Impact of stand age and species richness on inter-annual variability (IAV) of EFPs

With successional time forests experience disturbances or single tree fall that allow different tree species or individuals in different sizes occupy the gaps, which results in temporal (e.g. phenology) or spatial heterogeneity of plant traits. Also, diversity often increases in addition to spatial complexity with stand age (Wirth, 2009). Thus the coexistence of species and their interaction with each other like resource use complementarity might make forests more robust to environmental changes. Generally, the idea that plant diversity has a positive effect on the stability or resilience of ecosystems has a long history and has been the subject of many studies (Bengtsson *et al.*, 1997, McGradySteed *et al.*, 1997, Mcnaughton, 1993, Naeem & Li, 1997). Since the impact of forest on the atmospheric carbon dioxide (Malhi *et al.*, 1999) is relevant in the context of climate change mitigation (Schulze *et al.*, 2000), it is very relevant to understand how forest could be more resilient. Is it structural, taxonomic or ontogenetic diversity of forests lending them resilience?

Following the results of the second paper, in this paper I investigate the cause of the differences of magnitude of the IAV of ecosystem GPPsat at the FLUXNET sites. The IAV of ecosystem GPPsat is still not well understood. This can hamper the predictability of the global carbon cycle, since the total uptake of CO_2 by ecosystems via photosynthesis (i.e. GPP) is one of the most important fluxes in the global carbon cycle.

Since there are only a few sites that collected plant traits over several years, it was not possible to study the IAV of ecosystem functional properties such as GPPsat in relation to plant traits. Therefore, I used stand age and species richness of the sites as means to have a clue whether the vegetation at the sites is also influencing the differences in the IAV existing between the forest sites.

In this study (See Figure 6), I explore the link of the inter-annual magnitude of ecosystem GPPsat as a proxy for ecosystem stability with the properties of the vegetation at the site; here stand age, species richness, LAI, canopy height and cover. In the study I use a variety of data sources, from remote sensing information to ecosystem level CO_2 fluxes, and also consider and discuss a series of potential confounding factors (air temperature, precipitation, soil water and nutrient availability), in particular the role of climate and structural differences of the different forest sites as potential drivers as well.

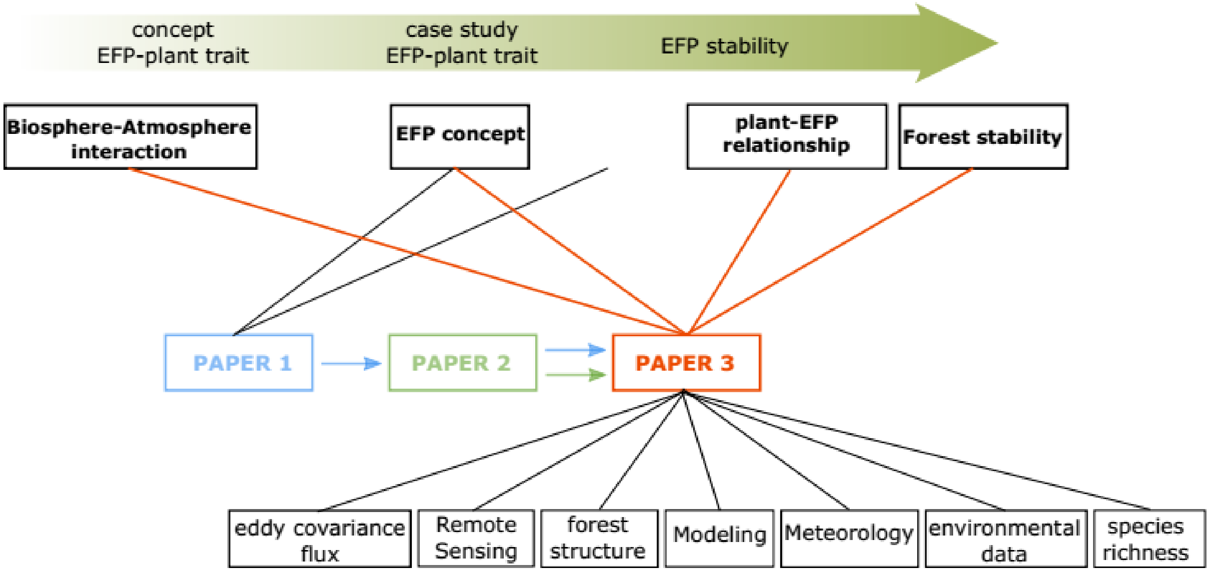

Figure 6: Framework demonstrating topics covered, data sources, methodological approaches and previous study (Paper 1 and Paper 2) employed in the development of paper 3 of this dissertation (Musavi *et al.* (2017), Nature Ecology and Evolution).

2 General methods

For the purpose of this thesis I did a lot of data collection and treatment. Data for species composition at the sites and plant traits were collected from TRY, FLUXNET, and additional literature search and by request from site principle investigators (PIs). For the estimation of EFPs I used micrometeorological data (flux) from FLUXNET and FAPAR and LAI from online available remote sensing products that were available at the institute. Detailed explanations are given in the following sections;

2.1 Collection of species cover and ancillary data

First, the ancillary database of FLUXNET was downloaded. A preliminary analysis of the database showed that there were inconsistencies in the way principle investigators (PIs) of the different sites reported the ancillary data. Especially for the abundance of the species, some reported cover based on litter collection, biomass, good guess or tree count and some reported the overstory and understory cover adding up to 100% and some estimated the cover separately for each layer.

Therefore, I checked all papers published about the sites for additional information. Still there were gaps and inconsistencies. Gaps were filled using PFT categories from the FLUXNET ancillary database. In the ancillary database the cover of understory and overstory vegetation is given at the PFT level. For sites with no cover information I divided the total cover which was defined for the understory of a given PFT equally between species relating to understory and did the same for overstory. In some cases that PIs were contacted, they replied and confirmed the information on the species and cover.

In the last paper I use species richness information. I sorted the plant species according to their cover, from the one with highest cover to the lowest and considered only the number of species that had a cumulative cover of 90%.

2.2 Site selection

Sites were included in the study, which had information on species occurrence and their abundance at the sites and did not experience disturbances for the time scale of the data. In case there was a disturbance in a year at a site, I removed that year of data. In case of Paper 2 I used sites that replied to the leaf sampling request (see 2.6) and also had the GPP and (global solar radiation) Rg data of the year of sampling and were not disturbed. Sites and individual years were also removed if the quality of estimates for ecosystem of GPPsat was insufficient (see below).

2.3 Micrometeorological data

I used the half hourly flux data from eddy-covariance sites. The GPP values used in my study are computed using the commonly used algorithm of Reichstein *et al.* (2005) as method for partitioning NEE into TER and GPP. The algorithm computes GPP by extrapolating night time NEE data (night time TER) 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.

2. 4 EFP – Ecosystem photosynthesis capacity

To study the relationship between EFPs and plant traits, one should consider exploring the link between each EFP and plant traits individually. This is due to the fact that ecosystem properties are usually influenced by a group of plant traits (de Bello *et al.*, 2010, Diaz *et al.*, 2006, Eviner & Chapin, 2003, Lavorel & Garnier, 2002).

CO_2 is one of the most important greenhouse gases and the subject of many climate change mitigation plans. The terrestrial biomass and its soil store more carbon than it is contained in the carbon dioxide of the atmosphere (Koerner, 2003). GPP is the "gateway" for energy and carbon driving ecosystem processes (Gilmanov *et al.*, 2003). With an increase in future drought events and a decrease in GPP, ecosystems might act as carbon sources and contribute to positive carbon-climate feedbacks, e.g. the summer drought 2003 over Europe (Ciais *et al.*, 2005, Cox *et al.*, 2000, Dufresne *et al.*, 2002). Therefore, ecosystem photosynthesis capacity, i.e. the GPP potential of the ecosystem at its activity peak is an important intrinsic biogeochemical property of the ecosystem and that is the reason I chose this EFP for my study.

Utilizing an ecosystem level light response curves I estimated site-level annual photosynthetic capacity (GPPsat) using half-hourly GPP estimates and Rg or absorbed photosynthetic active radiation (APAR) (Musavi, 2016). For the light response curve I had two choices; using the rectangular hyperbola model

$$GPP = \frac{\alpha A_{max} Q}{\alpha Q + A_{max}}$$

where α is the initial slope of the light response curve, Amax is the plateau of the light response curve, GPP is the half-hourly GPP values, and Q is the incoming radiation used to drive the model. Or using the nonrectangular hyperbolic light response curve (NHLRC) model (Gilmanov *et al.*, 2003)

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

where the parameters are the same as in the rectangular hyperbolic model and only the parameter θ is added, which is a curvature parameter ($0 \leq \theta \leq 1$). I used the latter one, because it provides more realistic estimates by providing a better fit (Lieth & Reynolds, 1987, Peat, 1970, Prioul & Chartier, 1977). The rectangular model sometimes did not converge to a saturation state and estimated unrealistic high values of A_{max} (Gilmanov *et al.*, 2003). Actually, when $\theta \rightarrow 1$ in the nonrectangular hyperbola model it becomes the rectangular hyperbola (Gilmanov *et al.*, 2003).

I fit NHLRC to GPP and Rg/APAR flux data of a 5-day moving window. Then model uses the flux data and the provided parameters, α, A_{max} and θ. The parameters are fitted to the data considering the dependence of GPP to light. The GPP is recalculated based on the fitted parameters and is then compared to the original GPP observations and so a fitting coefficient of determination is provided. The parameters are estimated by minimizing the model observation residual sum of square with the quasi-Newton optimization method that allows box constraints (Byrd *et al.*, 1995). To this purpose, I used the optim function implemented in R (http://CRAN.R-project.org/). I removed estimated model parameters with R^2 of the fitting lower than 0.6.

Since the model saturates slowly, I used an approximation of the maximum of GPP, deriving GPP at Rg of 1000 W/m^2 (2000 μmol m^{-2} s^{-1} in case of APAR) (Jacobs *et al.*, 2007), which is resulting in GPPsat the GPP at saturating light. The estimated parameters and GPPsat are attributed to the day at the center of the window. So a time series of daily values of GPPsat are derived for each year. Using estimates only when the performance of the fitting is good ($R^2 > 0.6$), I retain growing season data as the R^2 of the model fit was typically higher than 0.6 only within the growing season. To have the annual GPPsat, I extracted the 90th percentile of the time series.

2.5 APAR estimation

In this thesis, estimates of FAPAR and LAI (Pinty *et al.*, 2011a, Pinty *et al.*, 2011b) derived at 1 km spatial resolution by the joint research centre two-stream inversion package (JRC-TIP) (Pinty *et al.*, 2007) from the (moderate resolution imaging spectroradiometer) MODIS broadband visible and near-infrared surface albedo products (Schaaf *et al.*, 2002) are used to quantify the phenology of vegetation and changes in the structure of the ecosystem. The FAPAR product covers a sequence of 16 days periods with 1 km spatial resolution. Longitude and latitude of the FLUXNET sites are used to find the pixels where the towers are located and the time series of FAPAR of these pixels are used. The data of FAPAR and LAI are with gaps due to conditions like clouds and thus it is necessary to fill these data gaps before use. To this end, a distance correlation between the time series of the eight pixels around the central pixel where the towers are located is performed (Szekely *et al.*, 2007). The gaps are then filled using the data of the pixels with a correlation of $r > 0.75$ with the central pixel, prioritizing the pixels with highest correlation. The remaining gaps are filled with a spatiotemporal gap filling approach (v. Buttlar *et al.*, 2014). Then to move from 16 days periods sequence data to daily time series, I use a smoothing spline approach (Filippa *et al.*, 2016, Migliavacca *et al.*, 2011). FAPAR is the fraction of photo synthetic active radiation (PAR) that is absorbed by the plants. Thus APAR time series are derived by multiplying FAPAR by PAR (Rg is converted to PAR).

2.6 Leaf sampling for plant trait estimation

In 2012 we started to collaborate with a group of scientist from Vrije Univeristy of Amsterdam. They had started a quest for *in-situ* plant samples from the FLUXNET sites to measure different plant traits. They wanted to compare the *in-situ* plant traits to different fluxes at the sites. We shared our data and knowledge on the topic and also the suggestion of using EFPs instead of fluxes directly from our side. I assisted in contacting PIs for ancillary data and also in collecting leaf samples from a site located in Hainich forest. To ensure high data quality, it was very important that the samples were collected as standardized as possible. Therefore a sampling protocol was sent to the PIs of the sites while considering minimum effort required from the PIs in order to maximize the reply rates. The leaf sampling protocol was based on the TCO "Protocols for Vegetation Sampling and Data Submission" from Law *et al.* (2008) and the paper from Cornelissen *et al.* (2003). For the selection of plants, PIs were asked to only sample from trees, shrubs and herbaceous species that are present in the footprint of the flux tower and ideally, they were asked to obtain samples from the 5-10 most abundant species. If the whole canopy of the site was accessible to the samplers (for example small trees for which the top can be reached with pruners), samples from 10 different individuals per species were asked. In practice, the number of trees that were going to be sampled was dependent on the accessibility of the canopy, which for forests is probably limited to the position of the flux tower. In this case, PIs were asked to sample for as many as possible individual trees that can be reached from the tower (e.g. using elongated pruners/clippers if available).

Sampling was preferred to be done at the peak of the growing season. Only fully developed and, non-damaged leaves that were not in senescence should have been sampled. No understory was included in the sampling of forests, as the understory has no fully sunlit leaves. For grasslands, as well as for crops, or sites with a very low vegetation cover, only fully sunlit leaves were asked to be sampled. When there were shrubs or trees intermixed with grassland (like a savanna), trees were sampled according to the way described for forests (top and bottom of the canopy), while from herbaceous plants, only fully sunlit leaves were sampled. For conifers, a suitable foliar sample is a shoot that retains all years of foliage, but that included current season's growth only if that is fully extended (not fully develop growth from the year was to be excluded from the sample). Non-vascular species such as bryophytes and liverworts were not included in the samples.

The leaf traits were measured in the lab at the Vrije University of Amsterdam. Due to leaf shrinkage, PIs were asked to measure the leaf area of the samples while they were still fresh. This step was essential for measuring the leaf mass per area (LMA).

In situ leaf samples from the selected sites were collected in the period 2011–2012. In summary plant traits related to photosynthesis at ecosystem scale, specifically leaf nutrient content and stoichiometry of the nutrients, were measured (Sardans & Penuelas, 2012): leaf nitrogen content per dry mass (Nmass or per 100 g leaf dry mass: N%), leaf nitrogen content per leaf area (Narea, g/m^2), leaf phosphorus content per leaf dry mass (Pmass, mg/g) and per leaf area (Parea, g/m^2), leaf carbon content per leaf dry mass (C, mg/g), leaf C/N ratio (C/N, g/g), leaf carbon and nitrogen stable isotope concentration (δ13C, δ15N), leaf dry mass per leaf area (LMA), leaf nitrogen phosphorous ratio (N/P), and specific leaf area (SLA, mm/mg).

2.7 Collecting plant trait estimations from TRY and auxiliary database of FLUXNET

I extracted the plant species information of the FLUXNET sites from the auxiliary database of FLUXNET. Then I cleaned up the list and replaced English plant names and species codes by scientific species names. In many cases I updated the list doing a literature search. Then trait data from TRY were extracted using these scientific species names. In order to test whether the traits were extracted properly I checked the range of trait values and compared trait-trait correlations. In addition, the auxiliary database of FLUXNET was also used to extract existing plant traits reported at the sites. These data was then unified for their units.

2.8 Other auxiliary data

Data from climate, environmental and ecosystem structure variables where collected from different sources. Canopy cover was extracted from the MODIS vegetation continues fields product (DiMiceli *et al.*, 2011). Canopy height was extracted from Simard *et al.* (2011) study. Soil nutrient availability classes were derived from Fernandez-Martinez et al., 2014. Air temperature, water availability index and cumulative precipitation were ERA-Interim climate data downscaled at the FLUXNET sites (http://www.bgc-jena.mpg.de/~MDIwork/meteo/index.php). In addition, average stand age was extracted from the auxiliary database of FLUXNET.

2.9 Data analysis

Description of the statistical methods used in this dissertation is given in more detail in each of the peer-reviewed articles in section 3 (original contributions). The analyses were conducted in R platform (R Core Team 2014) and the scripts were written by me, with occasional support from co-authors. In case of the peer-review article 3 the whole script is also available online.

3 ORIGINAL CONTRIBUTIONS

3.1 Paper 1

Talie Musavi, Miguel D. Mahecha, Mirco Migliavacca, Markus Reichstein, Martine Janet van de Weg, Peter M. van Bodegom, Michael Bahn, Christian Wirth, Peter B. Reich, Franziska Schrodt, Jens Kattge, (2015): The imprint of plants on ecosystem functioning: A data-driven approach. International Journal of Applied Earth Observation and Geoinformation. 43, 119–131. doi: 10.1016/j.jag.2015.05.009.

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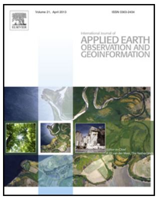

The imprint of plants on ecosystem functioning: A data-driven approach

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ABSTRACT

Terrestrial ecosystems strongly determine the exchange of carbon, water and energy between the biosphere and atmosphere. These exchanges are influenced by environmental conditions (e.g., local meteorology, soils), but generally mediated by organisms. Often, mathematical descriptions of these processes are implemented in terrestrial biosphere models. Model implementations of this kind should be evaluated by empirical analyses of relationships between observed patterns of ecosystem functioning, vegetation structure, plant traits, and environmental conditions. However, the question of how to describe the imprint of plants on ecosystem functioning based on observations has not yet been systematically investigated. One approach might be to identify and quantify functional attributes or responsiveness of ecosystems (often very short-term in nature) that contribute to the long-term (i.e., annual but also seasonal or daily) metrics commonly in use. Here we define these patterns as "ecosystem functional properties", or EFPs. Such as the ecosystem capacity of carbon assimilation or the maximum light use efficiency of an ecosystem. While EFPs should be directly derivable from flux measurements at the ecosystem level, we posit that these inherently include the influence of specific plant traits and their local heterogeneity. We present different options of upscaling in situ measured plant traits to the ecosystem level (ecosystem vegetation properties – EVPs) and provide examples of empirical analyses on plants' imprint on ecosystem functioning by combining in situ measured plant traits and ecosystem flux measurements. Finally, we discuss how recent advances in remote sensing contribute to this framework.

1. Introduction

The structure and functioning of terrestrial ecosystems are formed by environmental (e.g., climatic and edaphic) constraints, as well as the legacy of ecosystem development. Historical processes such as evolution, migration, and disturbances are encoded in the community structure of biota (i.e., plant or soil organism communities, their horizontal and vertical structure and temporal dynamics). In turn, the biotic structure shapes the biogeochemical functioning of ecosystems, i.e., nutrient turnover, water cycling, and carbon storage potential amongst others (Field et al., 1992; Friend and Cox 1995; Schlesinger 1997; Chapin et al., 1998). To put it in other words: responses of biogeochemical processes to environmental conditions are modulated by the local properties of organismic communities (Field et al., 1992). The interacting effects of organismic responses and biophysics at the ecosystem level ultimately shape ecosystem feedbacks to the climate system as manifested in the exchange of energy and greenhouse gases and cycling of chemical compounds (Bonan, 2008).

Commonly used terrestrial biosphere models implement biogeochemical and biophysical processes according to our understanding derived, in large part, from plant organ level observations, and use parameters that are often based on observable plant traits. Plant traits are measurable features at the individual organ or organism level such as morphological, anatomical, phys-

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Definitions used throughout the manuscript

Ecosystem functional property (EFP)	Indicators of ecosystem functional state. Quantities that characterize ecosystem processes and responses in an integrated and comparable manner (Reichstein et al. 2014).
Ecosystem vegetation property (EVP)	Indicators, characterizing the properties of the vegetation in the context of an ecosystem.
Eddy covariance (EC)	A micrometeorological method to measure exchanges of heat, mass, and momentum between a surface and the overlying atmosphere (Baldocchi et al., 2001), based on the covariance between turbulent fluctuations of the vertical wind and the scalar fluctuation, of the quantity of trace gases of interest (Baldocchi et al., 1988; Foken and Wichura, 1996; Aubinet et al., 2000; Baldocchi, 2008).
Ecosystem flux	The exchange of matter and energy between an ecosystem and the atmosphere per unit time measured with the eddy covariance technique (Luyssaert et al., 2009; Reshef et al., 2011).
FLUXNET	A network of regional networks, which coordinates regional and global analysis of observations from EC tower sites. (http://fluxnet.ornl.gov/).
TRY	A network of vegetation scientists, which provides a global archive of plant traits (http://www.try-db.org).
Plant functional type (PFT)	Plant functional type is a term that groups plants according to a limited number of plant attributes of life form, phylogeny, or morphology (Box, 1996).

iological or phenological traits (Violle et al., 2007). Measurements of plant traits have frequently been used for model development and parameterization, such as leaf carboxylation capacity (Vc_{max}), maximum CO_2 assimilation rates (A_{max}), and nitrogen content per leaf area (e.g., White et al., 2000; Kattge et al., 2009; Goll et al., 2012). However, the representation of plant biodiversity in common terrestrial biosphere models is very limited and rarely goes beyond differentiating ten to fifteen (depending on the model) plant functional types (PFTs). This approach largely ignores variability of characteristics within individual PFTs (but see van Bodegom et al., 2012; Reich et al., 2014; Reichstein et al., 2014). The increasing availability of relevant information on plant traits offers unprecedented opportunities for introducing more detailed functional diversity in global models of the terrestrial biosphere (Brovkin et al., 2012; van Bodegom et al., 2012; Wang et al., 2012; Pavlick et al., 2013; Verheijen et al., 2013). Functional diversity is defined herein as the variability within and among locations of both the trait mean and trait variance due to differences among organs, individuals, or species; or through time. Models that explicitly represent functional diversity will provide even more detailed predictions of plants' imprint on ecosystem processes (Scheiter et al., 2013).

Advancing model structures should be accompanied by developing a sound independent model-benchmarking system (Luo et al., 2012). However, even if the next generation of models integrate trait diversity and their effects on biogeochemical and biogeophysical processes (Reu et al., 2011; Scheiter et al., 2013; Pavlick et al., 2013), we anticipate that the biodiversity feedbacks will be particularly difficult to evaluate. We therefore assume that independent empirical analyses on the linkage of plant traits to emergent ecosystem scale properties will be needed and should remain independent from the model assumptions. Therefore, motivation for data driven, empirical analyses of plant characteristics in combination with ecosystem level exchanges of carbon, water, and energy are twofold.

First, the identification of robust empirically derived biodiversity effects on ecosystem functioning can become valuable for model benchmarking, and allow for testing whether the assumed relationships between plant traits and ecosystem functions in models are comparable to those observed (e.g., Luo et al., 2012). Second, it is important to identify key characteristics of plants that influence ecosystem functions, which might not have been considered yet. These are beneficial, both to facilitate a better understanding of the sensitivity of ecosystem exchanges of matter and energy to long-term environmental changes (including feedbacks to vegetation, soil and climate), while also being applicable to quantifying and understanding ecosystem services that are linked to ecosystem functions and processes (de Bello et al., 2010). Soil biota also has an important role in ecosystem processes (Neher 1999; Wall and Moore, 1999). However, information about soil biota is difficult to access via in situ measurements and hardly available via remote sensing (hereafter RS, but see Fisher et al., submitted), hence here we focus on plants.

The topic of how plants influence ecosystem functioning and how to predict ecosystem functions from 'effect traits' (sensu Lavorel and Garnier, 2002) has been discussed for several decades in the literature and is sometimes considered a "holy grail" in ecology (Grime 1979; Southwood 1988; Chapin et al., 2000; Lavorel and Garnier, 2002). Conceptual studies in this direction usually emphasize the relationships existing between plant traits and ecosystem processes or functions, but often are not explicit about the ecosystem functions and processes, nor how they could be estimated from ecosystem level observations and ultimately linked with plant traits. Moreover, in these literatures, the ecosystem functions are heavily dominated by snap-shot or annually integrated measurements of state variables or component processes, such as net primary production (NPP), leaf area index (LAI), or standing biomass, which are integrated over numerous component processes (see Hooper et al., 2005). Standing biomass, as an example, is the result of the physiological balance of the fluxes of photosynthesis and respiration, carbon allocation, organ-level growth and mortality, and biotic and abiotic losses, such as herbivory and storm breakage respectively. Trait influences on these component processes – typically fluxes of matter and energy – may be strong, but may remain hidden when relating traits to only state variables. A group of plant traits might influence changes of standing biomass, but it is also important to understand their influence on the processes resulting in the standing biomass. To overcome such limitations, we propose to link plant traits with essential features of ecosystem functioning, which can be derived from observations of ecosystem energy and matter fluxes – the direct result of relevant ecosystem processes like e.g., photosynthesis, respiration, or evapotranspiration.

In this conceptual paper, we highlight opportunities – so far not fully explored in ecology – arising by consolidating information on plant species characteristics (in situ and remotely sensed) and ecosystem fluxes at local to global scale. First, we introduce a conceptual framework that defines ecosystem functional properties (EFPs) as variables of ecosystem functioning that include physiological processes and their responses to the environment (Section 2). Then, we introduce top-down (Section 3.1) and bottom-up (Section 3.2 and 3.3) scaling approaches to match the temporal and spatial scales of observed plant traits and EFPs. In the final part, we will discuss how remotely sensed information can be effectively used in this context (Section 4). Overall, we will propose pathways to empirically analyze the intrinsic biotic controls of terrestrial ecosystems and

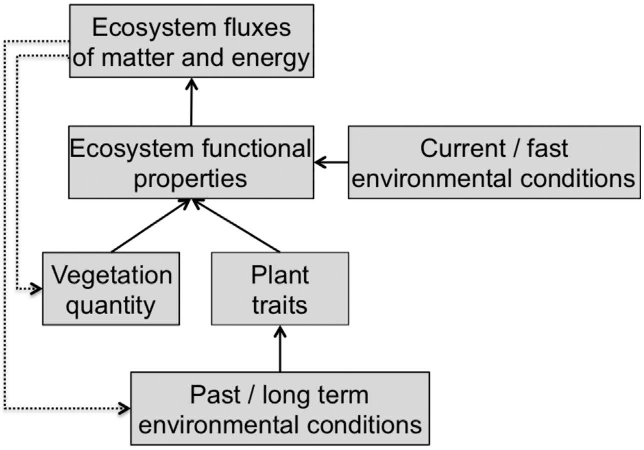

Fig. 1. Concept for mapping plant traits via ecosystem functional properties onto ecosystem fluxes, separating slow and fast changing environmental conditions. The concept is based on the hypothesis that plant traits adapt to long term, slowly changing environmental conditions, like seasonal or annual mean or extreme conditions. Together with vegetation quantity (e.g., biomass or LAI) plant traits determine ecosystem functional properties (EFPs). Fast changing environmental conditions, like diurnal or seasonal variation, determine ecosystem fluxes of matter and energy via the EFPs. Ecosystem fluxes determine changes of vegetation quantity, and may feedback on long term environmental conditions. We propose that the concept can be generalized, replacing vegetation quantity and plant traits by organisms quantity and organisms traits.

its effect on ecosystem functioning. We expect these new pathways to contribute to our understanding of which plant traits or plant trait combinations control spatiotemporal variations of functions occurring at the ecosystem scale, in interaction with climate and environmental factors.

2. The imprint of plants on ecosystem functioning: a conceptual basis for a data driven approach

Ecosystem functional properties (hereafter EFPs) should capture process attributes or responsiveness of ecosystems (often very short-term in nature) that contribute to the long-term (i.e., annual but also seasonal or daily) metrics commonly in use. Reichstein et al. (2014) defined EFPs “as quantities that characterize ecosystem processes and responses in an integrated and comparable manner” (page 13698). Thus EFPs are both conceptual in nature and quantifiable from ecosystem processes, and are analogous to ecophysiological leaf-level characteristics or relate to physical and ecohydrological characteristics important for land surface–atmosphere interactions (Reichstein et al., 2014). Following this definition, EFPs should provide relevant process characteristics, for instance maximum flux rate, flux rates under standardized environmental conditions (base rate), or the slope of changing rates given changes in environmental drivers (e.g., light response or temperature responses; sensitivities), or the fraction of such characteristics. EFPs can consequently be used to characterize variations in key processes, like photosynthesis, respiration, or evapotranspiration, or their relationship, like water use efficiency of photosynthesis (the amount of carbon gained by water transpired). As they characterize specific ecosystem processes, EFPs can be derived from observable ecosystem fluxes (the observable components of the processes), from the quantity (e.g., abundance) and characteristics (plant traits) of the organisms (the operators of the processes), or potentially inferred via RS at ecosystem level (Fig. 1). In general terms, EFPs can be understood as empirically derived equivalents at the ecosystem scale to parameters (at ecosystem scale) in terrestrial biosphere models. In relation to aggregated plant trait observations, EFPs thus enable us to examine the influence of biotic and abiotic controls on the various components of the processes (Fig. 1).

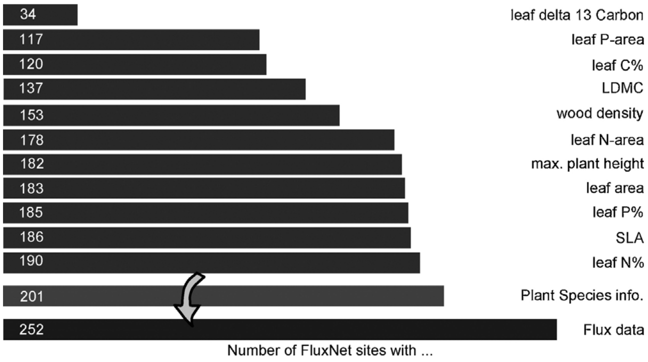

Fig. 2. The number of FLUXNET sites with traits in TRY. Bottom: Number of sites with available flux data in the FLUXNET La Thuile database. The second bar provides the number of sites with information of dominant plant species available in the FLUXNET ancillary database. The arrow indicates that we could use plant traits at the sites only by knowing which species exist at these sites. The remaining numbers on each bar are showing the number of FLUXNET sites for which the plant trait on the left side is available from TRY database for at least one of the site-species. (Traits from Table 1 are shown here).

So far, empirical analyses of the relationships between plant traits and ecosystem functions have been primarily limited to ecosystems or regional scales (Pierce et al., 1994; Kergoat et al., 2008; Ollinger et al., 2008; Cleveland et al., 2011; Reich 2012), or to whatever is available from the literature (e.g., Green et al., 2003). This is, in part, due to limited measures in biomes, but also because the relevant data (e.g., plant traits and ecosystem level fluxes) were not always measured simultaneously and have largely not been curated via central repositories. Nowadays, more data for primary ecosystem functions and organism traits are becoming available through RS data and initiatives like FLUXNET (the global network of ecosystem level observations of carbon, water, and energy fluxes on terrestrial ecosystems, Baldocchi, 2008) and TRY (a global archive of plant traits, Kattge et al., 2011). A first intersection of the plant species data from FLUXNET and TRY shows that, for more than 100 sites belonging to FLUXNET, we can gather information on a specific plant trait (e.g., specific leaf area, SLA) of the dominant species at the sites from TRY (Fig. 2). Moreover, the data reported in FLUXNET and TRY cover a variety of climatic conditions, as shown Fig. 3, which makes these empirical analyses possible at a global scale.

Ground-based measurements of plant traits are commonly conducted in ecological studies, but are usually limited in space and in time because of resource constraints (i.e., laborious and time consuming measurements). Moreover, plant traits are usually measured at the leaf or plant level, so in order for them to represent the vegetation of an ecosystem, they need to be upscaled to ecosystem vegetation properties (hereafter referred to as EVP). Here we introduce potential upscaling schemes for in situ measured plant traits to provide the information about biotic controls corresponding to EFPs (see Section 3.2). The developments in the field of RS over the last few decades allows us to retrieve plant traits, which in most cases are integrated at the ecosystem level (EVP) and in some cases continuous in time (Homolová et al., 2013). This is particularly important where the temporal variability of plant traits is relevant. In addition EFPs can as well be retrieved from RS (see Section 4).

3. Matching scales

3.1. Top-down

One of the challenges of the proposed methodology is that ecosystem fluxes measured with eddy covariance techniques are

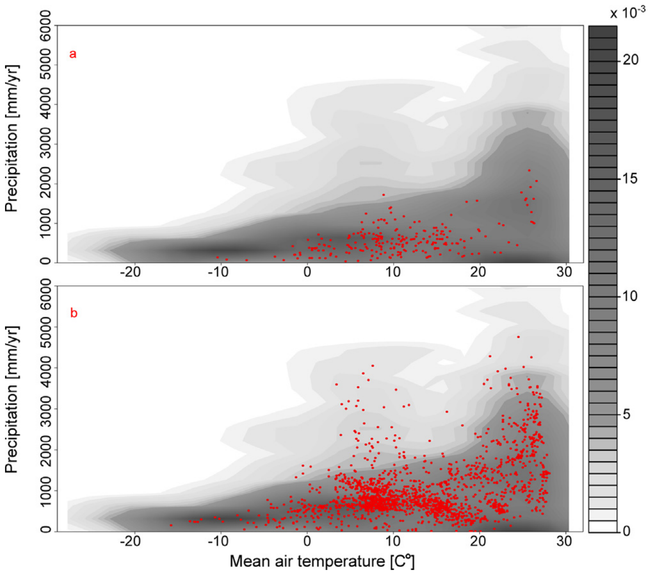

Fig. 3. The distribution of (a) FLUXNET sites, (b) measurement locations from TRY (of various plant traits) in climate space spanned by mean annual temperature and mean annual precipitation. Kernel density estimation was used to show the density of land surface pixels at 0.5° × 0.5° resolution for the two variables.

not directly comparable with plant traits because they do not vary at the same time scale. To grasp the relationship between plant traits, fluxes, environmental drivers (climate) and soil pools we need to carefully consider the time-scale.

While many plant traits (e.g., leaf mass per leaf area (LMA), gram leaf nitrogen to 100 gram leaf mass (%N)) typically vary mostly at weekly, seasonal, or longer time scales (Ma et al., 2010), ecosystem fluxes measure short-term responses (<1 h) but respond to meteorological and environmental conditions at time scales ranging from minutes to seasonal, interannual, and longer and can be integrated at those time scales (Richardson et al., 2007; Stoy et al., 2009). Meteorological drivers such as temperature, precipitation, solar radiation, and snow-cover explain a substantial part of the temporal (in particular daily to seasonal) and spatial variability of observed fluxes (e.g., Dunn et al., 2007; Urbanski et al., 2007). On longer time scales (seasonal, annual) fluxes might lag behind the meteorological factors (Stoy et al., 2009; see also Ogle et al., 2015 for memory effect in ecosystem processes) and for time scales longer than two weeks, fluxes of net ecosystem exchange (NEE) and gross primary production (GPP) are relatively less variable than the meteorological factors (Stoy et al., 2009). This has been attributed to the fact that fluxes are processed by plants, with plant traits changing on longer time scales (e.g., Ordoñez et al., 2009; van Ommen Kloeke et al., 2012; Verheijen et al., 2013). At seasonal and inter-annual scales, it therefore becomes more complicated to attribute multi-scale variability in ecosystem-atmosphere fluxes to hydrometeorological conditions only (Mahecha et al., 2007, 2010; Stoy et al., 2009; Reich, 2010). Thus, in addition to the dominant control of plants and pools on spatial variability of fluxes (e.g., between flux tower variability, e.g., Reichstein et al., 2003), they can possibly also influence the temporal variability of fluxes.

While fluxes of physiological properties such as NEE, GPP, ecosystem respiration, or evapotranspiration are measured with eddy covariance techniques and are readily available in half-hourly time scales, we can use them to derive EFPs that vary over longer time scales (Reichstein et al., 2014), comparable to plant traits. Proposed EFPs in Table 1 can be considered as an integrator of ecosystem functioning less variable in time than the fluxes themselves. By using the concept of EFPs, it is possible to eliminate the high temporal flux variations related to the short term climate variability (e.g., temperature and global radiation) and to standardize for environmental conditions. This approach to control for short-term variation of environmental conditions would be in analogy to suggestions for standardized trait measurements (e.g., Grime 1988; Cornelissen et al., 2003a; Perez-Harguindeguy et al., 2013).

An example for an EFP is optimum light use efficiency (LUE) derived from GPP and normalized by the fraction of absorbed photosynthetic active radiation (fPAR) (Kergoat et al., 2008). LUE is correlated to mean annual temperature at FLUXNET sites, but the correlation fades when this EFP is compared with the temperature corresponding to the time when the GPP flux was retained to compute LUE (Kergoat et al., 2008), because physiological characteristics of the EFP (here LUE) cancel short-term environmental variability. This kind of behavior is expected for other EFPs as well (Table 1). Therefore, EFPs provide empirical estimates of long-term changes of ecosystem functional states, and allow the link with plant traits and the comparison across sites.

Another example for an EFP is the photosynthetic capacity of an ecosystem, which is the potential maximum photosynthesis of the ecosystem over a given period. We suggest the use of GPP1000, which is the GPP or assimilated CO_2 of the ecosystem at 1000 W/m^2 of global incoming radiation (Rg) (e.g., Ruimy et al., 1995; Falge et al., 2001). GPP1000 can be derived by fitting non-rectangular hyperbolic light response curves (e.g., Gilmanov et al., 2003) using half-hourly GPP values and Rg data. Quantified on an annual basis (i.e., 90th percentile of the GPP1000 – to exclude outliers), this EFP characterizes the photosynthetic capacity of an ecosystem (comparable to A_{max} at leaf scale), which typically occurs at the peak of the growing season, with favorable temperatures and the absence of severe water stress, while it ignores the diurnal and seasonal variability of the fluxes related to irradiance and other environmental conditions. It enables analyses of the inter-annual variability of the photosynthetic capacity and facilitates comparisons across sites. GPP1000 can as well be characterized at shorter time scales, e.g., seasonally, which would then allow monitoring seasonal variation of the ecosystem functional state. However, the seasonal variation of environmental properties – temperatures may be unfavorable, water may be limiting – complicates these analyses.

A third example is water use efficiency (WUE, the ratio between GPP and evapotranspiration) that can be considered as an EFP that links carbon and water cycling. However, WUE instantaneously declines with water vapor pressure deficit (VPD) in the atmosphere; therefore inherent or intrinsic WUE – standardized for VPD – would be a more appropriate EFP (e.g., Beer et al., 2009). But still the exact form of the influence of VPD remains unclear, because VPD influences leaf parameters such as stomatal conductance (Mott and Parkhurst, 1991; Buckley, 2005; Shope et al., 2008) and photosynthetic carbon uptake (Shirke and Pathre, 2004), differently.

We have provided examples of how EFPs can be derived from observed ecosystem fluxes to provide empirical estimates of ecosystem functional states. EFPs facilitate monitoring of seasonal to long-term changes of ecosystem functional states and allow comparisons across sites. EFPs provide the opportunity to link ecosystem functional states to information of the state of the biota, e.g., via plant traits. However, we also point out that one has to critically examine whether an EFP is indeed independent of short-term environmental fluctuations. In Table 1 we provide further examples of EFPs and from which data streams they can be derived.

In the following section we introduce in situ plant trait measurements, and describe how they can be used to derive vegetation properties at the ecosystem level (EVPs) and be directly comparable to EFPs.

Table 1
List of possible ecosystem functional properties (EFPs) that can be derived from eddy covariance fluxes, with related plant traits and stand characteristics that can be potentially used for deriving the EVPs.

Processes	Ecosystem functional properties (EFPs)	Description	Plant traits/stand characteristics
Photosynthesis	Ecosystem photosynthetic capacity ($GPP1000_{max}$)	Maximum ecosystem photosynthesis (e.g., GPP) standardized for light saturation, e.g., at light intensity of 1000 W/m2 (see Falge et al., 2001; Gilmanov et al., 2003).	Leaf photosynthetic capacity (Amax; Vc_{max}); leaf nitrogen content per leaf area or dry mass (N_{leaf}); leaf mass per area (LMA); N:P ratios LAI; Species abundance
	Potential light use efficiency (LUE_{max})	Maximum ratio between GPP and absorbed photosynthetic active radiation (APAR) at growing season (see Monteith, 1972; Kergoat et al., 2008).	A_{max}; Vc_{max}; N_{leaf}; LMA; plant height; leaf size; N:P ratios LAI; Species abundance; Canopy structure
	Nitrogen use efficiency (NUE)	Maximum GPP1000 divided by leaf nitrogen content	A_{max}; Vc_{max}; N_{leaf}, LMA; N_{plant}; wood density; N:P ratios LAI; Biomass; Species abundance
	Normalized GPP*	$GPP^{*} = GPP_{max} \frac{fPARc}{fPAR} \frac{\cos(\theta=0)}{\cos(\theta s)}$ Kergoat et al. (2008)	A_{max}; Vc_{max}; N_{leaf}; LMA; N:P ratios LAI; Biomass; Species abundance
	Carbon use efficiency (CUE)	1) Biomass production divided by GPP 2) NPP to GPP ratio (DeLucia et al., 2007). 3) 1-Rb/GPP (Mahecha et al., 2010).	A_{max}; Vc_{max}; N_{leaf}, LMA; wood density LAI; Biomass; Species abundance
Respiration	Basal ecosystem respiration (Rb): 1) Rb at day of Max GPP1000 2) Median of seasonal Rb 3) Maximum seasonal Rb	Maximum or median of ecosystem respiration (R_{eco}) at a reference temperature (15C) and at the time period of no water limitations (Lloyd and Taylor, 1994; Reichstein and Beer, 2008).	N_{leaf}; LMA; LDMC; RDMC; wood density LAI; Biomass (above and belowground)
	Sensitivity of Rb to GPP (Rb/GPP)	Slope of the relationship between Rb and GPP Mahecha et al. (2010)	N_{leaf}; LMA; LDMC; RDMC; wood density LAI; Biomass (above and belowground)
Evapotranspiration	Maximum ecosystem evapotranspiration (ET_{max})	Maximum of the seasonal ET measured	Maximum stomatal conductance (gs_{max}); sapwood area; wood density LAI; Tree diameter at breast height (DBH)
	Inherent water use efficiency (WUE_{in})	Slope of the relationship between GPP*VPD and ET Beer et al. (2009)	gs_{max}; N_{leaf}; LMA; sapwood area; Amax/gs, d13C LAI
	Intrinsic water use efficiency (WUE*i)	Seasonal GPP divided by surface conductance (Gs) GPP/Gs Beer et al. (2009)	gs_{max}; N_{leaf}; LMA; sapwood area; Amax/gs; d13C LAI
Biophysical properties	Energy use efficency	GPP_{1000}/(LE + H) at the peak of the growing season or 90th percentile GPP/(LE + H) at the peak of the growing season See also Reichstein et al. (2014)	A_{max}; Vc_{max}; N_{leaf}; LMA; N_{plant}; wood density; gs_{max} LAI; Canopy structure; Biomass
	Minimum seasonal Albedo	Albedo at the peak of the growing season Cescatti et al. (2012)	Leaf morphology (shape and size); N_{leaf} LAI

3.2. *Upscaling of in situ measured traits*

Plant traits are traditionally measured in situ and more recently also sensed remotely. In situ measurements of plant traits are performed on plant or plant organ level and need to be upscaled to the ecosystem level (EVPs) to correspond to EFPs (Fig. 4). Thus far, upscaling of plant traits to canopy or ecosystem level has been done mainly by weighting traits by abundance of species, allometry, or biomass (e.g., Garnier et al., 2004). These approaches make sense if the effects of the traits of individual plants are additive, like using the number of individuals to upscale individual biomass to community biomass (Violle et al., 2007). This strategy is also useful for upscaling plant traits such as traits based on concentration e.g., grams of nitrogen or phosphorous per leaf mass. But the functionality of traits does not always scale with the quantity (e.g., abundance) of organism. For example, while photosynthesis scales with the nitrogen content of leaves (Givnish, 1986), it also depends on the position of the leaves (or organ) in the canopy, which determines the ability of the leaf to capture light. Plant productivity per unit nutrient in the whole biomass is another example for the relevance of vegetation structure: it decreases with increasing total biomass due to shading within the canopy and allocation of nitrogen to photosynthetically inactive tissues (Kerkhoff and Enquist, 2006).

An alternative upscaling approach accounting for light absorption along the canopy employs involving LAI and plant height: assuming leaves at the top of the canopy contribute most to CO_2 assimilation as they receive most of the radiation (Field and Mooney, 1986). Therefore, a canopy strata-weighted measure is needed, as the comparatively larger contribution of species located

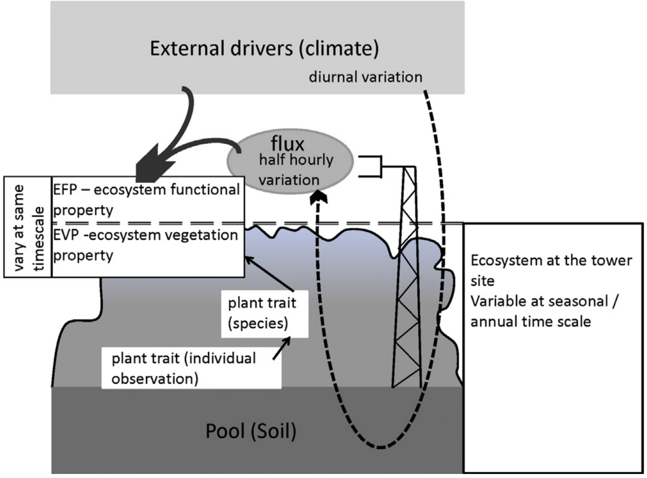

Fig. 4. Top-down and bottom up approaches to determine flux-based ecosystem functional properties (EFP) and trait-based ecosystem vegetation properties (EVPs). To link plant traits measured at the level of individual plants to EFPs, one first needs to upscale plant traits to ecosystem level.

towards the top of a canopy for carbon fixation or GPP needs to be accounted for. To include this strata-weighting when upscaling from plant to EVP, we propose to first weigh each species by its respective abundance plus the amount of radiation it receives using its relative height, thus discriminating for over/understory species. We use the Lambert–Beer law of extinction and implement the relative height (from 0 to 1) of the species:

$$W_s = A_s \times e^{k(1-H_s)} \text{for } s = 1, 2, 3, \ldots, n \qquad (1)$$

where W_s is the relative contribution (weight) of each species to the ecosystem trait, A_s is the abundance of the species, H_s is the relative height of the species, and k is the light extinction coefficient (Jones, 2014).

Given a number n of species in the ecosystem the value of the upscaled trait to ecosystem level (EVP) is computed as follow:

$$\text{EVP} = \text{LAI} \times \Sigma_{s=1}^{n} \text{Trait}_s \times W_s \qquad (2)$$

where LAI corresponds to the LAI of the ecosystem (m^2 leaf/m^2 ground) and Trait_s is the specific trait measured for a given species measured on leaf area basis. The resulting EVP will be at ecosystem scale and the unit will be per ground area. For example, by using Eqs. (1) and (2) it is possible to scale-up the nitrogen (N) content per leaf area (g/m^2) to the N concentration per ground area, the latter being the EVP, which can then be linked to the corresponding EFPs such as GPP1000 or LUE.

The advantage of this method of weighting traits by vertical structure rather by abundance is that it considers vegetation structure (i.e., plant height and LAI) and therefore incorporates the differences of plant species contributions to processes like ecosystem photosynthesis. Compared to abundance weighted means, a disadvantage of this more explicit approach is the need for additional data and that the additional parameters add more uncertainty.

Plant traits and the amount of vegetation, e.g., LAI or plant biomass, bear complementary information to explain ecosystem functioning (Fig. 3). As such, RS data of vegetation have the potential to benefit the framework. For example Reich (2012) showed that aboveground net primary production was well explained by LAI (which can increasingly be retrieved from RS, although it was not in that study) together with canopy N concentration (N%) derived from in situ measured leaf nitrogen concentration and species abundance. This approach preserves the structural and physiological differences of individual organisms or species within the ecosystem, and facilitates an analysis of the biodiversity imprint on ecosystem function.

While there is considerable intraspecific variation of plant traits, across large geographic scales, most of the trait variations are observed between species (Kattge et al., 2011; Violle et al., 2012; Albert, 2015). Therefore one outstanding question is whether data available from large integrated databases such as TRY can be used to characterize the trait of plant species occurring at specific sites (e.g., FLUXNET sites). To address this question, here we compare leaf nitrogen content per dry mass (N%) reported in the FLUXNET ancillary database for each site with N% derived from the TRY database (Fig. 5, Supplementary 1). The N% from the two different sources is highly correlated ($r = 0.72$) and follows a 1:1 relationship. This result is in agreement with growing evidence from independent results of similar studies (e.g., Cordlandwehr et al., 2013; Kazakou et al., 2014). This is encouraging, as it makes it possible to use general plant trait databases for a first inspection on trait influences on EFPs.

We furthermore tested if the correlation between an EFP derived from ecosystem fluxes and an EVP obtained by using information from TRY is similar to the one derived from traits measured at the sites. To this end, we provide an example correlating optimum daily LUE and canopy normalized GPP (reported as gross ecosystem exchange, GEE in Kergoat et al., 2008, see Table 1) with canopy N%. LUE and canopy normalized GPP are derived from eddy covariance fluxes from FLUXNET sites, including different PFTs. First we collected species composition and abundance at these sites from FLUXNET ancillary database and compared it with information from the literature (Supplementary 1). Then, for every species at the site, species-averaged N% was derived from TRY. Then canopy N% was estimated by abundance weighted mean of N% at each site. Canopy N% as the EVPs of the sites were then compared to the two EFPs (LUE and canopy normalized GPP). The results reported in Fig. 6 for LUE and canopy normalized GPP are comparable to the ones reported in Kergoat et al. (2008), indicating that is possible to use the species-averaged information reported in TRY to predict EFPs derived from specific sites. The results of Fig. 6 are even stronger considering that no filters based on climate or environmental conditions were applied to derive the average N% for each species. From Figs. 5 and 6, we conclude that strong patterns of plants' imprint on ecosystem function are likely similarly represented when using trait data from global databases.

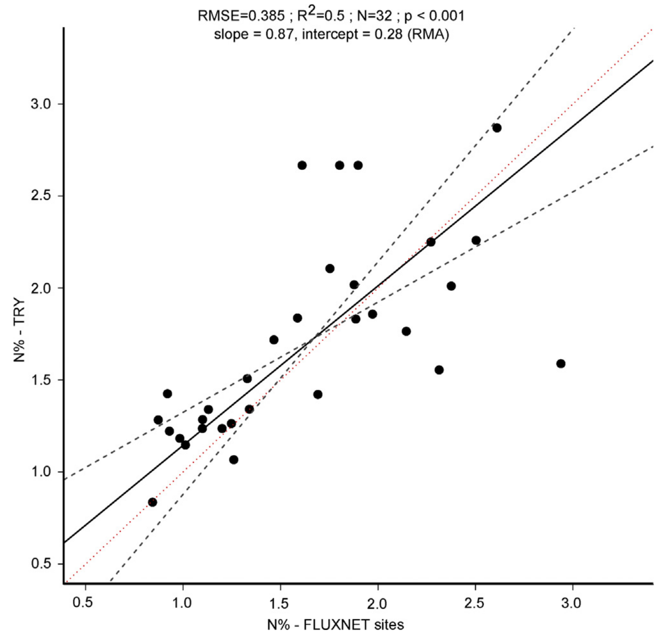

Fig. 5. Comparison of leaf nitrogen content per leaf dry mass (N%) reported in the FLUXNET ancillary database (N% – FLUXNET sites) and up-scaled using species mean trait values from the TRY database and species abundance from the FLUXNET ancillary database (N% – TRY). In case of more than one value reported in the FLUXNET ancillary database, we used the average N%. N% – TRY is based on species averaged values from the TRY database that were used for species at the sites. This values are then weighted by the abundance of the species (Table 1 in Supplementary). Slope and intercept were estimated by a reduced major axis (RMA) regression ($R = 0.72$).

3.3. *Spatial extrapolation of in situ measured traits*

Upscaling plant traits to continental or global scale will provide the possibility to study them directly in relation to remote sensed EFPs (see Section 4) available on global scales and EFPs derived from fluxes that are upscaled to global maps (Jung et al., 2011). One option to upscale plant traits measured in situ to global scales is to link the trait data with species distribution maps. One application of this approach produced trait maps across North and South America (Swenson et al., 2012). However, this technique faces two major issues: the heavily reliance on high quality species distribution data, which is not available for most of the world, and the issues related to species distribution models (SDM). For

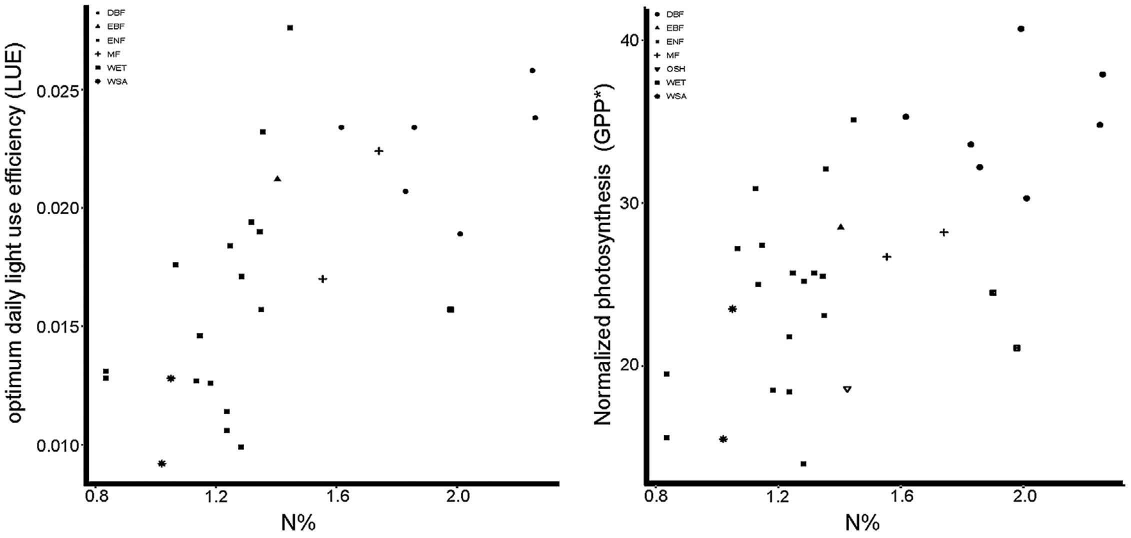

Fig. 6. Optimum daily light-use-efficiency (LUE, mol/mol) and canopy normalized photosynthesis (GPP*, μmols^{-1} m^{-2}) versus leaf nitrogen content per dry mass (N, %). LUE and GPP* are reported by Kergoat et al. (2008) for a range of eddy covariance sites with different dominant plant functional types (see labels). Leaf nitrogen content (N) is based on abundance weighted species mean trait values from the TRY database and species abundance from the FLUXNET ancillary database. The variance explained by N% are $R^2 = 0.41$ ($n = 28$, $p < 0.001$, intercept = 0.005 ± 0.003, slope = 0.01 ± 0.002) and $R^2 = 0.38$ ($n = 32$, $p < 0.001$, intercept = 10.3 ± 3.7, slope = 11.1 ± 2.5) for LUE and GPP*, respectively.

example, Henderson et al. (2014) tested the effect of using single species or multivariate modeling approaches on species distributions and found that the multivariate approach outperformed the single species approach by a large margin. The second issue is the assumption that species distributions are, on the one hand, in equilibrium with the environment of the respective organisms and that the traits, which are linked with species distribution data, on the other hand, reflect the whole of the species' trait spectrum. Trait values are known to be highly variable depending on the environmental conditions (Niinemets et al., 2015) with e.g., “tree-like” plant species reaching a much higher maximal height in warm, moist climates, than in cold and dry climates where they get a more “shrub-like” appearance with associated traits. However, as we have shown above, across PFTs and across large environmental gradients, the impact of intra-specific trait variability seems to be dominated by species turnover (Fig. 5, Cordlandwehr et al., 2013; Kazakou et al., 2014).

Another approach to avoid the use of species distribution data is to take advantage of the correlation between traits and environmental conditions and take the direct way. This is illustrated by van Bodegom et al. (2014) who produced global maps of some key traits using trait–environment relationships derived from linking climate and soil variables with community weighted mean trait values.

If a sufficient amount of in situ measured trait data is available, a third approach would be using interpolation techniques, for example Kriging or Gaussian process regression – an interpolation technique where Gaussian processes are taking into account prior covariance (e.g., trait–environment relationships) to model interpolated values. So far, this technique has been mainly applied in geosciences but rarely within macroecology (but see Hernandez-Stefanoni and Ponce-Hernandez, 2006; Henderson et al., 2014 for some examples).

4. Remote sensing of plant traits and EFPs

As discussed in Section 3 RS observations provide information about vegetation structural components, like LAI or vegetation biomass. In addition, RS observations in the visible to near-infrared region of the electromagnetic spectrum have great utility to gather information about plant traits at the ecosystem level – EVP (Homolová et al., 2013), plant physiological conditions, and in some cases direct information on functional aspects of the ecosystem (Hilker et al., 2008), i.e., on EFPs. The possibilities offered by new remote sensing techniques allowed several authors to develop new concept of optically distinguishable PFTs (“optical type” according to Ustin and Gamon (2010)) and to directly estimate EVPs beyond the concept of PFTs. Moreover, remote sensing could be a way to address the scaling approach to derive EVPs or better integrate in situ plant traits measurements (Asner et al., 2015). This would allow a more direct link between EFPs and EVP derived from remote sensing information (e.g., Ustin and Gamon, 2010). This information can be obtained at different spatial and temporal scales by using satellite products, airborne platforms with hyperspectral sensors, or by measuring them in the proximity of the surface (usually referred to as near-surface RS or proximal sensing) (Ustin et al., 2004; Gamon et al., 2006; Balzarolo et al., 2011). To explore the possibility of linking traits scaled at the ecosystem level to eddy covariance flux data and eventually EFPs, near surface RS and airborne hyperspectral data are most suited. In the Table 2 we list some literature examples of how plant traits, vegetation structural properties, and EFPs relevant for the proposed framework have been successfully retrieved.

Retrieval of plant traits from RS is well reported in the literature (for a review see Homolová et al., 2013). Yet obtaining plant traits time series or maps usable to predict EFPs from RS data is not straightforward. Plant traits and canopy properties that can be derived from RS data are mainly those that describe a relationship and interaction between absorbed/reflected light and vegetation structure/function (Roelofsen et al., 2014), i.e., structural traits affecting light scattering (e.g., Ustin, 2013). For instance, variations in foliar photosynthetic pigments affect mainly the spectrum in the visible region (400–700 nm), variations in leaf structure affect the near infrared region (700–1300 nm), while variations in water content and protein content (as well as other nutrients such as P) affect the shortwave infrared region (1300–2500 nm) (e.g., Mutangao and Kumar, 2007; Ramoelo et al., 2013). Therefore, the typology of plant traits and EVPs that can be retrieved via RS depends primarily on the spectral characteristics and resolution of the sensors.

One of the main criticisms in the use of RS information for the proposed approach is that scaling RS information from leaf

Table 2
List of plant traits, canopy structure, and EFPs that can be retrieved from RS at leaf and canopy ecosystem scale. Methods of estimation and associated references are also reported.

		Scale			
		Leaf		Canopy/Ecosystem	
		Method	Reference	Method	Reference
Plant traits	SLA or LMA	Inversion RTM	(Colombo et al., 2008; Asner et al., 2011)	Inversion RTM	(Asner et al., 2011)
	Vc_{max}	Inversion RTM	(Hobourg et al., 2013)	Combination RTM and SIF data;	(Zhang et al., 2014)
				Inversion RTM;	(Hobourg et al., 2013)
	N_{leaf}	Empirical regressions	(Martin et al., 2008; Ollinger et al., 2008)	Empirical regressions	(Martin et al., 2008; Ollinger et al., 2008; Fava et al., 2009)
		Inversion RTM and relationship with Chl a and b	(e.g., Zarco-Tejada et al., 2004)	Inversion RTM and relationship with Chl a and b	(e.g., Zarco-Tejada et al., 2004)
	Pigment Content (e.g., Chlorophyll a and b)	Inversion Radiative Transfer Model	(Houborg and Boegh, 2008)	Inversion radiative transfer model	(Hobourg and Boegh, 2008)
		Empirical models	(Gitelson, 2011)	Empirical models	(Hunt et al., 2013)
	Gs_{max}			Empirical models and infrared thermography	(Jones et al., 2002)
	Leaf dry matter (LDM)	Empirical methods	(Kokaly et al., 2009)	Empirical methods	(Kokaly et al., 2009)
Vegetation structural properties	LAI			Empirical Models	(Wardley and Curran, 1984; Zhang et al., 2014)
				Inversion RTM	(Meroni et al., 2004; Pinty et al., 2011)
	Canopy Height			LiDAR	(Kaartinen et al., 2012)
	Biomass			LiDAR and RADAR	(Tsui et al., 2013)
EFP	$Reco_{Tref}$			Empirical modeling (optical remote sensing and land surface temperature)	(Jägermeyr et al., 2014)
	LUE			Hyperspectral remote sensing	(Hilker et al., 2008; Garbulsky et al., 2014)
				SIF	(Porcar-Castel et al., 2014)
	Albedo			RTM	(Román et al., 2009; Cescatti et al., 2012)

to ecosystem level and vice versa is still challenging (Malenovský et al., 2013). At the leaf level, a variety of RS techniques and sensors has been largely applied to monitor key plant traits such as leaf chlorophyll a and b content (Gitelson et al., 2005; Dash and Curran, 2007; Houborg and Boegh, 2008), relative extractable water content in leaves (Colombo et al., 2008) and nutrient concentrations, in particular foliar nitrogen content (e.g., Zarco-Tejada et al., 2004). But at the ecosystem level, there are several confounding factors in addition to uncertainties related to the sensors used (e.g., spectral resolution). Several confounding factors that influence the upscaled results of the leaf level reflectance include: contamination of the signal by aerosols and clouds (in particular for airborne and satellite data), and the canopy structure and soil which affects accuracy of the retrieval of traits (e.g., le Maire et al., 2008; Knyazikhin et al., 2012). Thus, a key challenge is the separation of the leaf contribution associated with changes in plant traits (or a correlated variable) from those by canopy structure (Houborg et al. 2013). The main techniques currently used to upscale and downscale RS information from the leaf to the ecosystem level are physically based radiative transfer models, spectral mixing and unmixing techniques, and data fusion (Malenovský et al., 2007).

Radiative transfer models based on coupled leaf optics and canopy reflectance models are often used in inverse mode to estimate plant traits and canopy biochemistry (e.g., pigments, foliar N content) at ecosystem level from the reflectance observed with spectrometers or airborne/satellite platforms (Baret and Buis, 2008; Jacquemoud et al., 2009; Knyazikhin et al., 2012; Ustin, 2013). One typical example is the estimation of chlorophyll a and b, done by inverting leaf optical properties model (e.g., Jacquemoud and Baret, 1990) coupled with canopy directional reflectance models while accounting for canopy structure (e.g. the Scattering by Arbitrary Inclined Leaves model, SAILH). Despite their potential, the estimation of traits from radiative transfer models is not trivial, as it requires a heavy parameterization of the canopy structure characteristics. Moreover, the inverse problem is often ill-posed or prone to equifinality (e.g., Combal et al. 2003), hampering the correct estimation of the parameters (e.g., plant traits).

Empirical methods are also often used instead of radiative transfer models. These methods rely on the parameterization of a regression model between in situ plant traits observations and (1) reflectance in a portion of the electromagnetic spectrum sensitive to variations of the targeted trait, or (2) an arithmetic combination of different portions of the spectrum (i.e., vegetation indices) (e.g., Colombo et al., 2008; Chen et al., 2010). Empirical models can be built directly for canopy scale, or at the leaf level and upscaled to the canopy level. However, these methods are quite often site-specific and sampling condition dependent, sensor-specific (in particular dependent on the spectral resolution), might change in space and time, and the retrieval of leaf canopy traits is often hampered by the difficulty in decoupling the contributions of the targeted trait and LAI (e.g., Gobron et al. 1997; Colombo et al., 2008). Moreover, empirical methods have demonstrated to have less predictive power in many cases compared to radiative transfer and physically based models (Malenovský et al., 2013).

Many plant traits have been successfully estimated using RS data, such as canopy and leaf N%, and chlorophyll a and b content.

Yet the estimation of some relevant key traits is still problematic. For instance, White et al. (2000) emphasize that leaf mass per leaf area (LMA, the inverse of SLA) is one of the key parameters to accurately simulate the temporal variability of GPP and NPP with terrestrial biosphere models. However, the estimation of LMA from RS is far from precise. Homolová et al. (2013) reviewed the literature and reported an average relative RMSE of 45.0% (1sd 30.0%) for the LMA retrieval, regardless of the method used for the estimation. One of the main problems is that LMA estimations are sensitive to variations in the portion of the spectrum that is also affected by water absorption which can act as a confounding factor (e.g., Asner et al., 2011).

RS applications to estimate EFPs directly have not yet been fully explored. Albedo is one of the key EFPs (Table 1), and its variability in time and space can be globally retrieved through the use of near-surface and RS products. Nevertheless, current approaches for measuring in situ albedo are not adequate to describe mixed or highly heterogeneous landscapes such as mixed forests, open shrublands, savannas, and croplands (Cescatti et al., 2012). Also EFPs related to photosynthesis (e.g., LUE, Table 1) might be inferred by RS measurements such as sun-induced chlorophyll fluorescence (SIF, Porcar-Castell et al., 2014) and photochemical reflectance index (PRI) (Gamon et al., 1992), which have proven to be valuable methods for the direct assessment of plant photosynthesis, from the ecosystem scale (Meroni et al., 2009; Damm et al., 2010) to regional and global scale (e.g., Guanter et al., 2014). These measurements can in principle be used to directly estimate ecosystem LUE (Garbulsky et al., 2014), ecosystem maximum carboxylation rate (V_{cmax}) via empirical relationships (Houborg et al., 2013), or by inverting radiative transfer models simulating SIF, such as Soil Canopy Observation Photosynthesis Energy balance model – SCOPE (e.g., van der Tol et al. 2009; Zhang et al., 2014). Nevertheless, the estimation of these EFPs from time series of SIF or PRI is not a trivial task given the series of confounding factors that affect the signal at canopy and ecosystem scale, in particular the algorithm retrieval for SIF (e.g., Meroni et al., 2009), variation of LAI and directional effects (e.g., Garbulsky et al., 2014), and also the mechanistic understanding of the link between SIF and photosynthesis at the seasonal scale (Porcar-Castell et al., 2014). Still, it seems promising to infer direct information on parameters related to EFPs using RS.

5. Conclusions

We propose a pathway to empirically analyze the intrinsic biotic controls of terrestrial ecosystem functioning based on the conceptualization of ecosystem functional properties (EFPs) as indicators of ecosystem functional state. Since the variability of EFPs can only partly be explained by environmental drivers, we expect that biotic controls, represented by plant abundance and traits, measured in situ or via RS (ecosystem vegetation properties, EVPs) will explain an additional important component of the variation in ecosystem functioning. We provide examples how EFPs and biotic correspondents (here EVPs) can be derived from ecosystem fluxes, RS, and plant traits considering information on canopy structure. However, further work is necessary to test how to best derive EFPs, link these to EVPs, and assess the uncertainties associated to the different methods. We anticipate our framework will encourage the combination of ecosystem flux studies with EFPs, RS, and in situ observed plant traits (as EVPs), with the final goal to increase our understanding of how environmental drivers shape ecosystems and vice versa. The outcome of such empirical studies will complement complex predictive terrestrial biosphere models and help to better predict long term trajectories of ecosystem functioning and ecosystem services under climate change.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jag.2015.05.009

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The imprint of plants on ecosystem functioning: a data-driven approach - Supplementary information

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Species abundance at FLUXNET sites used to upscale leaf nitrogen concentration to canopy level (N%):

Leaf nitrogen concentration of the canopy (N%, Fig. 5 and Fig. 6) was calculated as community weighted mean (CWM), using species mean trait values from the TRY database. Site-specific species abundance information (Table A) was derived from the FLUXNET ancillary database, complemented by various literature sources. In case of many sites the abundance of overstory and understory species was reported separately (each adding to 100 percent). In these cases we used the information provided in Table B to assess the relative fraction of over and understory foliage for different Plant Functional Types (PFTs), e.g. for an evergreen needle leaf forest (ENF) we assume that 85% of the abundance is overstory and 15% understory. If no information on the position of the species in the canopy (over/under story) was provided in the FLUXNET ancillary database or literature we used the growth form of the species to assign them to the different stories (e.g. trees in a forest ecosystem are defined overstory).

Table A: Species relative abundance at FLUXNET sites. Species relative abundance is reported as ‘modified abundance’, because it is based on several sources. If no reference is provided, data have been taken from the FLUXNET ancillary database. Note that relative abundances do not need to add to 100, because only the relative contribution of a species is relevant to calculate the community weighted mean leaf nitrogen concentration.

Site ID	Species names	Story	modified abundance	PFT	Literature used for Species and abundance
AU-Tum	Eucalyptus delegatensis	over	50	EBF	-
AU-Tum	Eucalyptus dalrympleana	over	50	EBF	-
BE-Bra	Quercus rubra	over	6	MF	De Pury & Ceulemans 1997
BE-Bra	Picea abies	over	1.52	MF	De Pury & Ceulemans 1997
BE-Bra	Pinus nigra	over	13.84	MF	De Pury & Ceulemans 1997
BE-Bra	Prunus spinosa	under	0.5	MF	De Pury & Ceulemans 1997
BE-Bra	Pinus sylvestris	over	13.84	MF	De Pury & Ceulemans 1997
BE-Bra	Quercus robur	over	6	MF	De Pury & Ceulemans 1997
BE-Bra	Picea excelsa	over	1.52	MF	De Pury & Ceulemans 1997
BE-Bra	Populus tremuloides	over	2.16	MF	De Pury & Ceulemans 1997
BE-Bra	Betula pendula	over	0.64	MF	De Pury & Ceulemans 1997
BE-Bra	Fagus sylvestris	over	1.28	MF	De Pury & Ceulemans 1997
BE-Bra	Larix decidua	over	3.6	MF	De Pury & Ceulemans 1997
BE-Bra	Pseudotsuga menziesii	over	0.64	MF	-
BE-Bra	Rhododendron	under	1.66	MF	-
BE-Bra	Sorbus	under	1.16	MF	-
BE-Bra	Pinus nigra	under	0.08	MF	-
BE-Bra	Pinus sylvestris	under	0.08	MF	-
BE-Bra	Betula pendula	under	0.12	MF	-
BE-Bra	Populus tremuloides	under	0.06	MF	-
BE-Bra	Picea excelsa	under	0.02	MF	-
BE-Bra	Picea abies	under	0.02	MF	-
BE-Vie	Pseudotsuga menziesii	over	50	MF	-
BE-Vie	Fagus sylvatica	over	50	MF	-

CA-Gro	Thuja occidentalis	over	12.3	MF	Pejam et al. 2006
CA-Gro	Abies balsamea	over	9.15	MF	Pejam et al. 2006
CA-Gro	Betula papyrifera	over	31.49	MF	Pejam et al. 2006
CA-Gro	Picea mariana	over	12.3	MF	Pejam et al. 2006
CA-Gro	Picea glauca	over	10.48	MF	Pejam et al. 2006
CA-Gro	Populus tremuloides	over	24.28	MF	Pejam et al. 2006
CA-Man	Picea mariana	over	100	ENF	-
CA-Mer	Chamaedaphne calyculata	over	12.5	OSH	Lafleur et al. 2003
CA-Mer	Kalmia angustifolia	over	12.5	OSH	Lafleur et al. 2003
CA-Mer	Ledum groenlandicum	over	12.5	OSH	Lafleur et al. 2003
CA-Mer	Vaccinium myrtilloides	over	12.5	OSH	Lafleur et al. 2003
CA-Mer	Eriophorum vaginatum	under	12.5	OSH	Lafleur et al. 2003
CA-Mer	Sphagnum capillifolium	under	12.5	OSH	Lafleur et al. 2003
CA-Mer	Sphagnum fuscum	under	12.5	OSH	Lafleur et al. 2003
CA-Mer	Sphagnum magellanicum	under	12.5	OSH	Lafleur et al. 2003
CA-Oas	Corylus cornuta	under	20	DBF	Black et al. 2000
CA-Oas	Populus tremuloides	over	72	DBF	Black et al. 2000
CA-Oas	Populus balsamifera	over	8	DBF	Black et al. 2000
CA-Obs	Picea mariana	over	100	ENF	-
CA-Ojp	Pinus banksiana	over	85	ENF	-
CA-Ojp	Cladonia mitis	under	15	ENF	-
CA-SJ3	Cladina mitis	under	15	ENF	-
CA-SJ3	Pinus banksiana	over	85	ENF	-
CA-TP2	Quercus velutina	over	1	ENF	-
CA-TP2	Pinus resinosa	over	2	ENF	-
CA-TP2	Pinus strobus	over	97	ENF	-
CA-TP3	Quercus velutina	over	1	ENF	-
CA-TP3	Pinus strobus	over	94	ENF	-
CA-TP3	Pinus banksiana	over	5	ENF	-
CN-Do1	Phragmites australis	under	25.4	WET	Yan et al. 2008
CN-Do1	Spartina alterniflora	under	71.5	WET	Yan et al. 2008

CN-Do2	Spartina alterniflora	under	54.6	WET	Yan et al. 2008
CN-Do2	Phragmites australis	under	37.8	WET	Yan et al. 2008
CN-Do3	Scirpus mariqueter	under	6.8	WET	Yan et al. 2008
CN-Do3	Phragmites australis	under	14.7	WET	Yan et al. 2008
CN-Do3	Spartina alterniflora	under	48.4	WET	Yan et al. 2008
CN-Do3	Schoenoplectus maritimus	under	33	WET	-
CN-HaM	Kobresia tibetica	under	16.66	GRA	Kato et al. 2006, Kato et al. 2004
CN-HaM	Kobresia humilis	under	16.66	GRA	Kato et al. 2006, Kato et al. 2004, Fu et al. 2006
CN-HaM	Kobresia pygmaea	under	16.66	GRA	Kato et al. 2006, Kato et al. 2004
CN-HaM	Potentilla fruticosa	under	16.66	GRA	Kato et al. 2004, Fu et al. 2006
CN-HaM	Poa annua	under	16.66	GRA	Fu et al. 2006
CN-HaM	Festuca rubra	under	16.66	GRA	Fu et al. 2006
DE-Bay	Calamagrostis villosa	under	6.66	ENF	Staudt & Foken 2007
DE-Bay	Vaccinium myrtillus	under	6.66	ENF	Staudt & Foken 2007
DE-Bay	Oxalis acetosella	under	6.66	ENF	Staudt & Foken 2007
DE-Bay	Deschampsia flexuosa	under	6.66	ENF	Staudt & Foken 2007
DE-Bay	Dicranum scoparium	under	6.66	ENF	Staudt & Foken 2007
DE-Bay	Dryopteris dilatata	under	6.66	ENF	Staudt & Foken 2007
DE-Bay	Picea abies	over	60	ENF	Staudt & Foken 2007
DE-Tha	Pinus sylvestris	under	5.6	ENF	Bernhofer et al. 2003
DE-Tha	Betula	under	5.6	ENF	-
DE-Tha	Larix decidua	under	5.6	ENF	Bernhofer et al. 2003
DE-Tha	Deschampsia flexuosa	under	5.6	ENF	-
DE-Tha	Picea abies	over	72	ENF	Bernhofer et al. 2003
DE-Tha	Fagus sylvatica	under	5.6	ENF	Bernhofer et al. 2003
DK-Sor	Larix decidua	over	10	DBF	Pilegaard et al. 2001
DK-Sor	Picea abies	over	10	DBF	Pilegaard et al. 2001
DK-Sor	Mercurialis perennis	under	10	DBF	Pilegaard et al. 2001
DK-Sor	Anemone nemorosa	under	10	DBF	Pilegaard et al. 2001
DK-Sor	Fagus Sylvatica	over	60	DBF	Pilegaard et al. 2001
FI-Hyy	Vaccinium vitis-idaea	under	7.5	ENF	-

FI-Hyy	Betula pendula	over	3.5	ENF	-
FI-Hyy	Vaccinium myrtillus	under	7.5	ENF	-
FI-Hyy	Pinus sylvestris	over	75	ENF	-
FI-Hyy	Juniperus communis	over	1	ENF	-
FI-Hyy	Picea abies	over	7	ENF	-
FI-Kaa	Betula nana	over	5.71	WET	Aurela et al. 2002
FI-Kaa	Ledum palustre	over	5.71	WET	Aurela et al. 2002
FI-Kaa	Empetrum nigrum	under	5.71	WET	Aurela et al. 2002
FI-Kaa	Carex	under	60	WET	Aurela et al. 2002
FI-Kaa	Vaccinium uliginosum	under	5.71	WET	Aurela et al. 2002
FI-Kaa	Rubus chamaemorus	under	5.71	WET	Aurela et al. 2002
FI-Kaa	Vaccinium vitis-idaea	under	5.71	WET	Aurela et al. 2002
FI-Kaa	Salix	under	5.71	WET	Aurela et al. 2002
FR-Hes	Betula pendula	over	1.66	DBF	Granier et al. 2000
FR-Hes	Fagus sylvatica	over	90	DBF	Granier et al. 2000
FR-Hes	Carpinus betulus	over	1.66	DBF	Granier et al. 2000
FR-Hes	Quercus petraea	over	1.66	DBF	Granier et al. 2000
FR-Hes	Larix decidua	over	1.66	DBF	Granier et al. 2000
FR-Hes	Prunus avium	over	1.66	DBF	Granier et al. 2000
FR-Hes	Fraxinus excelsior	over	1.66	DBF	Granier et al. 2000
FR-LBr	Molinia caerulea	under	15	ENF	-
FR-LBr	Pinus pinaster	over	85	ENF	-
IT-Col	Fagus sylvatica	over	100	DBF	Valentini et al. 1996
IT-Cpz	Quercus ilex	over	80	EBF	Tirone et al. 2003
IT-Cpz	Phillyrea latifolia	under	2.22	EBF	Tirone et al. 2003
IT-Cpz	Pistacia lentiscus	under	2.22	EBF	Tirone et al. 2003
IT-Cpz	Erica arborea	under	2.22	EBF	Tirone et al. 2003
IT-Cpz	Cistus salvifolius	under	2.22	EBF	Tirone et al. 2003
IT-Cpz	Cistus incanus	under	2.22	EBF	Tirone et al. 2003
IT-Cpz	Clematis flammula	under	2.22	EBF	Tirone et al. 2003
IT-Cpz	Hedera helix	under	2.22	EBF	Tirone et al. 2003

IT-Cpz	Hedera helix	under	2.22	EBF	Tirone et al. 2003
IT-Cpz	Hedera helix	under	2.22	EBF	Tirone et al. 2003
IT-Ren	Picea abies	over	85	ENF	Cescatti and Marcolla 2004
IT-Ren	Pinus cembra	under	12	ENF	Cescatti and Marcolla 2004
IT-Ren	Larix decidua	over	3	ENF	Cescatti and Marcolla 2004
NL-Loo	Pseudotsuga menziesii	over	3	ENF	-
NL-Loo	Pinus sylvestris	over	89	ENF	-
NL-Loo	Quercus robur	over	1	ENF	-
NL-Loo	Betula pendula	over	4	ENF	-
RU-Fyo	Picea abies	over	86	ENF	Kurbatova et al. 2008
RU-Fyo	Betula pendula	over	14	ENF	Kurbatova et al. 2008
SE-Fla	Picea abies	over	83	ENF	http://www.ncoe-defrost.org/Flakaliden
SE-Fla	Pinus sylvestris	over	17	ENF	http://www.ncoe-defrost.org/Flakaliden
SE-Nor	Pinus sylvestris	over	65	ENF	Lagergren et al. 2008
SE-Nor	Vaccinium myrtillus	over	1	ENF	-
SE-Nor	Betula alba	over	1	ENF	-
SE-Nor	Picea abies	over	33	ENF	Lagergren et al. 2008
UK-Gri	Picea sitchensis	over	100	ENF	-
US-Bar	Fraxinus americana	over	6	DBF	-
US-Bar	Tsuga canadensis	over	15	DBF	Jenkins et al. 2007, http://www.fs.fed.us/ne/durham/4155/bartlett.htm
US-Bar	Populus grandidentata	over	6	DBF	-
US-Bar	Betula alleghaniensis	over	15	DBF	Jenkins et al. 2007, http://www.fs.fed.us/ne/durham/4155/bartlett.htm
US-Bar	Picea rubens	over	8	DBF	Jenkins et al. 2007, http://www.fs.fed.us/ne/durham/4155/bartlett.htm
US-Bar	Betula papyrifera	over	10	DBF	Jenkins et al. 2007, http://www.fs.fed.us/ne/durham/4155/bartlett.htm
US-Bar	Acer saccharum	over	15	DBF	Jenkins et al. 2007, http://www.fs.fed.us/ne/durham/4155/bartlett.htm
US-Bar	Acer rubrum	over	10	DBF	Jenkins et al. 2007, http://www.fs.fed.us/ne/durham/4155/bartlett.htm
US-Bar	Fagus grandifolia	over	15	DBF	Jenkins et al. 2007, http://www.fs.fed.us/ne/durham/4155/bartlett.htm
US-Blo	Pinus ponderosa	over	100	ENF	-
US-Brw	Arctophila fulva	under	33.33	WET	-
US-Brw	Dupontia fischeri	under	33.33	WET	-
US-Brw	Carex aquatilis	under	33.33	WET	-

US-Dk3	Ulmus alata	over	3	ENF	-
US-Dk3	Liquidambar styraciflua	over	3	ENF	-
US-Dk3	Pinus taeda	over	85	ENF	-
US-Dk3	Cornus florida	over	3	ENF	-
US-Dk3	Quercus alba	over	3	ENF	-
US-Dk3	Acer rubrum	over	3	ENF	-
US-Ha1	Betula alleghaniensis	over	13	DBF	-
US-Ha1	Hamamelis virginiana	over	12	DBF	-
US-Ha1	Acer rubrum	over	38	DBF	-
US-Ha1	Quercus rubra	over	21	DBF	-
US-Ha1	Acer pensylvanicum	over	11	DBF	-
US-Ha1	Tsuga canadensis	over	13	DBF	-
US-Ho1	Picea rubens	over	41	ENF	Hollinger et al. 2004
US-Ho1	Tsuga canadensis	over	25	ENF	Hollinger et al. 2004
US-Ho1	Abies balsamea	over	6.8	ENF	Hollinger et al. 2004
US-Ho1	Pinus strobus	over	6.8	ENF	Hollinger et al. 2004
US-Ho1	Thuja occidentalis	over	6.8	ENF	Hollinger et al. 2004
US-Ho1	Acer rubrum	over	6.8	ENF	Hollinger et al. 2004
US-Ho1	Betula papyrifera	over	6.8	ENF	Hollinger et al. 2004
US-Me2	Pinus ponderosa	over	85	ENF	-
US-Me2	Arctostaphylos patula	under	7.5	ENF	-
US-Me2	Purshia tridentata	under	7.5	ENF	-
US-Me4	Pteridium aquilinum	under	5	ENF	-
US-Me4	Fragaria vesca	under	2	ENF	-
US-Me4	Pinus ponderosa	over	85	ENF	-
US-Me4	Purshia tridentata	under	8	ENF	-
US-MMS	Acer saccharum	over	27	DBF	Schmid et al. 2000
US-MMS	Sassafras albidum	over	9.5	DBF	Schmid et al. 2000
US-MMS	Liriodendron tulipifera	over	19	DBF	Schmid et al. 2000
US-MMS	Quercus alba	over	9	DBF	Schmid et al. 2000
US-MMS	Quercus nigra	over	8.5	DBF	Schmid et al. 2000

US-MOz	Acer barbatum	over	12	DBF	-
US-MOz	Acer barbatum	under	5	DBF	-
US-MOz	Quercus velutina	under	1	DBF	-
US-MOz	Quercus velutina	over	5	DBF	-
US-MOz	Quercus muehlenbergii	over	9	DBF	-
US-MOz	Fraxinus americana	under	3	DBF	-
US-MOz	Juniperus virginiana	under	2.5	DBF	-
US-MOz	Juniperus virginiana	over	12	DBF	-
US-MOz	Ostrya virginiana	under	2.5	DBF	-
US-MOz	Carya ovata	over	8	DBF	-
US-MOz	Quercus alba	over	20	DBF	-
US-NR1	Picea engelmannii	over	28	ENF	-
US-NR1	Pinus contorta	over	26	ENF	-
US-NR1	Abies lasiocarpa	over	46	ENF	-
US-PFa	Abies balsamea	over	7.638	MF	Kenneth et al. 2003
US-PFa	Acer rubrum	over	1.553	MF	Kenneth et al. 2003
US-PFa	Acer saccharum	over	20.06	MF	Kenneth et al. 2003
US-PFa	Betula alleghaniensis	over	1.425	MF	Kenneth et al. 2003
US-PFa	Betula papyrifera	over	4.739	MF	Kenneth et al. 2003
US-PFa	Pinus resinosa	over	12.987	MF	Kenneth et al. 2003
US-PFa	Populus grandidentata	over	0.813	MF	Kenneth et al. 2003
US-PFa	Populus tremuloides	over	17.377	MF	Kenneth et al. 2003
US-PFa	Picea glauca	over	5.676	MF	Kenneth et al. 2003
US-PFa	Tilia americana	over	6.243	MF	Kenneth et al. 2003
US-SO2	Adenostoma sparsifolium	over	10	WSA	-
US-SO2	Adenostoma fasciculatum	over	90	WSA	-
US-SO3	Adenostoma fasciculatum	over	85	WSA	-
US-SO3	Adenostoma sparsifolium	over	5	WSA	-
US-SO3	Ceanothus greggii	over	10	WSA	-
US-UMB	Acer rubrum	over	21	DBF	-
US-UMB	Fagus grandifolia	under	3.2	DBF	-

US-UMB	Pinus strobus	over	3.2	DBF	-
US-UMB	Amelanchier	under	3.2	DBF	-
US-UMB	Betula papyrifera	over	3.2	DBF	-
US-UMB	Quercus rubra	over	28	DBF	-
US-UMB	Populus grandidentata	over	35	DBF	-
US-UMB	Populus tremuloides	over	3.2	DBF	-
US-WBW	Carya ovata	over	18	DBF	Verma et al. 1986
US-WBW	Acer rubrum	over	18	DBF	Baldocchi et al. 2003
US-WBW	Quercus prinus	over	18	DBF	Verma et al. 1986, Baldocchi et al. 2003
US-WBW	Quercus alba	over	18	DBF	Verma et al. 1986, Baldocchi et al. 2003
US-WBW	Liriodendron tulipifera	over	5	DBF	-
US-WBW	Pinus taeda	over	5	DBF	-
US-WBW	Acer saccharum	over	18	DBF	Baldocchi et al. 2003
US-WCr	Dirca palustris	over	4	DBF	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=101
US-WCr	Tilia americana	over	21	DBF	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=101
US-WCr	Adiantum pedatum	over	4	DBF	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=102
US-WCr	Betula alleghaniensis	over	4	DBF	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=103
US-WCr	Pteridium aquilinum	over	4	DBF	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=104
US-WCr	Caulophyllum thalictroides	over	4	DBF	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=105
US-WCr	Fraxinus pennsylvanica	over	3	DBF	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=106
US-WCr	Acer saccharum	over	56	DBF	http://ameriflux.ornl.gov/fullsiteinfo.php?sid=107
FR-Lq1	Agropiron repens	under	8	GRA	-
FR-Lq1	Heracleum strandilium	under	8	GRA	-
FR-Lq1	Crocus	under	8	GRA	-
FR-Lq1	Melandrium rubrum	under	8	GRA	-
FR-Lq1	Cerastium	under	8	GRA	-

FR-Lq1	Holcus lanatus	under	8	GRA	-
FR-Lq1	Heracleum sphondylium	under	8	GRA	-
FR-Lq1	Arrhenatherum elatius	under	8	GRA	-
FR-Lq1	Ornithogalum umbellatum	under	8	GRA	-
FR-Lq1	Ajuga reptens	under	8	GRA	-
FR-Lq1	Chaerophyllum japonicum	under	8	GRA	-
FR-Lq1	Agrostis capillaris	under	8	GRA	-
FR-Lq1	Phyteuma spicatum	under	8	GRA	-
FR-Lq2	Agrostis capillaris	under	7.14	GRA	-
FR-Lq2	Heracleum sphondylium	under	7.14	GRA	-
FR-Lq2	Cerastium	under	7.14	GRA	-
FR-Lq2	Agropiron repens	under	7.14	GRA	-
FR-Lq2	Bromus mollis	under	7.14	GRA	-
FR-Lq2	Phleum pratense	under	7.14	GRA	-
FR-Lq2	Senecio viscosus	under	7.14	GRA	-
FR-Lq2	Urtica dioica	under	7.14	GRA	-
FR-Lq2	Anthoxanthum odoratum	under	7.14	GRA	-
FR-Lq2	Dactylis glomerata	under	7.14	GRA	-
FR-Lq2	Lolium perenne	under	7.14	GRA	-
FR-Lq2	Conopodium majus	under	7.14	GRA	-
FR-Lq2	Taraxacum officinale	under	7.14	GRA	-
FR-Lq2	Santolina	under	7.14	GRA	-

Table B: Fraction of over and understory cover for the different PFTs of FLUXNET sites.

PFT	Cover	Story
CRO	0	Over
CRO	1	Under
CSH	0.6	Over
CSH	0.4	Under
DBF	0.8	Over
DBF	0.2	Under
EBF	0.8	Over
EBF	0.2	Under
ENF	0.85	Over
ENF	0.15	Under
GRA	0.5	Over
GRA	0.5	Under
MF	0.8	Over
MF	0.2	Under
OSH	0.5	Over
OSH	0.5	Under
SAV	0.5	Over
SAV	0.5	Under
WET	0.5	Over
WET	0.5	Under
WSA	0.5	Over
WSA	0.5	Under

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3.2 Paper 2

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ORIGINAL RESEARCH

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

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Abstract

The aim of this study was 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 (photosynthetically active radiation or absorbed photosynthetically active radiation). Although the effect of climate is minimized in these 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, eddy covariance, FLUXNET, interannual variability, photosynthetic capacity, plant traits, spatiotemporal variability, TRY database

1 | INTRODUCTION

Accurate predictions of land–atmosphere feedbacks under climate change require an in-depth understanding of how climatic and other environmental controls on ecosystem functioning are mediated by vegetation characteristics, diversity, and structure (Bonan, 2008). Eddy covariance (EC) measurements of carbon dioxide (CO_2), water, and energy fluxes are widely employed to monitor ecosystem processes and functions (Baldocchi et al., 2001). The increased 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, Mcintyre, Landsberg, & Forbes, 1997). However, plant traits and model parameters derived from EC data can be highly variable within PFTs and species (Alton, 2011; Groenendijk et al., 2011; Kattge et al., 2011; Reichstein, Bahn, Mahecha, Kattge, & Baldocchi, 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 (Pappas, Fatichi, & Burlando, 2016; Van Bodegom et al., 2012; Verheijen, Aerts, Bonisch, Kattge, & Van Bodegom, 2015) 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 spatiotemporal variation in traits and ecosystem functional 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, Knorr, Raddatz, & Wirth, 2009), whereas other plant traits could also be suitable candidates. Foliar phosphorus, for example, improves the model prediction of carbon fluxes as reported by Mercado et al. (2011), Goll et al. (2012), and Yang, Thornton, Ricciuto, and Post (2014).

The short-term (half-hourly to daily) variability of carbon fluxes measured with the EC technique is controlled by meteorological, environmental conditions (Richardson, Hollinger, Aber, Ollinger, & Braswell, 2007), and endogenous plant controls (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) variation of fluxes (Richardson et al., 2007; Stoy et al., 2009). Evaluating the relationship between plant traits and eddy covariance fluxes is not straight forward because the former is usually measured only a couple of times per year (mostly during the growing season), whereas the latter is measured continuously at half-hourly intervals. 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, such as carboxylation capacity (Vc_{max}), EFPs are less variable in time than the fluxes themselves, which makes them a suitable quantity to be linked to plant functional traits (Musavi et al., 2015; Reichstein et al., 2014). Therefore, EFPs can be used to characterize long-term variation in key process characteristics, such as 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 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, a number of studies linking plant traits and EFPs using a wide range of ecosystems are few (e.g., Kergoat, Lafont, Arneth, Le Dantec, & Saugier, 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 broadscale 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 are linked. Likewise, the uncertainties of the relationship between EFPs to plant functional traits related to the temporal dynamics of both ecosystem functioning and traits have not been evaluated before. This is the first time to our knowledge that the relationship between an EFP (here ecosystem photosynthetic capacity) derived from EC CO_2 fluxes and plant traits and the associated uncertainties have been systematically investigated for spatiotemporal variation and the relevance of synchronized observations. Using ecosystem photosynthetic capacity as an example for an EFP derived from selected FLUXNET sites, the goals of this study were as follows:

TABLE 1 Definitions of ecosystem photosynthetic capacity estimated using light response curve

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

In the column "Radiation," the independent variable used in Equation 1 is reported.

1. Providing an objective approach to characterize ecosystem photosynthetic capacity from different estimates of gross primary productivity (GPP) 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 their relationships (with a particular focus on leaf nitrogen content per leaf mass).
3. Identifying (a set of) plant traits that control the spatial variability (i.e., across sites) of ecosystem photosynthetic capacity.

2 | MATERIALS AND 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 photosynthetically active radiation (PAR) 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 interannual variation (IAV) were assumed as the most appropriate to characterize the EFP. These estimates of ecosystem photosynthetic capacity were correlated with 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 with a suite of other photosynthesis-related plant traits to identify those that control its spatial (i.e., across site) variability.

2.1 | 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) 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 previous years were used) and the flux data from the year of sampling. Depending on the site, different years of flux data were available in the La Thuile 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 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). As PAR was not always available at the selected sites, we derived PAR by multiplying global incoming shortwave radiation (Rg, Wm^{-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 daytime 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.

2.2 | MODIS TIP-FAPAR and leaf area index (LAI)—vegetation 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 et al., 2002) were used to quantify the vegetation phenology and changes in the structure of the ecosystem with 16-day temporal resolution (Musavi et al., 2015; Figure 1). 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

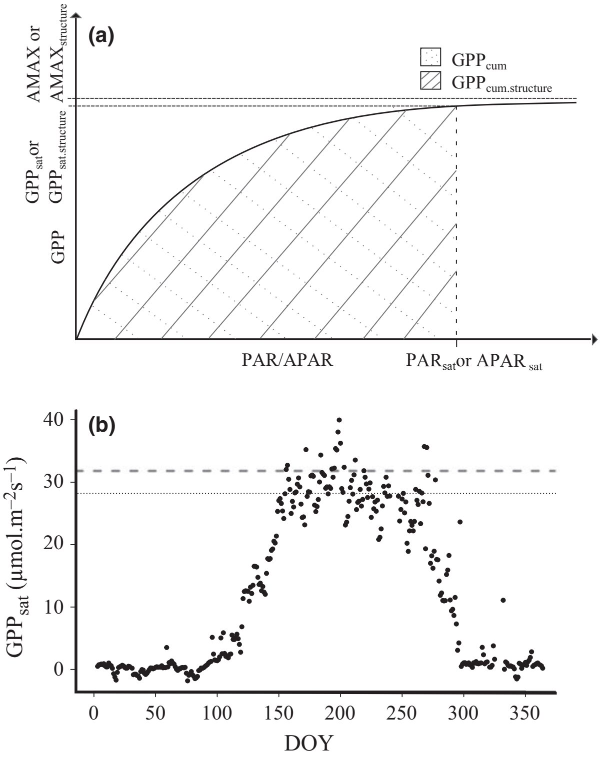

FIGURE 1 (a) Conceptual figure of the different estimates of ecosystem functional property (EFP) related to ecosystem photosynthetic capacity. Light response curves are fitted using GPP flux and PAR or APAR according to Table 1. (b) Time series of GPP_{sat} for 1 year. Higher values of GPP_{sat} occur during the growing season (usually around mid-spring to end-summer). For this study, we use the 90th percentile as the maximum GPP_{sat} of each year, which is indicated with the dashed line. For comparison the 60th percentile of GPP_{sat} is indicated with the dotted line

distance correlation between the time series of all pixels around the central pixel for each flux site (Szekely, Rizzo, & Bakirov, 2007). We subsequently chose pixels with a correlation of $r > .75$ with the central pixel. Afterward, 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, Zscheischler, & Mahecha, 2014). To derive daily time series of FAPAR, a smoothing spline approach was used to derive daily time series of FAPAR (see also Filippa et al., 2016; Migliavacca et al., 2011). FAPAR was then used to compute half-hourly APAR (absorbed photosynthetic active radiation) values (μmol m^{-2} s^{-1}). Annual maximum LAI was derived using the 90th percentile of the satellite retrieved estimates of LAI from JRC-TIP of the same year of sampling (Pinty et al., 2011a).

2.3 | Plant functional trait collection—vegetation characteristics

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

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 carried out mostly at peak growing season on fully developed and nondamaged 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. $\delta^{13}C$ was determined by an elemental analyzer (NC2500, ThemoQuest Italia, Rodana, Italy) coupled online 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 (e.g., for 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, SLA, and $\delta^{13}C$. 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, Westbeek, Cambridge, Lambers, & Pons, 1997; Bahn et al., 1999; Campbell et al., 2007; Cavender-Bares, Keen, & Miles, 2006; Coomes, Heathcote, Godfrey, Shepherd, & Sack, 2008; Cornelissen, 1996; Cornelissen et al., 2003a; Cornelissen, Diez, & Hunt, 1996; Cornelissen et al., 2004; Cornwell et al., 2008; Craine et al., 2009; Craine, Lee, Bond, Williams, & Johnson, 2005; Diaz et al., 2004; Freschet, Cornelissen, Van Logtestijn, & Aerts, 2010; Fyllas et al., 2009; Garnier et al., 2007; Han, Fang, Guo, & Zhang, 2005; Hickler, 1999; Kattge et al., 2011, 2009; Kazakou, Vile, Shipley, Gallet, & Garnier, 2006; Kerkhoff, Fagan, Elser, & Enquist, 2006; Kleyer et al., 2008; Laughlin, Leppert, Moore, & Sieg, 2010; Louault, Pillar, Aufrere, Garnier, & Soussana, 2005; Loveys et al., 2003; Medlyn et al., 1999; Messier, Mcgill, & Lechowicz, 2010; Meziane & Shipley, 1999; Niinemets, 2001; Ogaya & Penuelas, 2003; Onoda et al., 2011; Ordonez et al., 2010; Poorter, Niinemets, Poorter, Wright, & Villar, 2009; Poschlod, Kleyer, Jackel, Dannemann, & Tackenberg, 2003; Quested et al., 2003; Reich, Oleksyn, & Wright, 2009; Reich et al., 2008; Sack, Cowan, Jaikumar, & Holbrook, 2003; Sack, Melcher, Liu, Middleton, & Pardee, 2006; Shipley, 1995, 2002; Shipley & Vu, 2002; Vile, 2005; White, Thornton, Running, & Nemani, 2000; Willis et al., 2010; Wright et al., 2007, 2004, 2010.

2.4 | 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 nonrectangular hyperbolic light response curves (Gilmanov et al., 2003):

$$\mathrm{GPP} = \frac{1}{2\theta}\left(\alpha Q + A_{\max} - \sqrt{\left(\alpha Q + A_{\max}\right)^2 - 4\alpha A_{\max}\theta Q}\right) \quad (1)$$

where **α** is the initial slope of the light response curve, **θ** is the curvature parameter (ranging from 0 to 1), $\boldsymbol{A}_{\max}$ 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 stands for the amount of light that is absorbed by the leaves of the ecosystem.

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

Each light response curve fitting was used to derive the A_{max} parameter, the value of GPP at light saturation and the integral of the light response curve at light saturation (Falge et al., 2001). For light saturation, we defined a threshold of Rg of 1,000 Wm^2 (corresponding to PAR of 2,110 $\mu mol\ m^{-2}\ s^{-1}$) (see also Jacobs et al., 2007). This resulted in six different estimates describing ecosystem photosynthetic capacity: (1) A_{max}: parameter of the Equation 1; (2) $A_{max.structure}$: parameter of Equation 1 but with APAR as driving radiation to account for canopy structure; (3) GPP_{sat}: GPP at light saturation using PAR as driving radiation (4) $GPP_{sat.structure}$: as GPP_{sat} but with APAR as radiation variable; (5) GPP_{cum}: integral of the fitted light response until light saturation; and (6) $GPP_{cum.structure}$: as GPP_{sat} but using APAR as radiation until light saturation (Figure 1a, Table 1).

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

To extract the corresponding annual ecosystem photosynthetic capacity for each site-year, maximum and different percentiles (90th to 60th) of the time series of the estimated parameters were computed. Finally, the coefficient of variation (CV, Everitt, 1998) of the annual ecosystem photosynthetic capacity estimates was computed for each site. For example, at each site, we computed the annual value for GPP_{sat} (i.e., 90th 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 made using sites with at least 5 years of data. The average of annual ecosystem photosynthetic capacity of the selected estimates was used to relate to leaf functional traits.

2.5 | 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, for example, N%. N% is chosen here, as the relationship between N% and photosynthetic processes is well established (e.g., Field & Mooney, 1986; Reich, Walters, & Ellsworth, 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 supporting information (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 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, as it accounts for nonlinear 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.

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

3 | RESULTS

3.1 | 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 was the one that minimized the CV (i.e., the IAV) of most estimators (Figure 2). The maximum annual values showed the highest IAVs and therefore were not considered appropriate estimates of ecosystem photosynthetic capacity. The use of the 60th percentile for the extractions showed slightly higher IAV than the 90th percentile. Other percentiles such as 85, 80, 75, and 70 were also tested and had similar results to the 60 percentile (data not shown). However, considering that we were 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 $A_{max.structure}$ had the highest IAV regardless of how they were extracted annually. GPP_{cum} and GPP_{sat} had the lowest IAV, even though a detailed analysis revealed a substantial IAV for both estimators at some La Thuile sites (Figure 3). While GPP_{cum} is related to the whole growing season, GPP_{sat} is related mostly to the peak of growing season. However, GPP_{cum} and GPP_{sat} were strongly correlated (Table S1). $GPP_{cum.structure}$ and $GPP_{sat.structure}$, accounting for canopy structure, showed slightly higher IAV than GPP_{cum} and GPP_{sat}. As we aimed at developing a method to derive maximum ecosystem

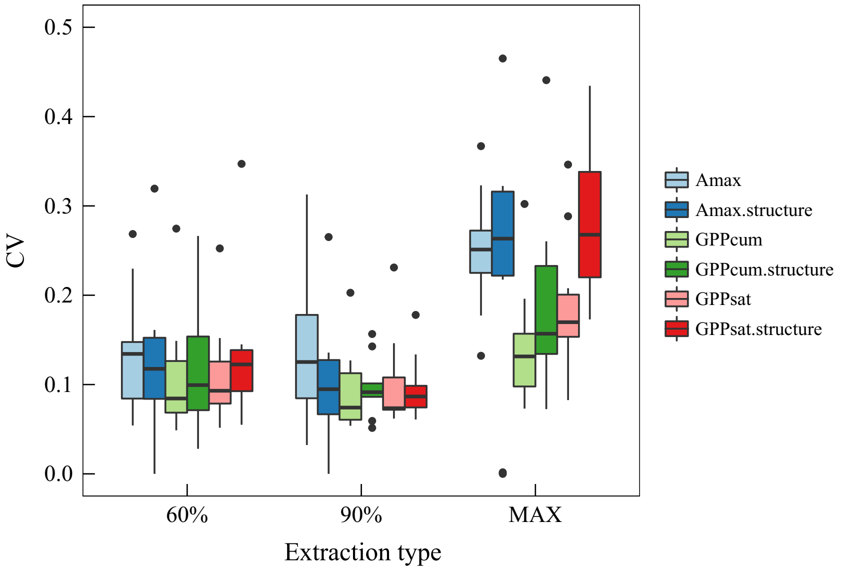

FIGURE 2 Comparison of mean and ranges of the different estimates of ecosystem photosynthetic capacity and different annual extractions. CV denotes the coefficient of variation (standard deviation/mean), which was calculated for every site. The results are based on sites with at least 5 years of available 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 denote low interannual variability). For explanations of the ecosystem photosynthetic capacity estimates described in the legend, see Table 1

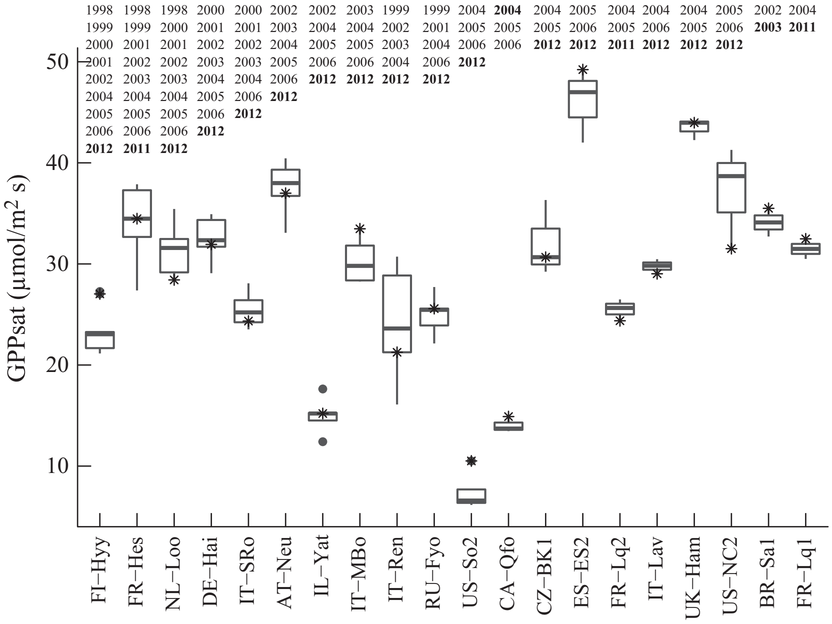

FIGURE 3 Boxplots of annual GPP_{sat} values derived from the La Thuile database for each FLUXNET site. The line across the boxplot shows the mean GPP_{sat} for each site, and the lower and upper boxes show the 25th and 75th percentiles of GPP_{sat}. The stars denote GPP_{sat} values of the respective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

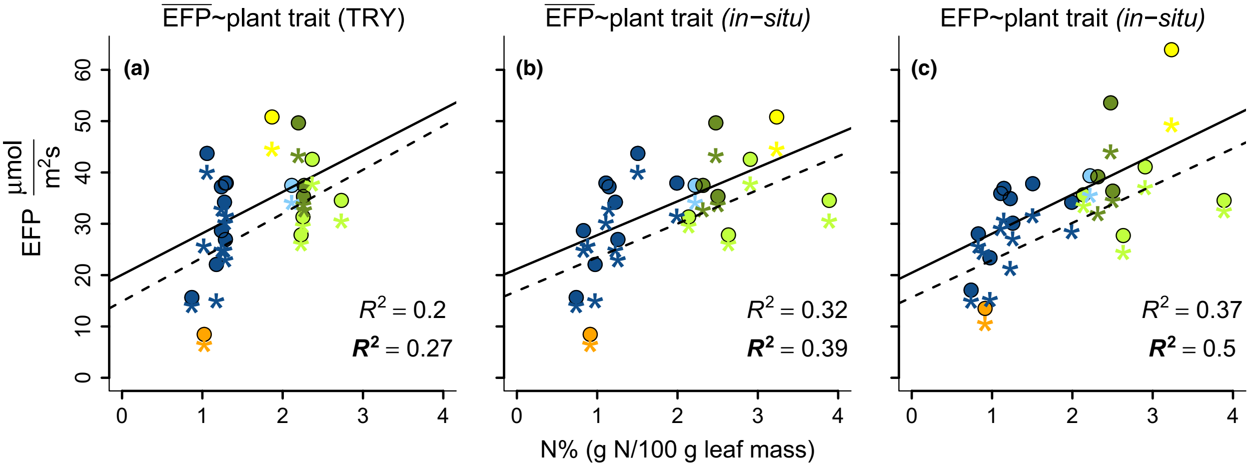

FIGURE 4 Relationship between a) GPP_{sat} and $GPP_{sat.structure}$ extracted from La Thuile and N% from TRY, b) GPP_{sat} and $GPP_{sat.structure}$ from La Thuile and N% in situ, c) GPP_{sat} and $GPP_{sat.structure}$ derived from the same year of the trait sampling and N% in situ. Y-axes are ecosystem 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 multiyear averages for each site. Bold R^2 and star symbols are for the relationships with ecosystem photosynthetic capacity estimates using PAR (GPP_{sat}). Nonbold R^2 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 Figure 4

Ecosystem photosynthetic capacity	Model	Distance correlation	R^2	adj. R^2	Intercept ± *SE*	Slope ± *SE*	*p*	RRMSE	EF	*df*
GPP_{sat}	N%	0.73	0.50	0.47	15.67 ± 3.51	7.25 ± 1.71	.0005	26.2	0.31	1 + 18
$\overline{GPP}_{sat}$	N%	0.67	0.39	0.36	16.89 ± 3.95	6.57 ± 1.93	.003	29.09	0.18	1 + 18
$\overline{GPP}_{sat}$	$N\%^{TRY}$	0.56	0.27	0.23	14.88 ± 5.74	8.55 ± 3.28	.018	30.65	0.09	1 + 18
$GPP_{sat.structure}$	N%	0.63	0.37	0.34	20.45 ± 5	7.62 ± 2.39	.005	30	0.10	1 + 17
$\overline{GPP}_{sat.structure}$	N%	0.58	0.32	0.28	21.18 ± 4.87	6.59 ± 2.33	.01	25.5	−0.15	1 + 17
$\overline{GPP}_{sat.structure}$	$N\%^{TRY}$	0.47	0.20	0.15	20.08 ± 7.01	8.07 ± 3.94	.06	26.1	−0.20	1 + 17

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.

photosynthetic capacity robust to meteorological variability, we assessed 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 site-years did not change the results (Fig. S4). In addition, the estimated parameters, for example, GPP_{sat} were not strongly linked to climate variables (Fig. S8).

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

3.2 | Relationship between ecosystem photosynthetic capacity and plant functional traits

Using a linear relationship, the N% based on data from the TRY database explained 27% of the variance of site averaged GPP_{sat} (20% of $GPP_{sat.structure}$) (Figure 4a, Table 2). N% derived from TRY and in situ were strongly correlated (Fig. S5), and the R^2 of the relationship between N% and GPP_{sat}, and $GPP_{sat.structure}$ improved from 0.27 to 0.39 and from 0.20 to 0.32, respectively, when in situ N% was used (Figure 4b, Table 2). In addition, site averaged estimates of GPP_{sat} and $GPP_{sat.structure}$ were replaced by GPP_{sat} and $GPP_{sat.structure}$ from the years of in situ sampling R^2 increased to 0.50 and 0.37, respectively (Figure 4c, Table 2). The fit is even better when a nonlinear fit was used for Figure 4a,b (distance correlation increased from 0.56 to 0.73 for GPP_{sat} and from 0.47 to 0.63 for $GPP_{sat.structure,}$ See also Fig. S6). An ANCOVA test revealed that the relationship between ecosystem photosynthetic capacity and N% was significantly different between the levels of synchronization when GPP_{sat} (significantly different in slope and intercept, $p < .01$) or $GPP_{sat.structure}$ (only significantly different intercept, $p < .05$) was used to characterize ecosystem photosynthetic capacity. Similar improvements of the relationship of CWM

TABLE 3 Relationships between N%, LAI, and GPP$_{sat}$ tested

Variable	Model	Distance correlation	R^2	adj. R^2	Intercept ± *SE*	Slope ± *SE*	*p*	*df*	AIC
LAI	N%	0.70	0.48	0.45	0.34 ± 0.38	0.71 ± 0.18	.001	1 + 17	44
GPP$_{sat}$	LAI	0.57	0.28	0.24	20.10 ± 4.03	5.43 ± 2.09	.01	1 + 17	138
GPP$_{sat}$	N%	0.73	0.50	0.47	15.25 ± 3.79	7.41 ± 1.81	.0008	1 + 17	132
GPP$_{sat}$	LAI + N%	0.71	0.50	0.44	14.96 ± 3.98	N% 6.78 ± 2.58 LAI 0.87 ± 2.51	.004	2 + 16	134
GPP$_{sat}$	N% + LAI + LAI:N%	—	0.64	0.56	0.74 ± 6.94	N% 15.22 ± 4.22 LAI 10.33 ± 4.55 N%:LAI −4.71 ± 1.98	.001	3 + 15	129

The GPP$_{sat}$ is derived from the year at which the sampling of leaf N% was carried out. N% here is measured from in situ samples. LAI is the 90th percentile of the bimonthly LAI values retrieved from remote sensing and corresponds to the LAI of the sampling year as well (available for 19 sites).

TABLE 4 Results of the variable selection analyses conducted with a stepwise regression

Variable	Model	Distance correlation	R^2	adj. R^2	Intercept ± *SE*	Slope ± *SE*	*p*	*df*	AIC	EF
GPP$_{sat}$	C/N + P$_{area}^2$	0.67	0.61	0.55	41.62 ± 3.01	C/N −0.39 ± 0.08 P$_{area}^2$ 23.94 ± 16.20	.0009	2 + 15	119	0.18
GPP$_{sat.structure}$	C/N + P$_{area}^2$	0.65	0.54	0.48	49.02 ± 4.07	C/N −0.48 ± 0.12 P$_{area}^2$ 38.89 ± 22.22	.004	2 + 14	123	−0.28

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 GPP$_{sat}$ and only 17 have the two traits and GPP$_{sat.structure}$ measurements.

traits to GPP$_{sat}$ and GPP$_{sat.structure}$ were realized using other plant traits and synchronizing the plant traits with the ecosystem photosynthetic capacity estimates in time and space (Fig. S2). We also tested whether the improvement of this relationship was due to random effects. To do this, we randomly resampled the annual photosynthetic capacity (specifically GPP$_{sat}$ and GPP$_{sat.structure}$) to test whether the use of corresponding years statistically improves the relationship or not. The results confirmed that the best fit was obtained when the N% and the photosynthetic capacity estimate match in time and space (Table S2).

As 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 decreased but only by about 0.05 (Fig. S7).

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

3.3 | 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 showed that the variability of GPP$_{sat}$ and GPP$_{sat.structure}$ between sites is best explained by leaf C/N ratio and P$_{area}^2$ (considering AIC as the selection criteria). However, only C/N was a significant predictor for both of the ecosystem photosynthetic capacity estimates. The selected model explained 61% and 54% of the variance of GPP$_{sat}$ and GPP$_{sat.structure}$, respectively (Table 4).

4 | DISCUSSION

4.1 | 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 curves was suitable as it accounts for variation in radiation, which is one of the important parameters explaining variation in GPP (Van Dijk, Dolman, & Schulze, 2005). The estimation of the parameters using a moving window approach was also suitable because it accounts for variation in meteorological variables such as temperature and vapor pressure deficit. Among the parameters derived from the light response curve, A_{max} (or $A_{max.structure}$) had the largest IAV and was therefore the least suitable estimator for ecosystem photosynthetic capacity. This may have several reasons: The response of GPP to PAR/APAR does not exhibit a clear saturation and still tends to increase at high PAR/APAR and reaches A_{max} outside the range of PAR/APAR measurements. Therefore, small changes in the slope at high PAR/APAR may cause large deviations in A_{max} (Gilmanov et al., 2003). In periods of the year when the PAR/APAR is not high, or the numbers of data points at high PAR is limited, the A_{max} parameter is poorly constrained. In this case, the fit can be affected by random flux uncertainty that scales with the magnitude of fluxes and is not easily constrainable (Richardson et al., 2012). GPP_{sat} or GPP_{cum} showed much smaller IAV, and therefore, we suggest the use GPP_{sat} or GPP_{cum} derived with PAR or APAR (Falge et al., 2001; Lasslop et al., 2010; Ruimy, Jarvis, Baldocchi, & Saugier, 1995) as more robust estimators of ecosystem photosynthetic capacity than A_{max}. Our results also demonstrate that the use of higher percentiles (i.e., 90th) rather than the maximum for EFP extraction should be preferred as it was more robust to outliers.

4.2 | Linking plant functional traits and EFP estimates

Ecosystem functional properties are whole-ecosystem properties and thus depend on both ecosystem structure and function (Reichstein et al., 2014). As GPP depends on both the efficiency with which the absorbed energy is converted to chemical energy at leaf level (Monteith, 1972) and the canopy structure, GPP_{sat} variability ultimately depends on the variability of FAPAR (Reichstein et al., 2014). In this study, we accounted for this aspect using APAR in Equation 1 for the estimation of $GPP_{sat.structure}$. 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-day data (e.g., Kandasamy, Baret, Verger, Neveux, & Weiss, 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 (1 km) makes it uncertain; the footprints of FLUXNET sites are often smaller than a 1 km 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, Shipley, & Garnier, 2006), also known as “dominance hypothesis” (Grime, 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, Grassein, Schurr, Vieilledent, & Violle, 2011).

4.3 | 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, Figure 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 multiyear 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 were 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, for example, 10 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, Vicinelli, Ponti, Cantoni, & Magnani, 2005; Ma, Baldocchi, Mambelli, & Dawson, 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, Martin, Anderson, & Knapp, 2015). But the contribution of physiological vs. structural information in the remote sensing signals needs to be better understood (e.g., Homolova, Maenovsky, Clevers, Garcia-Santos, & Schaeprnan, 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.

4.4 | 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 (Perez-Priego et al., 2015; Sardans & Penuelas, 2013; Walker et al., 2014). While C has low variation during the growing season (e.g., Jayasekera & Schleser, 1991; Kattge et al., 2011; Ma et al., 2010), 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, Cescatti, Migliavacca, & Kustas, 2013) and to the amount of Ribulose-1,5-bisphosphate carboxylase/oxygenase enzymes that ultimately controls the photosynthetic rates and carbon uptake (Evans, 1989; Kattge et al., 2009). 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, O'brien, Dobberfuhl, & Dowling, 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, Jensen, Kyle, & Elser, 2007). As 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 upscaling 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 upscaling 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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CONFLICT OF INTEREST

None declared.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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

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

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

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

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

Figure S1 Time series of daily GPP_{sat}. Data filtering using the R^2 of the model fit shows that only 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.

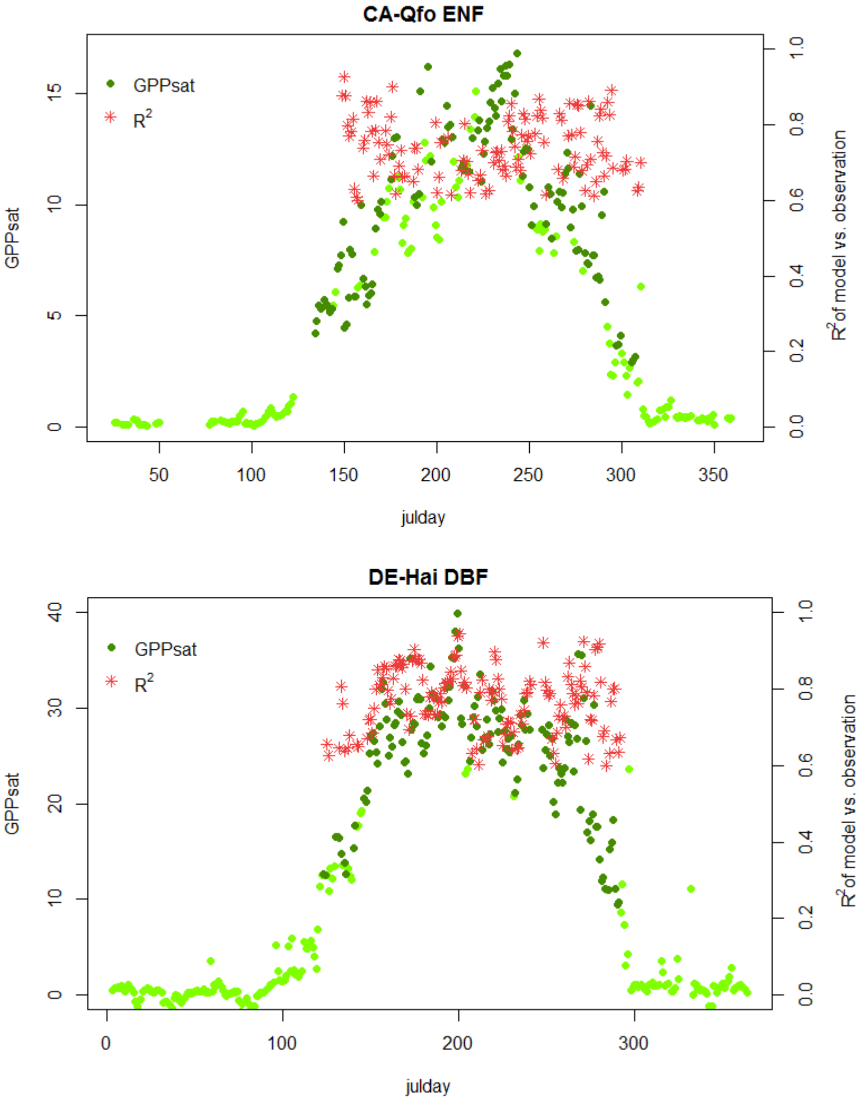
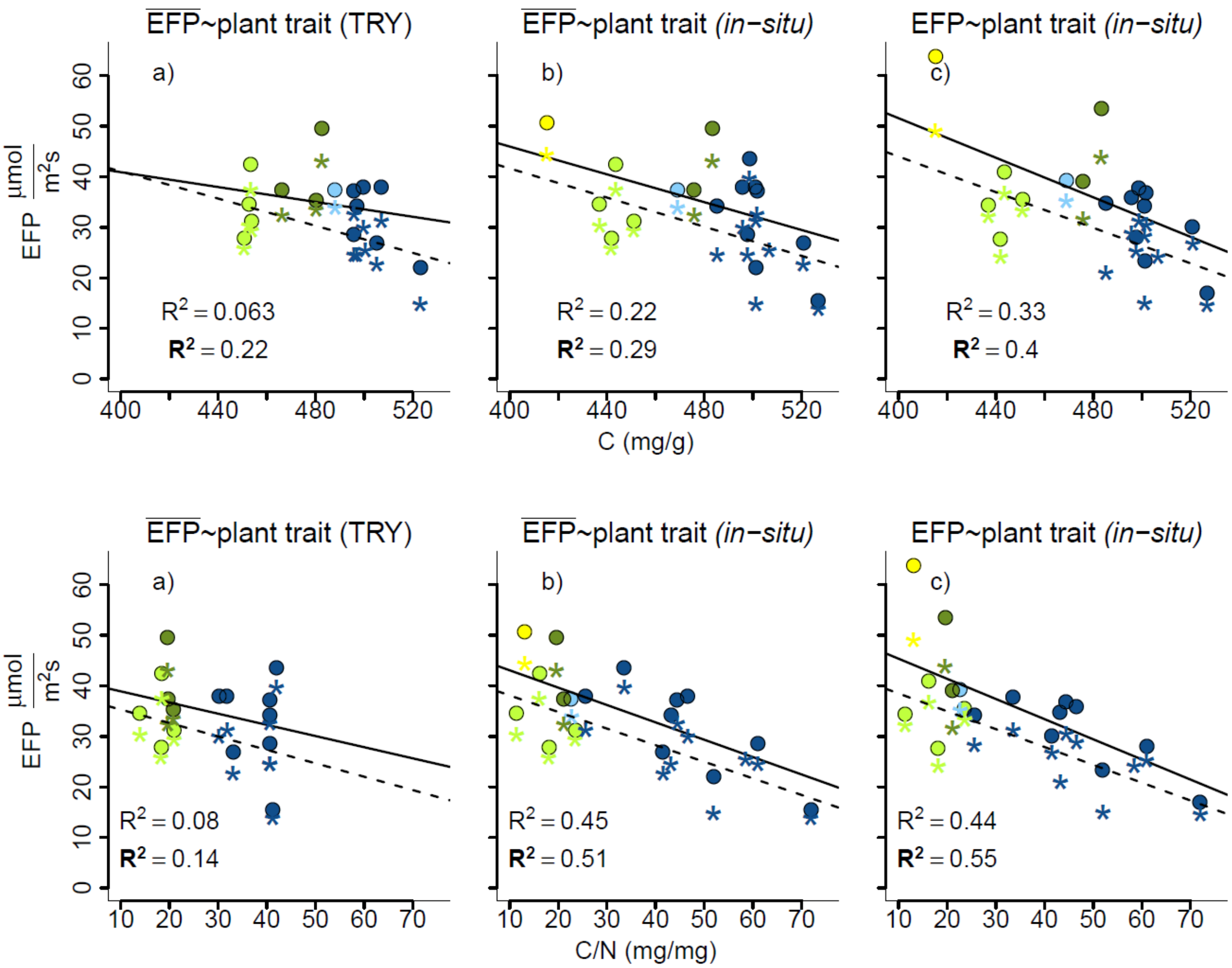
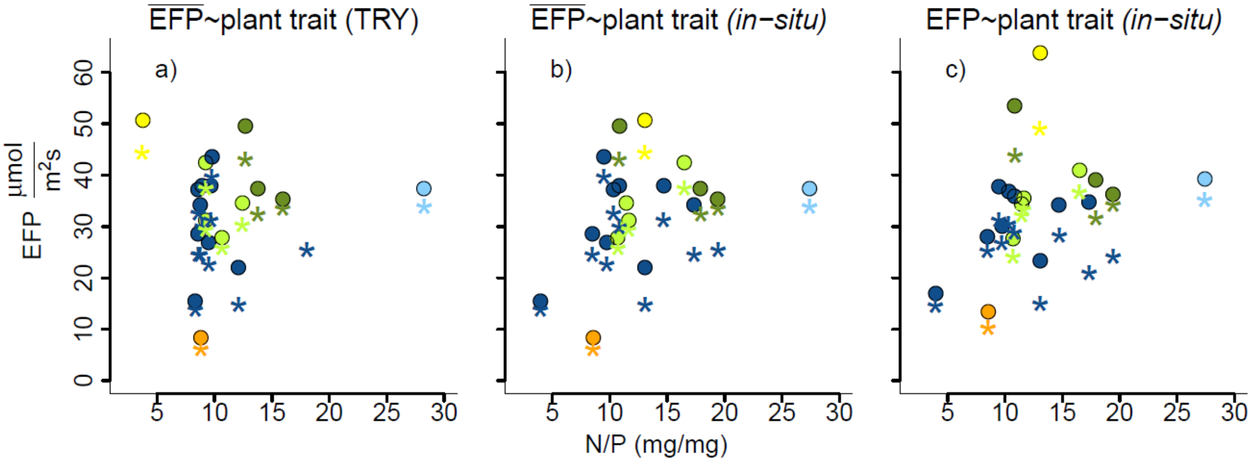
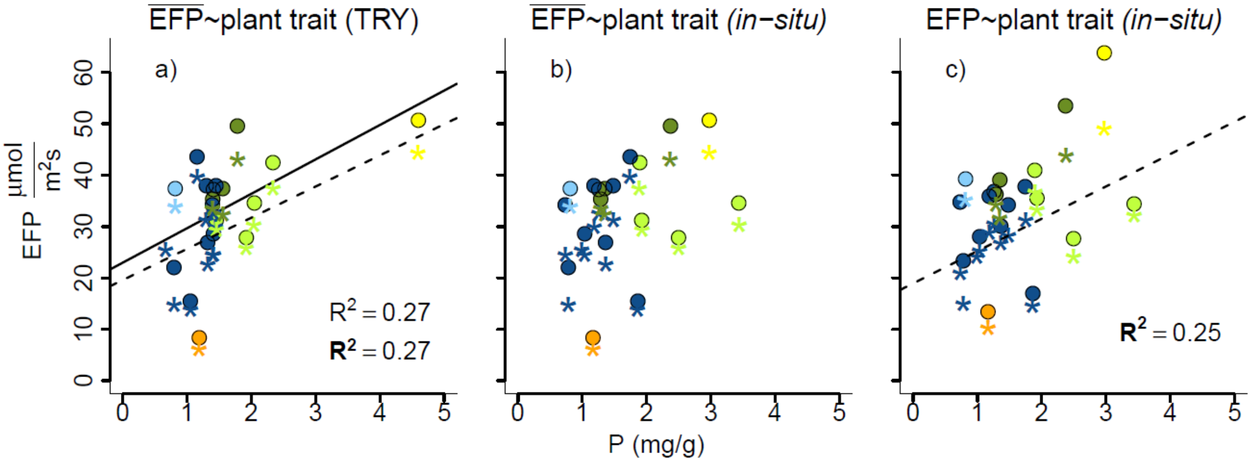


Figure S2 a) Relationship between GPP_{sat} and $GPP_{sat.structure}$ extracted from La Thuile and the trait from TRY. b) GPP_{sat} and $GPP_{sat.structure}$ from La Thuile and the trait from *in-situ* measurements. c) GPP_{sat} and $GPP_{sat.structure}$ derived from the same year of the trait sampling 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.




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


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

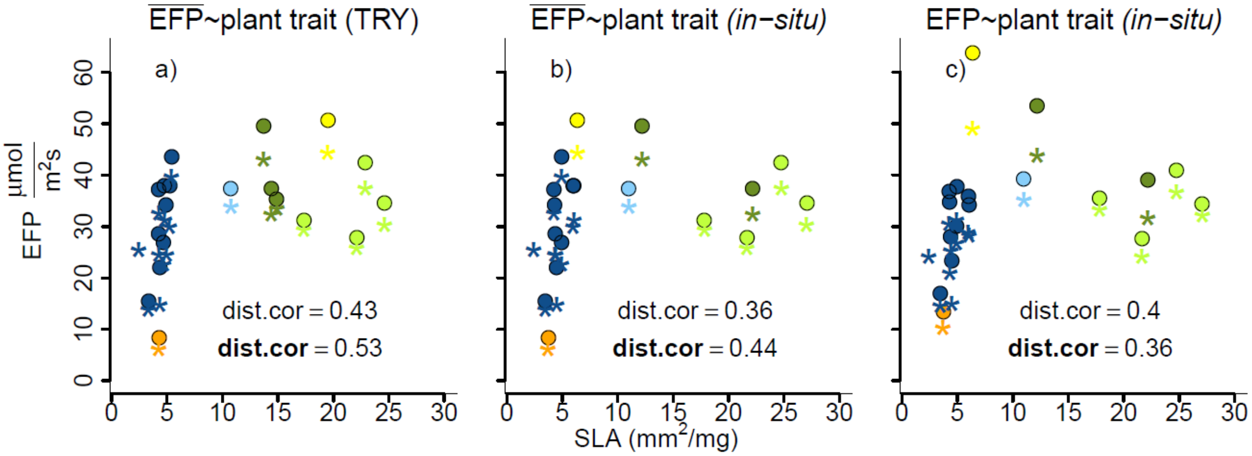

$\overline{EFP}$~plant trait (TRY)
$\overline{EFP}$~plant trait *(in−situ)*
EFP~plant trait *(in−situ)*
a)
b)
c)
EFP $\frac{\mu mol}{m^2 s}$
0
10
20
30
40
50
60
dist.cor = 0.43
dist.cor = 0.53
dist.cor = 0.36
dist.cor = 0.44
dist.cor = 0.4
dist.cor = 0.36
0
5
10
15
20
25
30
SLA (mm^2/mg)

Figure S3 Boxplots of annual GPP_{sat} values derived from the La Thuile database for each FLUXNET site. The red point denotes GPP_{sat} 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 GPP_{sat} estimates.

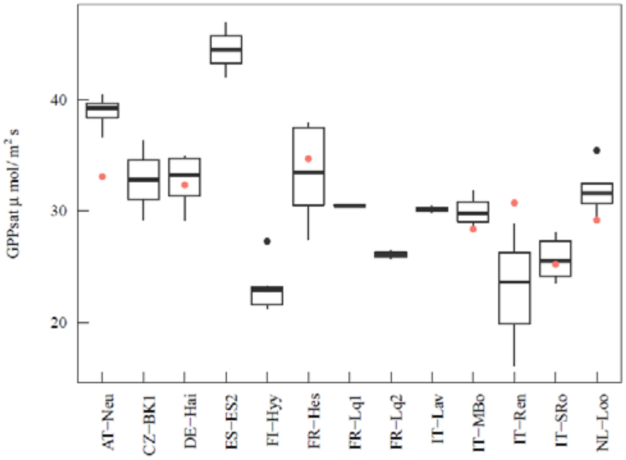


Figure S4 Relationship between a) GPP_{sat} and $GPP_{sat.structure}$ extracted from La Thuile and N% from TRY, b) GPP_{sat} and $GPP_{sat.structure}$ from La Thuile and N% *in-situ*. The Macro accent on the EFP indicates that the GPPsat and $GPP_{sat.structure}$ are the multi-year averages for each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

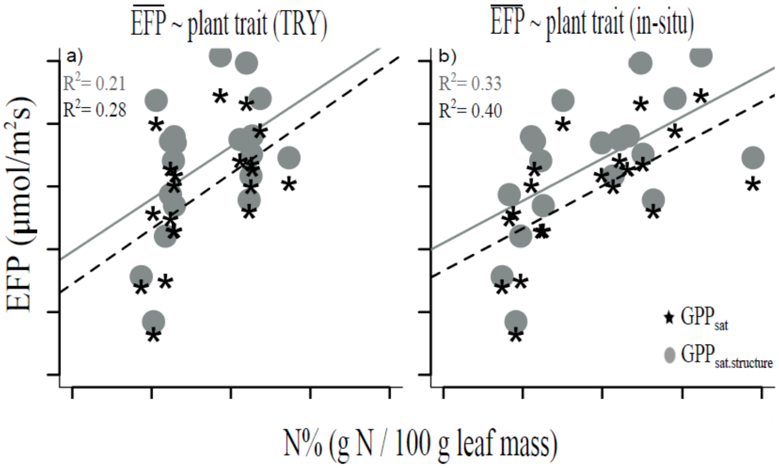


Figure S5 Summary of the fit between the *in-situ* measured and database derived community weighted mean of the plant traits. X-axes are plant traits from TRY and Y-axes are *in-situ* plant traits. The numbers on the left upper corner are the Pearson correlation coefficients between the two sources of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

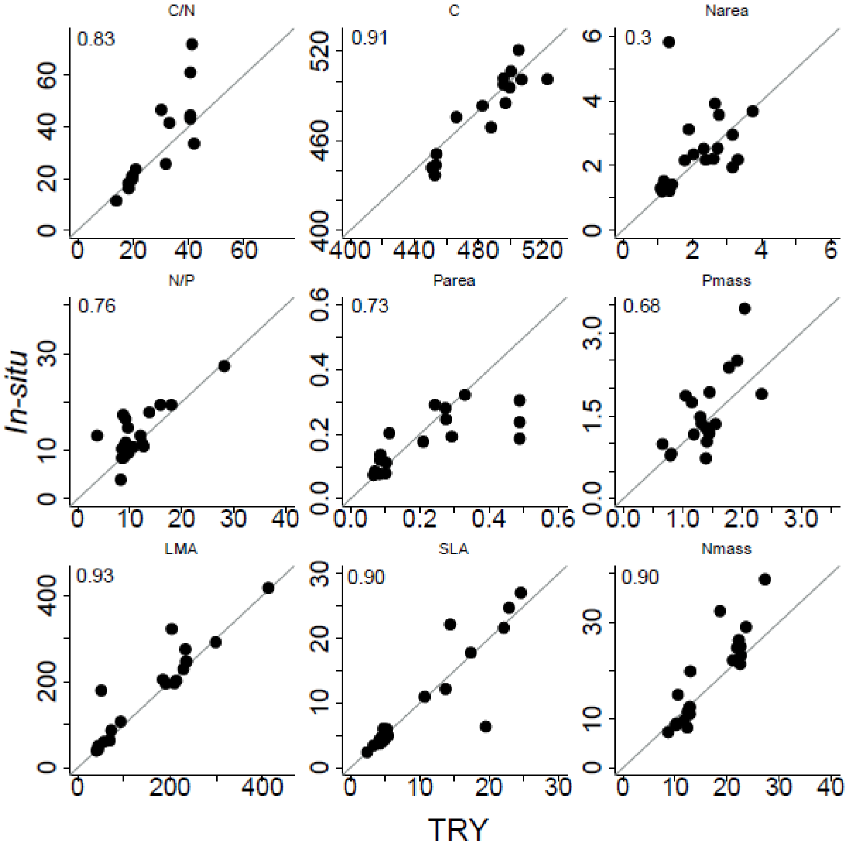


Figure S6 From left to right relationship between GPP_{sat} and $GPP_{sat.structure}$ extracted from La Thuile and N% from TRY. GPP_{sat} and $GPP_{sat.structure}$ from La Thuile and N% *in-situ*. GPP_{sat} and $GPP_{sat.structure}$ derived from the same year of the trait sampling and N% *in-situ*. The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

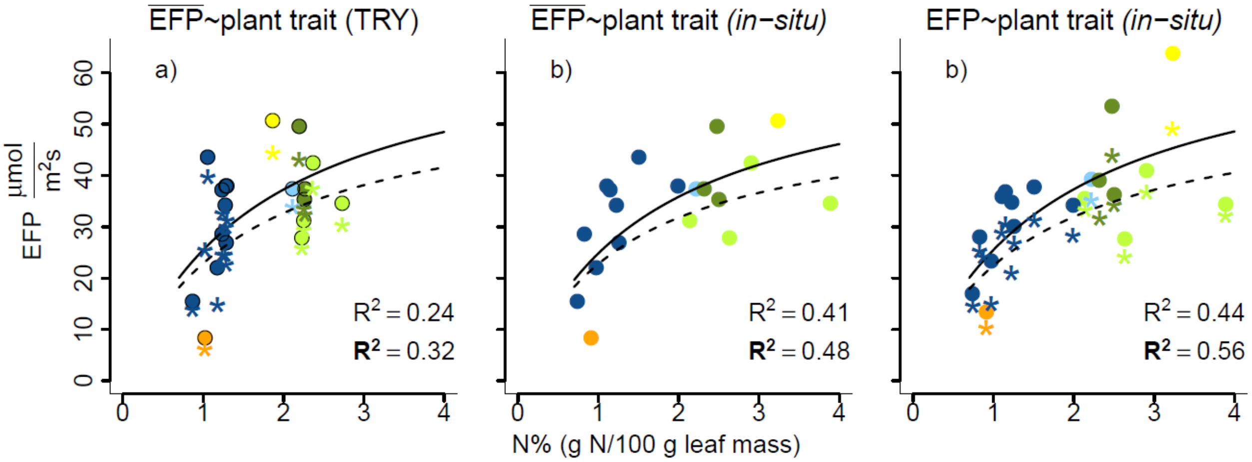


Figure S7 From left to right Relationship between GPP_{sat} and $GPP_{sat.structure}$ extracted from La Thuile and N% from TRY. GPP_{sat} and $GPP_{sat.structure}$ from La Thuile and N% *in-situ*. GPP_{sat} and $GPP_{sat.structure}$ derived from the same year of the trait sampling and N% *in-situ*. The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

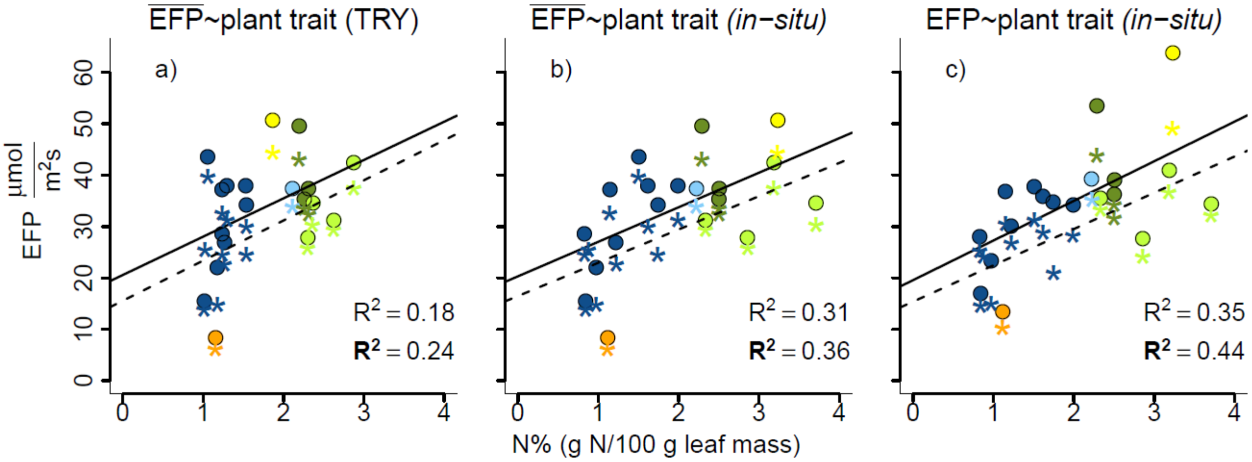


Figure S8 The extraction of GPP_{sat} considers the optimal conditions and thereby less correlated to climate variables. The fact that GPP_{sat} is the potential GPP at light saturation overcomes the direct effects of climate as well. The two figures below indicate that the difference between sites for 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.

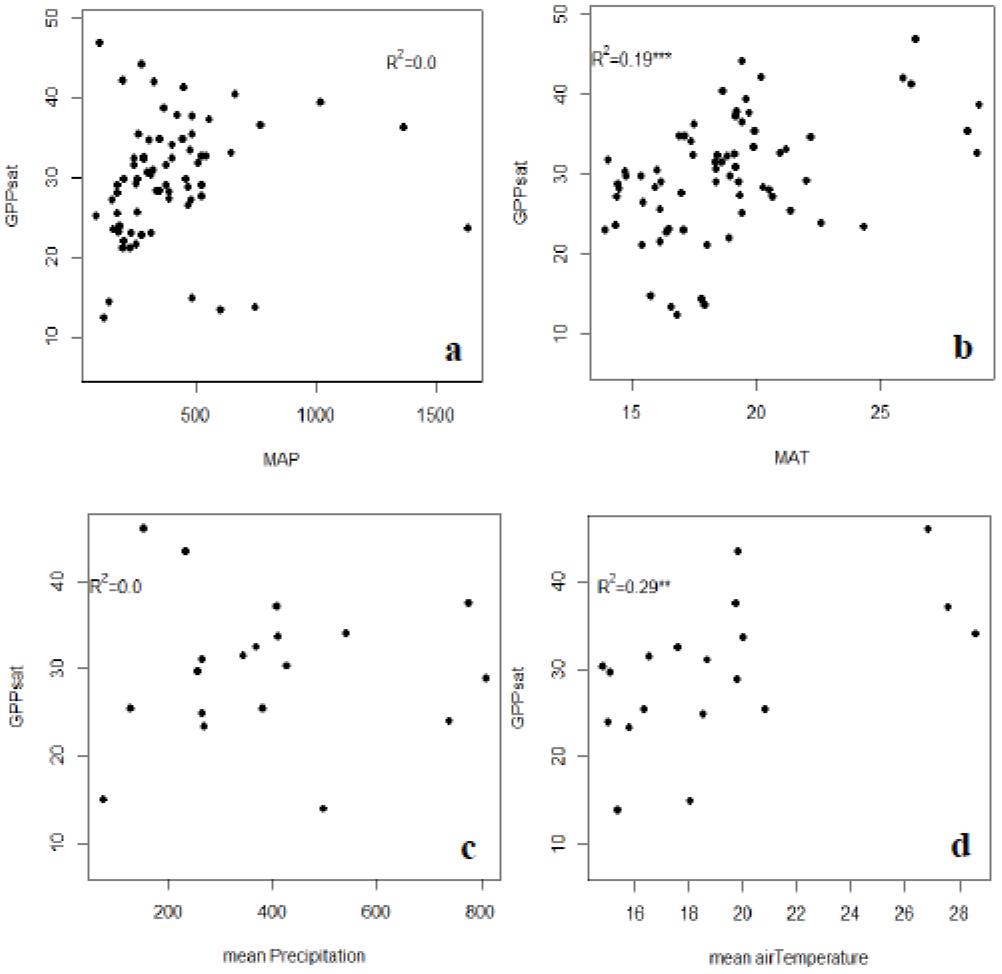
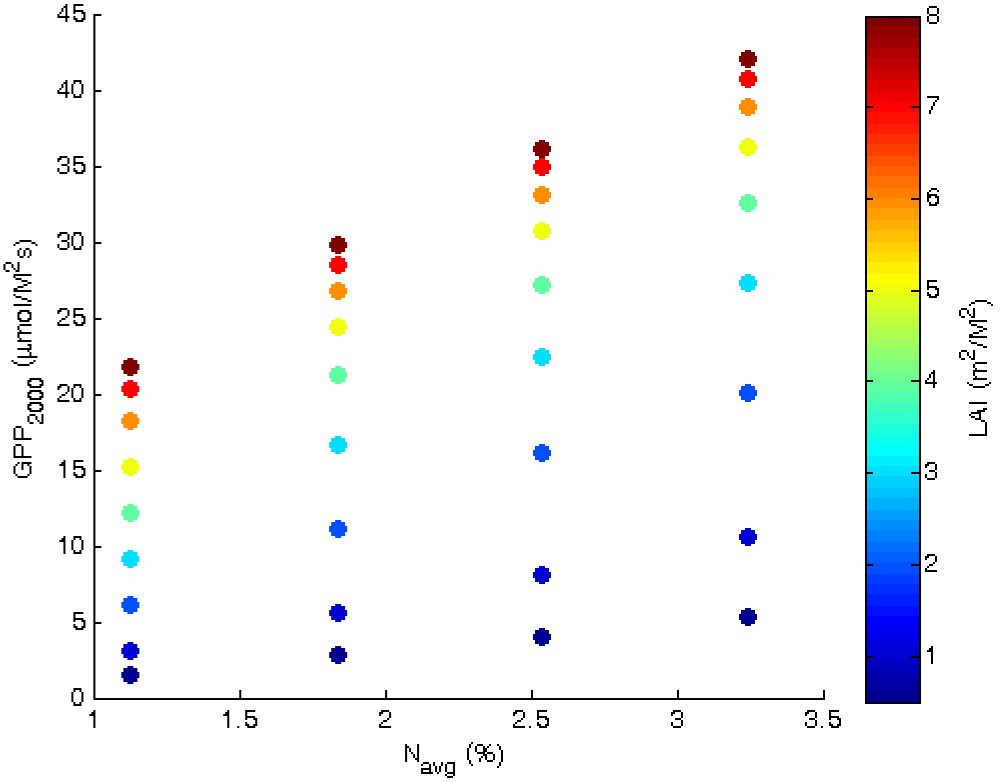


Figure S9 Relationship between N% (here total canopy nitrogen content divided by LAI) and photosynthetic capacity Simulations of GPP2000 were done using De Pury & Farquhar (1997) model, based on the combination of Farquhar photosynthesis model (Farquhar *et al.*, 1980) with the two-leaf big-leaf presentation 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%.



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SUPPLEMENTARY DATASETS

Table1 - InSitu_Traits

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

site.code	Species	Year	DOY	Trait_ID	Mean.trait	indv. No	SD.trait
AT-Neu	Dactylis glomerata	2012	163	C_N	15.08061	2	0.962553
AT-Neu	Phleum pratense	2012	163	C_N	15.92679	1	NA
AT-Neu	Ranunculus acris	2012	163	C_N	26.98908	2	17.2037
AT-Neu	Taraxacum officinale	2012	163	C_N	17.68594	5	3.795306
AT-Neu	Trifolium pratense	2012	163	C_N	20.22507	1	NA
AT-Neu	Trifolium repens	2012	163	C_N	10.37804	2	0.307294
AT-Neu	Dactylis glomerata	2012	163	leaf_C_concentration	446.7094	2	16.97156
AT-Neu	Dactylis glomerata	2012	163	d13c	-28.4662	2	0.08085
AT-Neu	Dactylis glomerata	2012	163	LMA	39.39881	5	6.7344
AT-Neu	Dactylis glomerata	2012	163	leaf_N_area	1.176335	2	0.148014
AT-Neu	Dactylis glomerata	2012	163	Nmass	29.71788	2	3.022199
AT-Neu	Dactylis glomerata	2012	163	SLA	25.58647	5	4.860679
AT-Neu	Phleum pratense	2012	163	leaf_C_concentration	436.4407	1	NA
AT-Neu	Phleum pratense	2012	163	d13c	-28.194	1	NA
AT-Neu	Phleum pratense	2012	163	LMA	46.13987	5	2.709169
AT-Neu	Phleum pratense	2012	163	leaf_N_area	1.264368	1	NA
AT-Neu	Phleum pratense	2012	163	Nmass	27.40293	1	NA
AT-Neu	Phleum pratense	2012	163	SLA	22.79159	5	2.11748
AT-Neu	Ranunculus acris	2012	163	leaf_C_concentration	470.9868	2	39.95076
AT-Neu	Ranunculus acris	2012	163	d13c	-27.561	2	1.712745
AT-Neu	Ranunculus acris	2012	163	LMA	42.65869	5	6.241266
AT-Neu	Ranunculus acris	2012	163	leaf_N_area	0.935478	2	0.583559
AT-Neu	Ranunculus acris	2012	163	Nmass	21.30819	2	12.10226
AT-Neu	Ranunculus acris	2012	163	SLA	23.97094	5	3.272
AT-Neu	Taraxacum officinale	2012	163	leaf_C_concentratio	433.1592	5	5.33136

				n			1
AT-Neu	Taraxacum officinale	2012	163	d13c	-29.6839	5	0.554004
AT-Neu	Taraxacum officinale	2012	163	LMA	39.56038	5	3.452819
AT-Neu	Taraxacum officinale	2012	163	leaf_N_area	1.003834	5	0.234314
AT-Neu	Taraxacum officinale	2012	163	Nmass	25.40617	5	5.395767
AT-Neu	Trifolium pratense	2012	163	leaf_P_area	0.04572	1	NA
AT-Neu	Taraxacum officinale	2012	163	SLA	25.2317	4	2.474402
AT-Neu	Trifolium pratense	2012	163	leaf_C_concentration	468.326	1	NA
AT-Neu	Trifolium pratense	2012	163	d13c	-29.7849	1	NA
AT-Neu	Trifolium pratense	2012	163	LMA	30.94863	5	6.647434
AT-Neu	Trifolium pratense	2012	163	leaf_N_area	1.325095	1	NA
AT-Neu	Trifolium pratense	2012	163	Nmass	42.81596		NA
AT-Neu	Trifolium pratense	2012	163	SLA	32.96022	5	7.121178
AT-Neu	Trifolium repens	2012	163	leaf_C_concentration	450.908	3	0.431882
AT-Neu	Trifolium repens	2012	163	d13c	-28.7664	2	0.499298
AT-Neu	Trifolium repens	2012	163	LMA	35.27049	5	4.311171
AT-Neu	Trifolium repens	2012	163	leaf_N_area	1.502233	2	0.07018
AT-Neu	Trifolium repens	2012	163	Nmass	44.67453	3	1.402267
AT-Neu	Trifolium repens	2012	163	SLA	29.12795	5	3.946757
AT-Neu	Dactylis glomerata	2012	163	leaf_P_area	0.065816	2	0.258688
AT-Neu	Ranunculus acris	2012	163	leaf_P_area	0.068563	2	0.051074
AT-Neu	Taraxacum officinale	2012	163	leaf_P_area	0.07954	5	0.041596
AT-Neu	Trifolium repens	2012	163	leaf_P_area	0.081365	2	0.011909
AT-Neu	Phleum pratense	2012	163	leaf_P_area	0.096777	1	NA
AT-Neu	Trifolium pratense	2012	163	leaf_P_dry	1.477303	1	NA
AT-Neu	Ranunculus acris	2012	163	leaf_P_dry	1.555154	2	1.080241
AT-Neu	Dactylis glomerata	2012	163	leaf_P_dry	1.674212	2	0.777246
AT-Neu	Phleum pratense	2012	163	leaf_N_P	13.06473	1	NA
AT-Neu	Taraxacum officinale	2012	163	leaf_N_P	13.8879	5	3.147552
AT-Neu	Ranunculus acris	2012	163	leaf_N_P	14.49603	2	2.2872
AT-Neu	Taraxacum officinale	2012	163	leaf_P_dry	1.996926	5	0.944416
AT-Neu	Phleum pratense	2012	163	leaf_P_dry	2.097474	1	NA

AT-Neu	Trifolium repens	2012	163	leaf_P_dry	2.344079	2	0.12449
AT-Neu	Dactylis glomerata	2012	163	leaf_N_P	20.36383	2	11.25897
AT-Neu	Trifolium repens	2012	163	leaf_N_P	16.11213	2	1.227039
AT-Neu	Trifolium pratense	2012	163	leaf_N_P	28.98252	1	NA
BR-Sa1	Prinostemma af. aspera	2003	258	leaf_P_dry	0.071589		NA
BR-Sa1	Abuta rufescens	2003	258	C_N	32.55427	1	NA
BR-Sa1	Abuta rufescens	2003	258	leaf_C_concentration	478.819		NA
BR-Sa1	Abuta rufescens	2003	258	d13c	-28.4071	1	NA
BR-Sa1	Abuta rufescens	2003	258	LMA	170.3835		NA
BR-Sa1	Abuta rufescens	2003	258	leaf_N_area	2.493774	1	NA
BR-Sa1	Abuta rufescens	2003	258	Nmass	14.70833	1	NA
BR-Sa1	Abuta rufescens	2003	258	SLA	5.869113		NA
BR-Sa1	Anomalocalyx uleanus	2003	75	C_N	24.45876	1	NA
BR-Sa1	Anomalocalyx uleanus	2003	75	leaf_C_concentration	450.4998		NA
BR-Sa1	Anomalocalyx uleanus	2003	75	d13c	-30.3119	1	NA
BR-Sa1	Anomalocalyx uleanus	2003	75	Nmass	18.41875	1	NA
BR-Sa1	Lecythis lurida	2003	75	leaf_P_dry	0.5763		NA
BR-Sa1	Anomalocalyx uleanus	2003	75	SLA	7.796664		NA
BR-Sa1	Anomalocalyx uleanus	2003	75	LMA	128.26		NA
BR-Sa1	Anomalocalyx uleanus	2003	75	leaf_N_area	2.352944	1	NA
BR-Sa1	Arrabidea prancei	2003	258	C_N	20.12087		NA
BR-Sa1	Arrabidea prancei	2003	258	leaf_C_concentration	504.95		NA
BR-Sa1	Arrabidea prancei	2003	258	d13c	-28.6808		NA
BR-Sa1	Arrabidea prancei	2003	258	LMA	125.4612		NA
BR-Sa1	Arrabidea prancei	2003	258	Nmass	25.09583		NA
BR-Sa1	Manilkara huberi	2003	75	leaf_P_dry	0.583984		NA
BR-Sa1	Arrabidea prancei	2003	258	SLA	7.970591		NA
BR-Sa1	Combretum	2003	258	C_N	21.91445		NA
BR-Sa1	Combretum	2003	258	leaf_C_concentration	469.8459		NA
BR-Sa1	Combretum	2003	258	d13c	-29.717		NA
BR-Sa1	Combretum	2003	258	LMA	58.32968		NA
BR-Sa1	Combretum	2003	258	leaf_N_area	3.128945		NA
BR-Sa1	Combretum	2003	258	Nmass	21.44		NA
BR-Sa1	Combretum	2003	258	SLA	17.14393		NA
BR-Sa1	Copaifera duckei	2003	258	C_N	19.89803		NA
BR-Sa1	Copaifera duckei	2003	75	C_N	20.84038		NA
BR-Sa1	Copaifera duckei	2003	258	leaf_C_concentration	503.2474		NA
BR-Sa1	Copaifera duckei	2003	75	leaf_C_concentration	517.0151		NA
BR-Sa1	Copaifera duckei	2003	258	d13c	-27.8879		NA
BR-Sa1	Copaifera duckei	2003	75	d13c	-28.6057		NA

BR-Sa1	Copaifera duckei	2003	258	LMA	90.8149	NA
BR-Sa1	Copaifera duckei	2003	75	LMA	124.0641	NA
BR-Sa1	Copaifera duckei	2003	258	leaf_N_area	1.247717	NA
BR-Sa1	Copaifera duckei	2003	258	leaf_N_area	2.30005	NA
BR-Sa1	Copaifera duckei	2003	258	Nmass	25.29132	NA
BR-Sa1	Copaifera duckei	2003	75	Nmass	24.80833	NA
BR-Sa1	Faramea platyneura	2003	75	leaf_P_dry	0.61472	NA
BR-Sa1	Copaifera duckei	2003	258	SLA	11.01141	NA
BR-Sa1	Copaifera duckei	2003	75	SLA	8.060347	NA
BR-Sa1	Cordia bicolor	2003	258	C_N	17.864	NA
BR-Sa1	Cordia bicolor	2003	258	leaf_C_concentration	466.1654	NA
BR-Sa1	Cordia bicolor	2003	258	d13c	-29.7751	NA
BR-Sa1	Cordia bicolor	2003	258	LMA	125.181	NA
BR-Sa1	Cordia bicolor	2003	75	leaf_N_area	3.02106	NA
BR-Sa1	Cordia bicolor	2003	258	Nmass	26.09524	NA
BR-Sa1	Sclerolobium paraense	2003	75	leaf_P_dry	0.624325	NA
BR-Sa1	Cordia bicolor	2003	258	SLA	7.988434	NA
BR-Sa1	Duguetia cadaverica	2003	75	C_N	17.49061	NA
BR-Sa1	Duguetia cadaverica	2003	75	leaf_C_concentration	464.5734	NA
BR-Sa1	Duguetia cadaverica	2003	75	d13c	-35.7321	NA
BR-Sa1	Duguetia cadaverica	2003	258	LMA	64.59305	NA
BR-Sa1	Duguetia cadaverica	2003	258	leaf_N_area	3.228568	NA
BR-Sa1	Duguetia cadaverica	2003	75	leaf_N_area	1.713026	NA
BR-Sa1	Duguetia cadaverica	2003	75	Nmass	26.56131	NA
BR-Sa1	Duguetia cadaverica	2003	258	SLA	15.48154	NA
BR-Sa1	Faramea platyneura	2003	258	C_N	16.6949	NA
BR-Sa1	Faramea platyneura	2003	75	C_N	18.24984	NA
BR-Sa1	Faramea platyneura	2003	258	leaf_C_concentration	346.3573	NA
BR-Sa1	Faramea platyneura	2003	75	leaf_C_concentration	388.8683	NA
BR-Sa1	Faramea platyneura	2003	258	d13c	-32.4739	NA
BR-Sa1	Faramea platyneura	2003	75	d13c	-32.6458	NA
BR-Sa1	Faramea platyneura	2003	258	LMA	66.30424	NA
BR-Sa1	Faramea platyneura	2003	258	LMA	79.61101	NA
BR-Sa1	Faramea platyneura	2003	258	leaf_N_area	1.364314	NA
BR-Sa1	Faramea platyneura	2003	75	leaf_N_area	1.852174	NA
BR-Sa1	Faramea platyneura	2003	258	Nmass	20.7463	NA
BR-Sa1	Faramea platyneura	2003	75	Nmass	21.30804	NA
BR-Sa1	Micropholis	2003	258	leaf_P_dry	0.637772	NA
BR-Sa1	Miconia acinodendron	2003	258	leaf_P_dry	0.639053	NA
BR-Sa1	Faramea platyneura	2003	258	SLA	15.08199	NA
BR-Sa1	Faramea platyneura	2003	258	SLA	12.56108	NA
BR-Sa1	Lecythis lurida	2003	75	C_N	25.405	NA

BR-Sa1	Lecythis lurida	2003	75	leaf_C_concentration	518.4738	NA
BR-Sa1	Lecythis lurida	2003	75	d13c	-29.6471	NA
BR-Sa1	Lecythis lurida	2003	75	LMA	135.8351	NA
BR-Sa1	Lecythis lurida	2003	75	leaf_N_area	2.754652	NA
BR-Sa1	Lecythis lurida	2003	75	Nmass	20.40833	NA
BR-Sa1	Protium puncticulatum	2003	258	leaf_P_dry	0.645456	NA
BR-Sa1	Lecythis lurida	2003	75	SLA	7.361869	NA
BR-Sa1	Lecythis	2003	258	C_N	20.71004	NA
BR-Sa1	Lecythis	2003	75	C_N	19.9124	NA
BR-Sa1	Lecythis	2003	258	leaf_C_concentration	465.3815	NA
BR-Sa1	Lecythis	2003	75	leaf_C_concentration	449.1628	NA
BR-Sa1	Lecythis	2003	258	d13c	-32.1056	NA
BR-Sa1	Lecythis	2003	75	d13c	-32.2835	NA
BR-Sa1	Lecythis	2003	258	LMA	98.6091	NA
BR-Sa1	Lecythis	2003	258	LMA	83.7238	NA
BR-Sa1	Lecythis	2003	258	leaf_N_area	2.21891	NA
BR-Sa1	Lecythis	2003	75	leaf_N_area	1.967279	NA
BR-Sa1	Lecythis	2003	258	Nmass	22.4713	NA
BR-Sa1	Lecythis	2003	75	Nmass	22.55694	NA
BR-Sa1	Faramea platyneura	2003	258	leaf_P_dry	0.65314	NA
BR-Sa1	Lecythis	2003	258	SLA	10.14105	NA
BR-Sa1	Lecythis	2003	258	SLA	11.94404	NA
BR-Sa1	Manilkara huberi	2003	258	C_N	35.0992	NA
BR-Sa1	Manilkara huberi	2003	75	C_N	40.32585	NA
BR-Sa1	Manilkara huberi	2003	258	leaf_C_concentration	514.83	NA
BR-Sa1	Manilkara huberi	2003	75	leaf_C_concentration	542.9203	NA
BR-Sa1	Manilkara huberi	2003	258	d13c	-29.6647	NA
BR-Sa1	Manilkara huberi	2003	75	d13c	-29.8505	NA
BR-Sa1	Manilkara huberi	2003	258	LMA	179.5436	NA
BR-Sa1	Manilkara huberi	2003	258	LMA	170.1594	NA
BR-Sa1	Manilkara huberi	2003	258	leaf_N_area	2.631965	NA
BR-Sa1	Manilkara huberi	2003	75	leaf_N_area	2.290636	NA
BR-Sa1	Manilkara huberi	2003	258	Nmass	14.66786	NA
BR-Sa1	Manilkara huberi	2003	75	Nmass	13.46333	NA
BR-Sa1	Sclerolobium paraense	2003	75	leaf_P_dry	0.668508	NA
BR-Sa1	Manilkara huberi	2003	258	SLA	5.569678	NA
BR-Sa1	Manilkara huberi	2003	258	SLA	5.876842	NA
BR-Sa1	Memora tanaeciicarpa	2003	258	C_N	20.23099	NA
BR-Sa1	Memora tanaeciicarpa	2003	258	leaf_C_concentration	468.0103	NA
BR-Sa1	Memora tanaeciicarpa	2003	258	d13c	-28.6675	NA
BR-Sa1	Memora tanaeciicarpa	2003	258	LMA	108.7717	NA

BR-Sa1	Memora tanaeciicarpa	2003	258	leaf_N_area	2.460774	NA
BR-Sa1	Memora tanaeciicarpa	2003	258	Nmass	23.13333	NA
BR-Sa1	Memora tanaeciicarpa	2003	258	SLA	9.193569	NA
BR-Sa1	Miconia acinodendron	2003	258	C_N	18.72748	NA
BR-Sa1	Miconia acinodendron	2003	75	C_N	18.02796	NA
BR-Sa1	Miconia acinodendron	2003	258	leaf_C_concentration	388.8814	NA
BR-Sa1	Miconia acinodendron	2003	75	leaf_C_concentration	389.8045	NA
BR-Sa1	Miconia acinodendron	2003	258	d13c	-35.1489	NA
BR-Sa1	Miconia acinodendron	2003	75	d13c	-34.6149	NA
BR-Sa1	Miconia acinodendron	2003	258	LMA	49.62648	NA
BR-Sa1	Miconia acinodendron	2003	75	LMA	42.92794	NA
BR-Sa1	Miconia acinodendron	2003	258	leaf_N_area	1.032903	NA
BR-Sa1	Miconia acinodendron	2003	258	Nmass	20.76528	NA
BR-Sa1	Miconia acinodendron	2003	75	Nmass	21.62222	NA
BR-Sa1	Lecythis	2003	258	leaf_P_dry	0.678753	NA
BR-Sa1	Miconia acinodendron	2003	258	SLA	20.15053	NA
BR-Sa1	Miconia acinodendron	2003	75	SLA	23.29485	NA
BR-Sa1	Micropholis	2003	258	C_N	29.46347	NA
BR-Sa1	Micropholis	2003	75	C_N	29.72877	NA
BR-Sa1	Micropholis	2003	258	leaf_C_concentration	491.4997	NA
BR-Sa1	Micropholis	2003	75	leaf_C_concentration	485.669	NA
BR-Sa1	Micropholis	2003	258	d13c	-29.6385	NA
BR-Sa1	Micropholis	2003	75	d13c	-29.0139	NA
BR-Sa1	Micropholis	2003	258	LMA	136.7962	NA
BR-Sa1	Micropholis	2003	75	LMA	138.4076	NA
BR-Sa1	Micropholis	2003	75	leaf_N_area	0.958051	NA
BR-Sa1	Micropholis	2003	258	leaf_N_area	2.282778	NA
BR-Sa1	Micropholis	2003	75	leaf_N_area	2.255402	NA
BR-Sa1	Micropholis	2003	258	Nmass	16.68167	NA
BR-Sa1	Micropholis	2003	75	Nmass	16.33667	NA
BR-Sa1	Manilkara huberi	2003	258	leaf_P_dry	0.700525	NA
BR-Sa1	Micropholis	2003	258	SLA	7.310145	NA
BR-Sa1	Micropholis	2003	75	SLA	7.225039	NA
BR-Sa1	Prinostemma af. aspera	2003	258	C_N	23.91961	NA
BR-Sa1	Prinostemma af. aspera	2003	258	leaf_C_concentration	436.6076	NA
BR-Sa1	Prinostemma af. aspera	2003	258	d13c	-28.8573	NA
BR-Sa1	Prinostemma af. aspera	2003	258	LMA	160.6403	NA
BR-Sa1	Prinostemma af. aspera	2003	258	LMA	95.25519	NA
BR-Sa1	Prinostemma af. aspera	2003	258	leaf_N_area	2.910567	NA
BR-Sa1	Prinostemma af. aspera	2003	258	Nmass	18.25313	NA
BR-Sa1	Sclerolobium paraense	2003	258	leaf_P_dry	0.715893	NA

BR-Sa1	Prinostemma af. aspera	2003	258	SLA	6.225087		NA
BR-Sa1	Prinostemma af. aspera	2003	258	SLA	10.49812		NA
BR-Sa1	Protium puncticulatum	2003	258	C_N	31.5554		NA
BR-Sa1	Protium puncticulatum	2003	75	C_N	32.24622		NA
BR-Sa1	Protium puncticulatum	2003	258	leaf_C_concentration	462.1113		NA
BR-Sa1	Protium puncticulatum	2003	75	leaf_C_concentration	457.3588		NA
BR-Sa1	Protium puncticulatum	2003	258	d13c	-31.6378		NA
BR-Sa1	Protium puncticulatum	2003	75	d13c	-33.6		NA
BR-Sa1	Protium puncticulatum	2003	75	LMA	98.44637		NA
BR-Sa1	Protium puncticulatum	2003	258	leaf_N_area	1.3979		NA
BR-Sa1	Protium puncticulatum	2003	75	leaf_N_area	1.394642		NA
BR-Sa1	Protium puncticulatum	2003	258	Nmass	14.64444		NA
BR-Sa1	Protium puncticulatum	2003	75	Nmass	14.18333		NA
BR-Sa1	Anomalocalyx uleanus	2003	75	leaf_P_dry	0.737664	1	NA
BR-Sa1	Micropholis	2003	75	leaf_P_dry	0.737664		NA
BR-Sa1	Protium puncticulatum	2003	75	SLA	10.15782		NA
BR-Sa1	Rinorea neglecta	2003	258	C_N	12.61557		NA
BR-Sa1	Rinorea neglecta	2003	75	C_N	12.10307		NA
BR-Sa1	Rinorea neglecta	2003	258	leaf_C_concentration	459.7148		NA
BR-Sa1	Rinorea neglecta	2003	75	leaf_C_concentration	461.1268		NA
BR-Sa1	Rinorea neglecta	2003	258	d13c	-35.3092		NA
BR-Sa1	Rinorea neglecta	2003	75	d13c	-36.2063		NA
BR-Sa1	Rinorea neglecta	2003	258	LMA	46.18053		NA
BR-Sa1	Rinorea neglecta	2003	75	LMA	42.08188		NA
BR-Sa1	Rinorea neglecta	2003	258	leaf_N_area	1.675471		NA
BR-Sa1	Rinorea neglecta	2003	75	leaf_N_area	1.557367		NA
BR-Sa1	Rinorea neglecta	2003	258	Nmass	36.44028		NA
BR-Sa1	Rinorea neglecta	2003	75	Nmass	38.1		NA
BR-Sa1	Protium puncticulatum	2003	75	leaf_P_dry	0.737664		NA
BR-Sa1	Abuta rufescens	2003	258	leaf_P_dry	0.745348	1	NA
BR-Sa1	Rinorea neglecta	2003	258	SLA	21.65415		NA
BR-Sa1	Rinorea neglecta	2003	75	SLA	23.76319		NA
BR-Sa1	Sclerolobium paraense	2003	258	C_N	24.02573		NA
BR-Sa1	Sclerolobium paraense	2003	75	C_N	21.50169		NA
BR-Sa1	Sclerolobium paraense	2003	258	C_N	25.7919		NA
BR-Sa1	Sclerolobium paraense	2003	75	C_N	24.06063		NA
BR-Sa1	Sclerolobium paraense	2003	258	leaf_C_concentration	501.0031		NA
BR-Sa1	Sclerolobium paraense	2003	75	leaf_C_concentration	514.9972		NA
BR-Sa1	Sclerolobium paraense	2003	258	leaf_C_concentration	505.3421		NA
BR-Sa1	Sclerolobium paraense	2003	75	leaf_C_concentration	504.8392		NA

BR-Sa1	Sclerolobium paraense	2003	258	d13c	-31.0521	NA
BR-Sa1	Sclerolobium paraense	2003	75	d13c	-31.0905	NA
BR-Sa1	Sclerolobium paraense	2003	258	d13c	-35.2251	NA
BR-Sa1	Sclerolobium paraense	2003	75	d13c	-34.3659	NA
BR-Sa1	Sclerolobium paraense	2003	258	LMA	107.1239	NA
BR-Sa1	Sclerolobium paraense	2003	75	LMA	117.462	NA
BR-Sa1	Sclerolobium paraense	2003	258	LMA	79.23593	NA
BR-Sa1	Sclerolobium paraense	2003	75	LMA	74.53946	NA
BR-Sa1	Sclerolobium paraense	2003	258	leaf_N_area	2.230341	NA
BR-Sa1	Sclerolobium paraense	2003	75	leaf_N_area	2.827665	NA
BR-Sa1	Sclerolobium paraense	2003	258	leaf_N_area	1.550742	NA
BR-Sa1	Sclerolobium paraense	2003	75	leaf_N_area	1.565412	NA
BR-Sa1	Sclerolobium paraense	2003	258	Nmass	20.85278	NA
BR-Sa1	Sclerolobium paraense	2003	75	Nmass	23.95148	NA
BR-Sa1	Sclerolobium paraense	2003	258	Nmass	19.59306	NA
BR-Sa1	Sclerolobium paraense	2003	75	Nmass	20.98196	NA
BR-Sa1	Duguetia cadaverica	2003	75	leaf_P_dry	0.772242	NA
BR-Sa1	Tachigali myrmecophila	2003	258	leaf_P_dry	0.791452	NA
BR-Sa1	Sclerolobium paraense	2003	258	SLA	9.334982	NA
BR-Sa1	Sclerolobium paraense	2003	75	SLA	8.51339	NA
BR-Sa1	Sclerolobium paraense	2003	258	SLA	12.62054	NA
BR-Sa1	Sclerolobium paraense	2003	75	SLA	13.41571	NA
BR-Sa1	Tachigali myrmecophila	2003	258	C_N	14.61992	NA
BR-Sa1	Tachigali myrmecophila	2003	258	C_N	13.7856	NA
BR-Sa1	Tachigali myrmecophila	2003	258	leaf_C_concentration	476.2439	NA
BR-Sa1	Tachigali myrmecophila	2003	258	leaf_C_concentration	493.8691	NA
BR-Sa1	Tachigali myrmecophila	2003	258	d13c	-30.8894	NA
BR-Sa1	Tachigali myrmecophila	2003	258	d13c	-29.4429	NA
BR-Sa1	Tachigali myrmecophila	2003	258	LMA	128.3358	NA
BR-Sa1	Tachigali myrmecophila	2003	258	LMA	110.1257	NA
BR-Sa1	Tachigali myrmecophila	2003	258	leaf_N_area	3.981593	NA
BR-Sa1	Tachigali myrmecophila	2003	258	leaf_N_area	4.008869	NA
BR-Sa1	Tachigali myrmecophila	2003	258	Nmass	32.575	NA
BR-Sa1	Tachigali myrmecophila	2003	258	Nmass	35.825	NA
BR-Sa1	Tachigali myrmecophila	2003	258	SLA	7.79206	NA
BR-Sa1	Tachigali	2003	258	SLA	9.080533	NA

	myrmecophila						
BR-Sa1	Tetrapterys sp.	2003	258	C_N	21.56494		NA
BR-Sa1	Tetrapterys sp.	2003	75	C_N	19.19469		NA
BR-Sa1	Tetrapterys sp.	2003	258	leaf_C_concentration	468.1029		NA
BR-Sa1	Tetrapterys sp.	2003	75	leaf_C_concentration	457.8633		NA
BR-Sa1	Tetrapterys sp.	2003	258	d13c	-26.8953		NA
BR-Sa1	Tetrapterys sp.	2003	75	d13c	-27.1547		NA
BR-Sa1	Tetrapterys sp.	2003	258	LMA	107.3704		NA
BR-Sa1	Tetrapterys sp.	2003	75	LMA	108.9292		NA
BR-Sa1	Tetrapterys sp.	2003	258	leaf_N_area	2.294783		NA
BR-Sa1	Tetrapterys sp.	2003	75	leaf_N_area	2.655185		NA
BR-Sa1	Tetrapterys sp.	2003	258	Nmass	21.70667		NA
BR-Sa1	Tetrapterys sp.	2003	75	Nmass	23.85365		NA
BR-Sa1	Cordia bicolor	2003	258	leaf_P_dry	0.827951		NA
BR-Sa1	Tetrapterys sp.	2003	258	SLA	9.313556		NA
BR-Sa1	Tetrapterys sp.	2003	75	SLA	9.180273		NA
BR-Sa1	Lecythis	2003	75	leaf_P_dry	0.829872		NA
BR-Sa1	Miconia acinodendron	2003	75	leaf_P_dry	0.851003		NA
BR-Sa1	Arrabidea prancei	2003	258	leaf_P_dry	0.92208		NA
BR-Sa1	Memora tanaeciicarpa	2003	258	leaf_P_dry	0.952816		NA
BR-Sa1	Rinorea neglecta	2003	258	leaf_P_dry	1.00557		NA
BR-Sa1	Rinorea neglecta	2003	75	leaf_P_dry	1.01813		NA
BR-Sa1	Tachigali myrmecophila	2003	258	leaf_P_dry	1.03734		NA
BR-Sa1	Combretum	2003	258	leaf_P_dry	1.09497		NA
BR-Sa1	Copaifera duckei	2003	75	leaf_P_dry	1.178213		NA
BR-Sa1	Sclerolobium paraense	2003	258	leaf_P_dry	1.19102		NA
BR-Sa1	Tetrapterys sp.	2003	75	leaf_P_dry	1.22944		NA
BR-Sa1	Tetrapterys sp.	2003	258	leaf_P_dry	1.282268		NA
BR-Sa1	Copaifera duckei	2003	258	leaf_P_dry	1.447153		NA
CA-Qfo	Picea mariana	2004	260	leaf_C_concentration	522.75	6	4.983473
CA-Qfo	Picea mariana	2004	260	leaf_C_concentration	528.75	6	5.354157
CA-Qfo	Picea mariana	2004	260	leaf_C_concentration	523.5	6	5.068037
CA-Qfo	Picea mariana	2004	260	leaf_C_concentration	525.32	6	4.693826
CA-Qfo	Picea mariana	2004	260	leaf_C_concentration	531.7833	6	3.20588
CA-Qfo	Picea mariana	2004	260	leaf_C_concentration	528.2	5	4.520509
CA-Qfo	Picea mariana	2004	260	leaf_C_concentration	531.3	6	5.256234
CA-Qfo	Picea mariana	2004	260	leaf_C_concentration	526.24	5	5.397963
CA-Qfo	Picea mariana	2004	260	LMA	252.1415	6	40.2122

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CA-Qfo	Picea mariana	2004	260	LMA	259.4226	6	35.72555
CA-Qfo	Picea mariana	2004	260	LMA	276.1936	5	22.76597
CA-Qfo	Picea mariana	2004	260	LMA	308.6999	5	37.73963
CA-Qfo	Picea mariana	2004	260	LMA	310.1596	6	42.00169
CA-Qfo	Picea mariana	2004	260	LMA	312.7054	5	31.43707
CA-Qfo	Picea mariana	2004	260	LMA	302.3314	6	47.445
CA-Qfo	Picea mariana	2004	260	LMA	320.0109	5	57.53132
CA-Qfo	Picea mariana	2004	260	leaf_N_area	1.895887	6	0.613965
CA-Qfo	Picea mariana	2004	260	leaf_N_area	1.904041	6	0.310821
CA-Qfo	Picea mariana	2004	260	leaf_N_area	2.296	5	0.466026
CA-Qfo	Picea mariana	2004	260	leaf_N_area	2.253339	5	0.386622
CA-Qfo	Picea mariana	2004	260	leaf_N_area	2.156212	6	0.275629
CA-Qfo	Picea mariana	2004	260	leaf_N_area	2.014709	5	0.371308
CA-Qfo	Picea mariana	2004	260	leaf_N_area	2.329155	6	0.325681
CA-Qfo	Picea mariana	2004	260	leaf_N_area	2.114956	5	0.472206
CA-Qfo	Picea mariana	2004	260	Nmass	7.383333	6	1.178841
CA-Qfo	Picea mariana	2004	260	Nmass	7.35	6	0.712039
CA-Qfo	Picea mariana	2004	260	Nmass	7.2	6	6.324555
CA-Qfo	Picea mariana	2004	260	Nmass	7.32	6	1.025671
CA-Qfo	Picea mariana	2004	260	Nmass	6.966667	6	0.476095
CA-Qfo	Picea mariana	2004	260	Nmass	6.44	6	0.887694
CA-Qfo	Picea mariana	2004	260	Nmass	7.75	6	0.816701
CA-Qfo	Picea mariana	2004	260	Nmass	6.6	6	0.827647
CA-Qfo	Picea mariana	2004	260	SLA	4.047762	6	0.621051
CA-Qfo	Picea mariana	2004	260	SLA	3.918073	6	0.558167
CA-Qfo	Picea mariana	2004	260	SLA	3.277019	5	0.386599
CA-Qfo	Picea mariana	2004	260	SLA	3.225188	5	0.703247
CA-Qfo	Picea mariana	2004	260	SLA	3.276725	6	0.46944

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CA-Qfo	Picea mariana	2004	260	SLA	3.224809	5	0.335422
CA-Qfo	Picea mariana	2004	260	SLA	3.380371	6	0.560971
CA-Qfo	Picea mariana	2004	260	SLA	3.225188	5	0.703247
CA-Qfo	Pinus banksiana	2004	260	leaf_C_concentration	510.2	6	9.068627
CA-Qfo	Pinus banksiana	2004	260	leaf_C_concentration	525.6333	6	6.400208
CA-Qfo	Pinus banksiana	2004	260	leaf_C_concentration	515.6	6	5.754998
CA-Qfo	Pinus banksiana	2004	260	leaf_C_concentration	523.5	6	9.902525
CA-Qfo	Pinus banksiana	2004	260	leaf_C_concentration	532	6	7.331576
CA-Qfo	Pinus banksiana	2004	260	leaf_C_concentration	530.2167	6	9.828615
CA-Qfo	Pinus banksiana	2004	260	LMA	252.2163	6	18.24265
CA-Qfo	Pinus banksiana	2004	260	LMA	261.0103	6	21.08705
CA-Qfo	Pinus banksiana	2004	260	LMA	279.3199	6	33.29114
CA-Qfo	Pinus banksiana	2004	260	LMA	289.4805	5	26.13076
CA-Qfo	Pinus banksiana	2004	260	LMA	302.6139	6	28.58304
CA-Qfo	Pinus banksiana	2004	260	LMA	308.2892	6	33.62481
CA-Qfo	Pinus banksiana	2004	260	leaf_N_area	2.624927	6	0.303174
CA-Qfo	Pinus banksiana	2004	260	leaf_N_area	2.507099	6	0.27662
CA-Qfo	Pinus banksiana	2004	260	leaf_N_area	2.798011	6	0.478049
CA-Qfo	Pinus banksiana	2004	260	leaf_N_area	2.703644	5	0.752066
CA-Qfo	Pinus banksiana	2004	260	leaf_N_area	2.879595	6	0.616819
CA-Qfo	Pinus banksiana	2004	260	leaf_N_area	2.949305	6	0.588919
CA-Qfo	Pinus banksiana	2004	260	Nmass	10.38333	6	0.526941
CA-Qfo	Pinus banksiana	2004	260	Nmass	9.65	6	1.270827
CA-Qfo	Pinus banksiana	2004	260	Nmass	9.983333	6	1.026483
CA-Qfo	Pinus banksiana	2004	260	Nmass	9.4	6	2.636285
CA-Qfo	Pinus banksiana	2004	260	Nmass	9.45	6	1.557883
CA-Qfo	Pinus banksiana	2004	260	Nmass	9.583333	6	1.828023
CA-Qfo	Pinus banksiana	2004	260	SLA	3.982233	6	0.28894

CA-Qfo	Pinus banksiana	2004	260	SLA	3.85439	6	0.34413
CA-Qfo	Pinus banksiana	2004	260	SLA	3.621027	6	0.415174
CA-Qfo	Pinus banksiana	2004	260	SLA	3.478943	5	0.339643
CA-Qfo	Pinus banksiana	2004	260	SLA	3.329662	6	0.321231
CA-Qfo	Pinus banksiana	2004	260	SLA	3.278862	6	0.387279
CA-Qfo	Picea mariana	2004	260	leaf_P_dry	0.993958	5	0.121484
CA-Qfo	Pinus banksiana	2004	260	leaf_P_dry	1.53	6	0.118491
CA-Qfo	Pinus banksiana	2004	260	leaf_P_dry	1.558333	6	0.168928
CA-Qfo	Pinus banksiana	2004	260	leaf_P_dry	1.616667	6	0.130945
CA-Qfo	Picea mariana	2004	260	leaf_P_dry	1.644	5	0.498478
CA-Qfo	Pinus banksiana	2004	260	leaf_P_dry	1.712	5	0.350885
CA-Qfo	Picea mariana	2004	260	leaf_P_dry	1.781667	6	0.423859
CA-Qfo	Picea mariana	2004	260	leaf_P_dry	1.798	5	0.576429
CA-Qfo	Picea mariana	2004	260	leaf_P_dry	1.902	5	0.541175
CA-Qfo	Pinus banksiana	2004	260	leaf_P_dry	1.973333	6	0.179741
CA-Qfo	Pinus banksiana	2004	260	leaf_P_dry	2	6	0.514471
CA-Qfo	Picea mariana	2004	260	leaf_P_dry	2.108333	6	0.571679
CA-Qfo	Picea mariana	2004	260	leaf_P_dry	2.17	6	0.500879
CA-Qfo	Picea mariana	2004	260	leaf_P_area	0.518685	5	0.194863
CA-Qfo	Picea mariana	2004	260	leaf_P_area	0.553253	6	0.150266
CA-Qfo	Picea mariana	2004	260	leaf_P_dry	2.635	6	0.3895
CA-Qfo	Picea mariana	2004	260	leaf_P_area	0.559374	6	0.131783
CA-Qfo	Picea mariana	2004	260	leaf_P_area	0.575945	5	0.119933
CA-Qfo	Picea mariana	2004	260	leaf_P_area	0.587089	5	0.264637
CA-Qfo	Picea mariana	2004	260	leaf_P_area	0.635053	6	0.180815
CA-Qfo	Picea mariana	2004	260	leaf_P_area	0.638495	5	0.168144
CA-Qfo	Picea mariana	2004	260	leaf_P_area	0.673245	6	0.185574
CZ-BK1	Picea abies	2012	220	leaf_P_dry	0.806736		NA
CZ-	Picea abies	2012	220	C_N	41.37248	4	4.27497

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CZ-BK1	Picea abies	2012	220	C_N	40.64111	4	6.289726
CZ-BK1	Picea abies	2012	220	C_N	44.86464	4	6.508777
CZ-BK1	Picea abies	2012	220	C_N	45.60159	4	4.343973
CZ-BK1	Picea abies	2012	220	C_N	46.03571	4	3.948523
CZ-BK1	Picea abies	2012	220	C_N	47.80298	4	5.566159
CZ-BK1	Picea abies	2012	220	leaf_C_concentration	507.556	4	9.370307
CZ-BK1	Picea abies	2012	220	leaf_C_concentration	502.085	4	12.20735
CZ-BK1	Picea abies	2012	220	leaf_C_concentration	499.6901	4	5.224272
CZ-BK1	Picea abies	2012	220	leaf_C_concentration	498.5571	4	8.259694
CZ-BK1	Picea abies	2012	220	leaf_C_concentration	505.7366	4	5.219117
CZ-BK1	Picea abies	2012	220	leaf_C_concentration	496.8913	4	6.606992
CZ-BK1	Picea abies	2012	220	d13c	-27.2352	4	0.401536
CZ-BK1	Picea abies	2012	220	d13c	-28.272	4	0.434903
CZ-BK1	Picea abies	2012	220	d13c	-27.8752	4	0.228163
CZ-BK1	Picea abies	2012	220	d13c	-28.4993	4	1.103449
CZ-BK1	Picea abies	2012	220	d13c	-29.9434	4	0.685578
CZ-BK1	Picea abies	2012	220	d13c	-29.176	4	0.464839
CZ-BK1	Picea abies	2012	220	LMA	272.085	6	120.1019
CZ-BK1	Picea abies	2012	220	LMA	304.2067	6	130.7844
CZ-BK1	Picea abies	2012	220	LMA	160.8045	6	66.51289
CZ-BK1	Picea abies	2012	220	LMA	173.2987	6	74.07605
CZ-BK1	Picea abies	2012	220	LMA	337.691	6	141.7467
CZ-BK1	Picea abies	2012	220	LMA	228.7344	6	97.68917
CZ-BK1	Picea abies	2012	220	leaf_N_area	3.536911	4	0.477163
CZ-BK1	Picea abies	2012	220	leaf_N_area	4.068378	4	0.554953
CZ-BK1	Picea abies	2012	220	leaf_N_area	1.843508	4	0.273095
CZ-BK1	Picea abies	2012	220	leaf_N_area	1.970654	4	0.211989

CZ-BK1	Picea abies	2012	220	leaf_N_area	3.896405	4	0.440227
CZ-BK1	Picea abies	2012	220	leaf_N_area	2.426662	4	0.226194
CZ-BK1	Picea abies	2012	220	Nmass	12.35417	4	1.130254
CZ-BK1	Picea abies	2012	220	Nmass	12.55304	4	1.718576
CZ-BK1	Picea abies	2012	220	Nmass	11.31882	4	1.66653
CZ-BK1	Picea abies	2012	220	Nmass	11.02353	4	1.271188
CZ-BK1	Picea abies	2012	220	Nmass	11.04416	4	0.910048
CZ-BK1	Picea abies	2012	220	Nmass	10.50392	4	1.253047
CZ-BK1	Picea abies	2012	220	SLA	3.536341	4	0.542311
CZ-BK1	Picea abies	2012	220	SLA	3.085808	4	0.100357
CZ-BK1	Picea abies	2012	220	SLA	2.84488	4	0.161149
CZ-BK1	Picea abies	2012	220	SLA	6.15151	4	0.456781
CZ-BK1	Picea abies	2012	220	SLA	5.622321	4	0.658339
CZ-BK1	Picea abies	2012	220	SLA	4.351419	4	0.576262
CZ-BK1	Picea abies	2012	220	leaf_N_P	7.979308	4	4.008193
CZ-BK1	Picea abies	2012	220	leaf_N_P	8.938038	4	3.625359
CZ-BK1	Picea abies	2012	220	leaf_P_dry	1.168988		NA
CZ-BK1	Picea abies	2012	220	leaf_P_dry	1.179793		NA
CZ-BK1	Picea abies	2012	220	leaf_N_P	9.739276	4	1.729412
CZ-BK1	Picea abies	2012	220	leaf_N_P	9.876813	4	3.439689
CZ-BK1	Picea abies	2012	220	leaf_P_dry	1.29224		NA
CZ-BK1	Picea abies	2012	220	leaf_N_P	10.70829	4	1.23494
CZ-BK1	Picea abies	2012	220	leaf_P_dry	1.41187		NA
CZ-BK1	Picea abies	2012	220	leaf_P_dry	1.706121		NA
CZ-BK1	Picea abies	2012	220	leaf_P_area	0.248312	4	0.09941
CZ-BK1	Picea abies	2012	220	leaf_P_area	0.264235	4	0.073137
CZ-BK1	Picea abies	2012	220	leaf_P_area	0.271539	4	0.108039
CZ-BK1	Picea abies	2012	220	leaf_N_P	14.82132	4	4.823984

CZ-BK1	Picea abies	2012	220	leaf_P_area	0.286298	4	0.096417
CZ-BK1	Picea abies	2012	220	leaf_P_area	0.377704	4	0.115888
CZ-BK1	Picea abies	2012	220	leaf_P_area	0.383014	4	0.064817
DE-Hai	Fagus sylvatica	2012	200	leaf_P_area	0.037865	4	0.005153
DE-Hai	Fagus sylvatica	2012	200	leaf_P_area	0.084183	4	0.009987
DE-Hai	Acer pseudoplatanus	2012	200	leaf_P_area	0.086216	3	0.010508
DE-Hai	Fagus sylvatica	2012	200	leaf_P_dry	1.025637	4	0.165748
DE-Hai	Acer pseudoplatanus	2012	200	C_N	18.88458	3	0.377186
DE-Hai	Acer pseudoplatanus	2012	200	C_N	14.61611	3	2.519437
DE-Hai	Acer pseudoplatanus	2012	200	leaf_C_concentration	464.7467	3	0.381813
DE-Hai	Acer pseudoplatanus	2012	200	leaf_C_concentration	455.0534	3	14.29387
DE-Hai	Acer pseudoplatanus	2012	200	d13c	-26.7708	3	0.501056
DE-Hai	Acer pseudoplatanus	2012	200	d13c	-30.2263	3	1.734747
DE-Hai	Acer pseudoplatanus	2012	200	LMA	84.04394	3	15.74983
DE-Hai	Acer pseudoplatanus	2012	200	LMA	32.4547	3	6.396047
DE-Hai	Acer pseudoplatanus	2012	200	leaf_N_area	2.064683	3	0.3577
DE-Hai	Acer pseudoplatanus	2012	200	leaf_N_area	1.00823	3	0.068314
DE-Hai	Acer pseudoplatanus	2012	200	Nmass	24.61659	3	0.506172
DE-Hai	Acer pseudoplatanus	2012	200	Nmass	31.70587	3	4.979227
DE-Hai	Acer pseudoplatanus	2012	200	SLA	12.2169	3	2.550017
DE-Hai	Acer pseudoplatanus	2012	200	SLA	31.72759	3	6.975987
DE-Hai	Fagus sylvatica	2012	200	C_N	24.6419	4	1.95332
DE-Hai	Fagus sylvatica	2012	200	C_N	20.54084	4	1.656818
DE-Hai	Fagus sylvatica	2012	200	leaf_C_concentration	487.6802	3	6.283017
DE-Hai	Fagus sylvatica	2012	200	leaf_C_concentration	477.9896	3	3.458201
DE-Hai	Fagus sylvatica	2012	200	d13c	-29.8687	4	1.047166
DE-Hai	Fagus sylvatica	2012	200	d13c	-33.3165	4	0.879891
DE-Hai	Fagus sylvatica	2012	200	LMA	83.67241	4	16.57177
DE-Hai	Fagus sylvatica	2012	200	LMA	26.75151	4	1.04736

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DE-Hai	Fagus sylvatica	2012	200	leaf_N_area	1.645544	4	0.20301
DE-Hai	Fagus sylvatica	2012	200	leaf_N_area	0.62458	4	0.040113
DE-Hai	Fagus sylvatica	2012	200	Nmass	19.88262	4	1.575109
DE-Hai	Fagus sylvatica	2012	200	Nmass	23.38182	4	1.853911
DE-Hai	Fraxinus excelsior	2012	200	leaf_P_area	0.09284	3	0.036691
DE-Hai	Fagus sylvatica	2012	200	SLA	12.29412	4.00E+00	2.323902
DE-Hai	Fagus sylvatica	2012	200	SLA	37.42468	4	1.485888
DE-Hai	Fraxinus excelsior	2012	200	C_N	21.05662	3	2.751209
DE-Hai	Fraxinus excelsior	2012	200	C_N	16.18066	3	1.67475
DE-Hai	Fraxinus excelsior	2012	200	leaf_C_concentration	466.7636	3	4.84613
DE-Hai	Fraxinus excelsior	2012	200	leaf_C_concentration	457.5171	3	12.46472
DE-Hai	Fraxinus excelsior	2012	200	d13c	-26.1473	3	0.50679
DE-Hai	Fraxinus excelsior	2012	200	d13c	-28.0728	3	1.231292
DE-Hai	Fraxinus excelsior	2012	200	LMA	120.7352	3	13.13755
DE-Hai	Fraxinus excelsior	2012	200	LMA	63.52553	3	41.84403
DE-Hai	Fraxinus excelsior	2012	200	leaf_N_area	2.682324	3	0.123888
DE-Hai	Fraxinus excelsior	2012	200	leaf_N_area	1.748655	3	1.012616
DE-Hai	Fraxinus excelsior	2012	200	Nmass	22.40804	3	2.770385
DE-Hai	Fraxinus excelsior	2012	200	Nmass	28.41854	3	2.076634
DE-Hai	Fraxinus excelsior	2012	200	SLA	8.347255	3	0.893045
DE-Hai	Fraxinus excelsior	2012	200	SLA	19.93495	3	9.57074
DE-Hai	Fraxinus excelsior	2012	200	leaf_P_dry	1.157334	3	0.16646
DE-Hai	Acer pseudoplatanus	2012	200	leaf_P_area	0.119962	3	0.013456
DE-Hai	Fraxinus excelsior	2012	200	leaf_P_area	0.14	3	0.026316
DE-Hai	Fagus sylvatica	2012	200	leaf_P_dry	1.416966	4	0.19738
DE-Hai	Acer pseudoplatanus	2012	200	leaf_P_dry	1.442893	3	0.125787
DE-Hai	Acer pseudoplatanus	2012	200	leaf_N_P	11.82988	3	1.789791
DE-Hai	Fraxinus excelsior	2012	200	leaf_P_dry	1.618078	3	0.362296
DE-Hai	Fagus sylvatica	2012	200	leaf_N_P	16.62389	4	1.375027
DE-Hai	Acer pseudoplatanus	2012	200	leaf_N_P	17.12704	3	1.15084

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DE-Hai	Fraxinus excelsior	2012	200	leaf_N_P	18.02492	3	3.10412
DE-Hai	Fraxinus excelsior	2012	200	leaf_N_P	19.61414	3	3.760937
DE-Hai	Fagus sylvatica	2012	200	leaf_N_P	19.65988	4	2.66104
DE-Hai	Acer pseudoplatanus	2012	200	leaf_P_dry	2.767742	3	0.889357
ES-ES2	Oryza sativa	2012	200	C_N	13.10593	20	1.874795
ES-ES2	Oryza sativa	2012	200	leaf_C_concentration	415.3668	20	4.850238
ES-ES2	Oryza sativa	2012	200	d13c	-27.8135	20	0.451654
ES-ES2	Oryza sativa	2012	200	LMA	179.358	20	63.71504
ES-ES2	Oryza sativa	2012	200	leaf_N_area	5.820197	20	2.302391
ES-ES2	Oryza sativa	2012	200	Nmass	32.34508	20	4.874341
ES-ES2	Oryza sativa	2012	200	SLA	6.379126	20	2.686352
ES-ES2	Oryza sativa	2012	200	leaf_N_P	13.0811	20	1.658532
ES-ES2	Oryza sativa	2012	200	leaf_P_area	0.521963	20	0.172626
ES-ES2	Oryza sativa	2012	200	leaf_P_dry	2.977446	20	0.437799
FI-Hyy	Picea abies	2012	302	leaf_N_P	8.349045	3	0.905318
FI-Hyy	Picea abies	2012	302	C_N	42.92493	3	16.51984
FI-Hyy	Picea abies	2012	302	C_N	50.65461	3	1.234745
FI-Hyy	Picea abies	2012	302	d13c	-29.4498	3	0.561158
FI-Hyy	Picea abies	2012	302	d13c	-28.2744	3	0.452142
FI-Hyy	Picea abies	2012	302	LMA	145.8689	3	44.08688
FI-Hyy	Picea abies	2012	302	LMA	241.7197	3	23.36703
FI-Hyy	Picea abies	2012	302	leaf_N_area	1.750313	3	0.214222
FI-Hyy	Picea abies	2012	302	leaf_N_area	2.38986	3	0.207573
FI-Hyy	Picea abies	2012	302	Nmass	13.34134	3	6.661114
FI-Hyy	Picea abies	2012	302	Nmass	9.894405	3	0.190481
FI-Hyy	Pinus sylvestris	2012	302	C_N	40.86391	7	3.872324
FI-Hyy	Pinus sylvestris	2012	302	C_N	39.98853	7	3.245345
FI-Hyy	Pinus sylvestris	2012	302	d13c	-29.8382	7	0.361092

FI-Hyy	Pinus sylvestris	2012	302	d13c	-28.493	7	0.655481
FI-Hyy	Pinus sylvestris	2012	302	LMA	174.1229	9	31.10548
FI-Hyy	Pinus sylvestris	2012	302	LMA	233.8305	9	22.46148
FI-Hyy	Pinus sylvestris	2012	302	leaf_N_area	2.092912	7	0.2387
FI-Hyy	Pinus sylvestris	2012	302	leaf_N_area	3.156287	6	0.317742
FI-Hyy	Pinus sylvestris	2012	302	Nmass	12.60366	7	1.053132
FI-Hyy	Pinus sylvestris	2012	302	Nmass	12.93537	6	0.891739
FI-Hyy	Picea abies	2012	302	leaf_P_dry	1.16488	3	0.084584
FI-Hyy	Pinus sylvestris	2012	302	leaf_N_P	9.018417	7	2.873457
FI-Hyy	Picea abies	2012	302	leaf_P_dry	1.192703	3	0.105645
FI-Hyy	Pinus sylvestris	2012	302	leaf_N_P	10.3648	7	2.69319
FI-Hyy	Pinus sylvestris	2012	302	leaf_P_dry	1.296396	7	0.38507
FI-Hyy	Picea abies	2012	302	leaf_P_area	0.172284	3	0.061216
FI-Hyy	Picea abies	2012	302	leaf_N_P	11.76899	3	6.800815
FI-Hyy	Pinus sylvestris	2012	302	leaf_P_dry	1.505415	7	0.505568
FI-Hyy	Pinus sylvestris	2012	302	leaf_P_area	0.218395	7	0.077706
FI-Hyy	Picea abies	2012	302	leaf_P_area	0.289031	3	0.043997
FI-Hyy	Pinus sylvestris	2012	302	leaf_P_area	0.363864	7	0.133522
FR-Hes	Fagus sylvatica	2011	228	leaf_P_area	0.049432	10	0.005291
FR-Hes	Fagus sylvatica	2011	228	leaf_P_area	0.06538	10	0.006998
FR-Hes	Fagus sylvatica	2003	167	C_N	19.96234	10	1.461301
FR-Hes	Fagus sylvatica	2003	167	C_N	19.39384	10	1.097209
FR-Hes	Fagus sylvatica	2003	167	C_N	18.55018	10	0.821906
FR-Hes	Fagus sylvatica	2003	228	C_N	22.68104	10	1.600873
FR-Hes	Fagus sylvatica	2003	228	C_N	21.19025	10	0.864256
FR-Hes	Fagus sylvatica	2003	228	C_N	21.30297	10	1.370329
FR-Hes	Fagus sylvatica	2003	167	leaf_C_concentration	482.8148	10	4.59945
FR-Hes	Fagus sylvatica	2003	167	leaf_C_concentration	480.0098	10	4.795202
FR-Hes	Fagus sylvatica	2003	167	leaf_C_concentration	477.77	10	4.696741

FR-Hes	Fagus sylvatica	2003	228	leaf_C_concentration	493.4956	10	7.849371
FR-Hes	Fagus sylvatica	2003	228	leaf_C_concentration	484.7656	10	11.98208
FR-Hes	Fagus sylvatica	2003	228	leaf_C_concentration	479.8913	10	6.638828
FR-Hes	Fagus sylvatica	2003	167	d13c	-28.34	12	0.52
FR-Hes	Fagus sylvatica	2003	167	d13c	-29.7	12	0.72
FR-Hes	Fagus sylvatica	2003	167	d13c	-31.04	16	0.92
FR-Hes	Fagus sylvatica	2003	167	LMA	84.04962	10	7.956937
FR-Hes	Fagus sylvatica	2003	167	LMA	50.29261	10	5.596207
FR-Hes	Fagus sylvatica	2003	167	LMA	38.02426	10	8.393933
FR-Hes	Fagus sylvatica	2003	228	LMA	65.30419	10	7.615242
FR-Hes	Fagus sylvatica	2003	228	LMA	41.3009	10	4.627143
FR-Hes	Fagus sylvatica	2003	228	LMA	32.6902	10	4.933893
FR-Hes	Fagus sylvatica	2003	167	leaf_N_area	2.03957	10	0.218319
FR-Hes	Fagus sylvatica	2003	167	leaf_N_area	1.253578	10	0.19434
FR-Hes	Fagus sylvatica	2003	167	leaf_N_area	0.973476	10	0.241521
FR-Hes	Fagus sylvatica	2003	228	leaf_N_area	1.421711	10	0.138736
FR-Hes	Fagus sylvatica	2003	228	leaf_N_area	0.947908	10	0.129935
FR-Hes	Fagus sylvatica	2003	228	leaf_N_area	1.023964	10	0.115868
FR-Hes	Fagus sylvatica	2003	167	Nmass	24.29625	10	1.646009
FR-Hes	Fagus sylvatica	2003	167	Nmass	24.82667	10	1.487996
FR-Hes	Fagus sylvatica	2003	167	Nmass	25.87167	10	1.148872
FR-Hes	Fagus sylvatica	2003	228	Nmass	21.84717	10	1.420194
FR-Hes	Fagus sylvatica	2003	228	Nmass	22.90467	10	0.929113
FR-Hes	Fagus sylvatica	2003	228	Nmass	22.61483	10	1.519123
FR-Hes	Fagus sylvatica	2003	167	SLA	12.00034	10	1.189663
FR-Hes	Fagus sylvatica	2003	167	SLA	20.11803	10	2.305044
FR-Hes	Fagus sylvatica	2003	167	SLA	27.20246	10	4.580571
FR-Hes	Fagus sylvatica	2003	228	SLA	15.50075	10	1.766879
FR-Hes	Fagus sylvatica	2003	228	SLA	24.50607	10	2.878502

FR-Hes	Fagus sylvatica	2003	228	SLA	31.18253	10	4.310205
FR-Hes	Fagus sylvatica	2011	228	leaf_P_area	0.109265	10	0.011696
FR-Hes	Fagus sylvatica	2011	228	leaf_P_dry	1.212121	10	0.192198
FR-Hes	Fagus sylvatica	2011	228	leaf_P_dry	1.283026	10	0.173357
FR-Hes	Fagus sylvatica	2011	228	leaf_P_dry	1.373162	10	0.186933
FR-Hes	Fagus sylvatica	2011	228	leaf_N_P	18.84094	10	2.689269
FR-Hes	Fagus sylvatica	2011	228	leaf_N_P	19.35009	10	2.545167
FR-Hes	Fagus sylvatica	2011	228	leaf_N_P	20.04441	10	2.377334
FR-Lq1	Lolium perenne	2011	167	leaf_P_area	0.081088		NA
FR-Lq1	Poa trivialis	2011	167	leaf_P_area	0.085208		NA
FR-Lq1	Agrostis capillaris	2011	167	leaf_P_area	0.090364		NA
FR-Lq1	Festuca rubra	2011	167	leaf_N_P	8.528292		NA
FR-Lq1	Agrostis capillaris	2011	167	C_N	10.95421	1	NA
FR-Lq1	Agrostis capillaris	2011	167	Nmass	40.2135	1	NA
FR-Lq1	Agrostis capillaris	2011	167	leaf_C_concentration	440.5071		NA
FR-Lq1	Agrostis capillaris	2011	167	SLA	37.75862	#REF!	NA
FR-Lq1	Agrostis capillaris	2011	167	d13c	-30.2334		NA
FR-Lq1	Agrostis capillaris	2011	167	LMA	26.48402	1	NA
FR-Lq1	Agrostis capillaris	2011	167	leaf_N_area	1.065015	1	NA
FR-Lq1	Dactylis glomerata	2011	167	C_N	10.47599	1	NA
FR-Lq1	Dactylis glomerata	2011	167	leaf_C_concentration	441.037		NA
FR-Lq1	Dactylis glomerata	2011	167	d13c	-28.4634		NA
FR-Lq1	Dactylis glomerata	2011	167	LMA	44.13284	1	NA
FR-Lq1	Dactylis glomerata	2011	167	leaf_N_area	1.857983	1	NA
FR-Lq1	Dactylis glomerata	2011	167	Nmass	42.09979	1	NA
FR-Lq1	Dactylis glomerata	2011	167	SLA	22.65886		NA
FR-Lq1	Festuca rubra	2011	167	C_N	17.6382		NA
FR-Lq1	Festuca rubra	2011	167	leaf_C_concentration	433.8001		NA
FR-Lq1	Festuca rubra	2011	167	d13c	-29.2014		NA
FR-Lq1	Festuca rubra	2011	167	LMA	83.69565	1	NA
FR-Lq1	Festuca rubra	2011	167	Nmass	24.59436		NA
FR-Lq1	Festuca rubra	2011	167	SLA	11.94805		NA
FR-Lq1	Lolium perenne	2011	167	C_N	12.2183	1	NA
FR-Lq1	Lolium perenne	2011	167	leaf_C_concentration	431.407		NA
FR-Lq1	Lolium perenne	2011	167	d13c	-31.1567		NA
FR-Lq1	Lolium perenne	2011	167	LMA	31.44105	1	NA
FR-Lq1	Lolium perenne	2011	167	leaf_N_area	1.110129	1	NA

FR-Lq1	Lolium perenne	2011	167	Nmass	35.30825	1	NA
FR-Lq1	Lolium perenne	2011	167	SLA	31.80556		NA
FR-Lq1	Poa pratensis	2011	167	C_N	11.63088	1	NA
FR-Lq1	Poa pratensis	2011	167	leaf_C_concentration	435.548		NA
FR-Lq1	Poa pratensis	2011	167	d13c	-28.3208		NA
FR-Lq1	Poa pratensis	2011	167	LMA	44.57547	1	NA
FR-Lq1	Poa pratensis	2011	167	leaf_N_area	1.669242	1	NA
FR-Lq1	Poa pratensis	2011	167	Nmass	37.44755	1	NA
FR-Lq1	Poa pratensis	2011	167	SLA	22.43386		NA
FR-Lq1	Poa trivialis	2011	167	C_N	10.3498	1	NA
FR-Lq1	Poa trivialis	2011	167	leaf_C_concentration	424.2212		NA
FR-Lq1	Poa trivialis	2011	167	d13c	-30.2614		NA
FR-Lq1	Poa trivialis	2011	167	LMA	27.1028	1	NA
FR-Lq1	Poa trivialis	2011	167	leaf_N_area	1.110899	1	NA
FR-Lq1	Poa trivialis	2011	167	Nmass	40.98835	1	NA
FR-Lq1	Poa trivialis	2011	167	SLA	36.89655		NA
FR-Lq1	Trifolium repens	2011	167	C_N	11.21133	1	NA
FR-Lq1	Trifolium repens	2011	167	leaf_C_concentration	438.7993		NA
FR-Lq1	Trifolium repens	2011	167	d13c	-28.818		NA
FR-Lq1	Trifolium repens	2011	167	LMA	40.28103	1	NA
FR-Lq1	Trifolium repens	2011	167	leaf_N_area	1.576555	1	NA
FR-Lq1	Trifolium repens	2011	167	Nmass	39.1389	1	NA
FR-Lq1	Trifolium repens	2011	167	SLA	24.82558		NA
FR-Lq1	Trifolium repens	2011	167	leaf_N_P	9.714208		NA
FR-Lq1	Poa pratensis	2011	167	leaf_P_area	0.149261		NA
FR-Lq1	Dactylis glomerata	2011	167	leaf_P_area	0.156426		NA
FR-Lq1	Trifolium repens	2011	167	leaf_P_area	0.162294		NA
FR-Lq1	Poa pratensis	2011	167	leaf_N_P	11.18335		NA
FR-Lq1	Agrostis capillaris	2011	167	leaf_N_P	11.7859		NA
FR-Lq1	Dactylis glomerata	2011	167	leaf_N_P	11.87775		NA
FR-Lq1	Poa trivialis	2011	167	leaf_N_P	13.03747		NA
FR-Lq1	Lolium perenne	2011	167	leaf_N_P	13.6904		NA
FR-Lq1	Festuca rubra	2011	167	leaf_P_area	0.241366		NA
FR-Lq1	Lolium perenne	2011	167	leaf_P_dry	2.579051		NA
FR-Lq1	Festuca rubra	2011	167	leaf_P_dry	2.883855		NA
FR-Lq1	Poa trivialis	2011	167	leaf_P_dry	3.143888		NA
FR-Lq1	Poa pratensis	2011	167	leaf_P_dry	3.348509		NA
FR-Lq1	Agrostis capillaris	2011	167	leaf_P_dry	3.412002		NA
FR-Lq1	Dactylis glomerata	2011	167	leaf_P_dry	3.544424		NA
FR-Lq1	Trifolium repens	2011	167	leaf_P_dry	4.029037		NA
FR-Lq2	Anthoxanthum odoratum	2011	167	leaf_N_P	7.169347		NA
FR-Lq2	Veronica chamaes	2011	167	leaf_N_P	8.027137		NA

FR-Lq2	Agrostis capillaris	2011	167	leaf_P_area	0.09186		NA
FR-Lq2	Trisetum flavescens	2011	167	leaf_N_P	8.388727		NA
FR-Lq2	Poa pratensis	2011	167	leaf_P_area	0.094181		NA
FR-Lq2	Trifolium repens	2011	167	leaf_P_area	0.096926		NA
FR-Lq2	Holcus mollis	2011	167	leaf_P_area	0.100225		NA
FR-Lq2	Phleum pratense	2011	167	leaf_N_P	8.965471		NA
FR-Lq2	Phleum pratense	2011	167	leaf_P_area	0.106021		NA
FR-Lq2	Agrostis capillaris	2011	167	leaf_N_P	9.310038		NA
FR-Lq2	Agrostis capillaris	2011	167	C_N	18.5938		NA
FR-Lq2	Agrostis capillaris	2011	167	leaf_C_concentration	438.6718		NA
FR-Lq2	Agrostis capillaris	2011	167	Nmass	23.59236	1	NA
FR-Lq2	Agrostis capillaris	2011	167	SLA	27.58621		NA
FR-Lq2	Agrostis capillaris	2011	167	d13c	-28.7042		NA
FR-Lq2	Agrostis capillaris	2011	167	LMA	36.25	1	NA
FR-Lq2	Agrostis capillaris	2011	167	leaf_N_area	0.855223		NA
FR-Lq2	Anthoxanthum odoratum	2011	167	C_N	21.46742		NA
FR-Lq2	Anthoxanthum odoratum	2011	167	leaf_C_concentration	442.5438		NA
FR-Lq2	Anthoxanthum odoratum	2011	167	d13c	-28.4098		NA
FR-Lq2	Anthoxanthum odoratum	2011	167	Nmass	20.61467	1	NA
FR-Lq2	Anthoxanthum odoratum	2011	167	SLA	24.56522		NA
FR-Lq2	Anthoxanthum odoratum	2011	167	LMA	40.70796	1	NA
FR-Lq2	Anthoxanthum odoratum	2011	167	leaf_N_area	0.839181		NA
FR-Lq2	Dactylis glomerata	2011	167	C_N	17.95367		NA
FR-Lq2	Dactylis glomerata	2011	167	leaf_C_concentration	445.0463		NA
FR-Lq2	Dactylis glomerata	2011	167	d13c	-26.9065		NA
FR-Lq2	Dactylis glomerata	2011	167	LMA	61.95652	1	NA
FR-Lq2	Dactylis glomerata	2011	167	leaf_N_area	1.535816		NA
FR-Lq2	Dactylis glomerata	2011	167	Nmass	24.7886	1	NA
FR-Lq2	Anthoxanthum odoratum	2011	167	leaf_P_area	0.117051		NA
FR-Lq2	Dactylis glomerata	2011	167	SLA	16.14035		NA
FR-Lq2	Festuca rubra	2011	167	C_N	14.89127		NA
FR-Lq2	Festuca rubra	2011	167	leaf_C_concentration	445.4887		NA
FR-Lq2	Festuca rubra	2011	167	d13c	-29.4016		NA
FR-Lq2	Festuca rubra	2011	167	LMA	74.61538	1	NA
FR-Lq2	Festuca rubra	2011	167	leaf_N_area	2.232201		NA
FR-Lq2	Festuca rubra	2011	167	Nmass	29.9161	1	NA
FR-Lq2	Festuca rubra	2011	167	SLA	13.40206		NA
FR-Lq2	Holcus mollis	2011	167	C_N	9.054379		NA

FR-Lq2	Holcus mollis	2011	167	leaf_C_concentration	432.0598		NA
FR-Lq2	Holcus mollis	2011	167	d13c	-29.3834		NA
FR-Lq2	Holcus mollis	2011	167	LMA	30.05464	1	NA
FR-Lq2	Holcus mollis	2011	167	leaf_N_area	1.434157		NA
FR-Lq2	Holcus mollis	2011	167	Nmass	47.71833	1	NA
FR-Lq2	Holcus mollis	2011	167	SLA	33.27273		NA
FR-Lq2	Phleum pratense	2011	167	C_N	11.92004		NA
FR-Lq2	Phleum pratense	2011	167	leaf_C_concentration	453.2148		NA
FR-Lq2	Phleum pratense	2011	167	d13c	-28.7777		NA
FR-Lq2	Phleum pratense	2011	167	LMA	25	1	NA
FR-Lq2	Phleum pratense	2011	167	leaf_N_area	0.950531		NA
FR-Lq2	Phleum pratense	2011	167	Nmass	38.02124	1	NA
FR-Lq2	Phleum pratense	2011	167	SLA	40		NA
FR-Lq2	Poa pratensis	2011	167	C_N	28.0687		NA
FR-Lq2	Poa pratensis	2011	167	leaf_C_concentration	436.2976		NA
FR-Lq2	Poa pratensis	2011	167	d13c	-27.5906		NA
FR-Lq2	Poa pratensis	2011	167	LMA	69.03226	1	NA
FR-Lq2	Poa pratensis	2011	167	leaf_N_area	1.073032		NA
FR-Lq2	Poa pratensis	2011	167	Nmass	15.54392	1	NA
FR-Lq2	Poa pratensis	2011	167	SLA	14.48598		NA
FR-Lq2	Trifolium repens	2011	167	C_N	12.66694		NA
FR-Lq2	Trifolium repens	2011	167	leaf_C_concentration	443.6867		NA
FR-Lq2	Trifolium repens	2011	167	d13c	-29.2327		NA
FR-Lq2	Trifolium repens	2011	167	LMA	41.29032	1	NA
FR-Lq2	Trifolium repens	2011	167	leaf_N_area	1.446282		NA
FR-Lq2	Trifolium repens	2011	167	Nmass	35.02715	1	NA
FR-Lq2	Trifolium repens	2011	167	SLA	24.21875		NA
FR-Lq2	Trisetum flavescens	2011	167	C_N	15.92043		NA
FR-Lq2	Trisetum flavescens	2011	167	leaf_C_concentration	432.6281		NA
FR-Lq2	Trisetum flavescens	2011	167	d13c	-29.0063		NA
FR-Lq2	Trisetum flavescens	2011	167	LMA	47.85714	1	NA
FR-Lq2	Trisetum flavescens	2011	167	leaf_N_area	1.300489		NA
FR-Lq2	Trisetum flavescens	2011	167	Nmass	27.17439	1	NA
FR-Lq2	Trisetum flavescens	2011	167	SLA	20.89552		NA
FR-Lq2	Veronica chamaes	2011	167	C_N	19.53795		NA
FR-Lq2	Veronica chamaes	2011	167	leaf_C_concentration	456.529		NA
FR-Lq2	Veronica chamaes	2011	167	d13c	-28.4902		NA
FR-Lq2	Veronica chamaes	2011	167	LMA	49.04762	1	NA
FR-Lq2	Veronica chamaes	2011	167	leaf_N_area	1.14606		NA
FR-Lq2	Veronica chamaes	2011	167	Nmass	23.36627	1	NA
FR-Lq2	Veronica chamaes	2011	167	SLA	20.38835		NA

FR-Lq2	Veronica chamaes	2011	167	leaf_P_area	0.142773		NA
FR-Lq2	Dactylis glomerata	2011	167	leaf_P_area	0.147098		NA
FR-Lq2	Trisetum flavescens	2011	167	leaf_P_area	0.155028		NA
FR-Lq2	Dactylis glomerata	2011	167	leaf_N_P	10.44073		NA
FR-Lq2	Festuca rubra	2011	167	leaf_P_area	0.170876		NA
FR-Lq2	Poa pratensis	2011	167	leaf_P_dry	1.364299		NA
FR-Lq2	Poa pratensis	2011	167	leaf_N_P	11.39334		NA
FR-Lq2	Festuca rubra	2011	167	leaf_N_P	13.06325		NA
FR-Lq2	Holcus mollis	2011	167	leaf_N_P	14.30932		NA
FR-Lq2	Trifolium repens	2011	167	leaf_N_P	14.92153		NA
FR-Lq2	Festuca rubra	2011	167	leaf_P_dry	2.290096		NA
FR-Lq2	Trifolium repens	2011	167	leaf_P_dry	2.347423		NA
FR-Lq2	Dactylis glomerata	2011	167	leaf_P_dry	2.374221		NA
FR-Lq2	Agrostis capillaris	2011	167	leaf_P_dry	2.534078		NA
FR-Lq2	Anthoxanthum odoratum	2011	167	leaf_P_dry	2.875391		NA
FR-Lq2	Veronica chamaes	2011	167	leaf_P_dry	2.910909		NA
FR-Lq2	Trisetum flavescens	2011	167	leaf_P_dry	3.239393		NA
FR-Lq2	Holcus mollis	2011	167	leaf_P_dry	3.334773		NA
FR-Lq2	Phleum pratense	2011	167	leaf_P_dry	4.240853		NA
IL-Yat	Pinus halepensis	2012	240	leaf_P_dry	0.590383	3	0.051093
IL-Yat	Pinus halepensis	2012	240	leaf_P_dry	0.714082	5	0.092466
IL-Yat	Pinus halepensis	2012	240	leaf_P_dry	0.806746	5	0.098389
IL-Yat	Pinus halepensis	2012	240	leaf_P_dry	0.900461	3	0.024157
IL-Yat	Pinus halepensis	2012	240	leaf_P_dry	0.91408	3	0.31781
IL-Yat	Pinus halepensis	2012	240	leaf_N_P	9.462832	3	0.76687
IL-Yat	Pinus halepensis	2012	240	leaf_P_area	0.139408	3	0.021455
IL-Yat	Pinus halepensis	2012	240	C_N	50.30009	5	4.48295
IL-Yat	Pinus halepensis	2012	240	C_N	57.5181	3	4.831451
IL-Yat	Pinus halepensis	2012	240	C_N	48.47455	3	3.825886
IL-Yat	Pinus halepensis	2012	240	C_N	51.54356	3	4.15562
IL-Yat	Pinus halepensis	2012	240	C_N	51.79733	5	3.989628
IL-Yat	Pinus halepensis	2012	240	leaf_C_concentration	498.0505	5	4.177593
IL-Yat	Pinus halepensis	2012	240	leaf_C_concentration	487.8026	3	3.262707
IL-Yat	Pinus halepensis	2012	240	leaf_C_concentration	508.7611	3	3.666426
IL-Yat	Pinus halepensis	2012	240	leaf_C_concentration	511.4616	3	2.944634
IL-Yat	Pinus halepensis	2012	240	leaf_C_concentration	500.4189	5	5.844529

IL-Yat	Pinus halepensis	2012	240	d13c	-23.4941	5	0.270234
IL-Yat	Pinus halepensis	2012	240	d13c	-23.1754	3	0.183062
IL-Yat	Pinus halepensis	2012	240	d13c	-23.0718	3	0.140584
IL-Yat	Pinus halepensis	2012	240	d13c	-23.6521	3	0.278398
IL-Yat	Pinus halepensis	2012	240	d13c	-23.4152	5	0.496414
IL-Yat	Pinus halepensis	2012	240	LMA	206.4635	10	19.57178
IL-Yat	Pinus halepensis	2012	240	LMA	231.8154	10	20.43527
IL-Yat	Pinus halepensis	2012	240	LMA	245.796	10	43.65894
IL-Yat	Pinus halepensis	2012	240	LMA	218.7845	10	51.92938
IL-Yat	Pinus halepensis	2012	240	LMA	238.0347	10	27.54429
IL-Yat	Pinus halepensis	2012	240	LMA	234.31	10	41.19025
IL-Yat	Pinus halepensis	2012	240	leaf_N_area	2.204972	5	0.2505
IL-Yat	Pinus halepensis	2012	240	leaf_N_area	1.84442	3	0.364856
IL-Yat	Pinus halepensis	2012	240	leaf_N_area	2.498498	3	0.288265
IL-Yat	Pinus halepensis	2012	240	leaf_N_area	2.169383	5	0.142615
IL-Yat	Pinus halepensis	2012	240	leaf_N_area	2.33897	3	0.137626
IL-Yat	Pinus halepensis	2012	240	Nmass	9.966533	5	0.914187
IL-Yat	Pinus halepensis	2012	240	Nmass	8.517701	3	0.658001
IL-Yat	Pinus halepensis	2012	240	Nmass	10.53613	3	0.776658
IL-Yat	Pinus halepensis	2012	240	Nmass	9.964653	3	0.777418
IL-Yat	Pinus halepensis	2012	240	Nmass	9.70668	5	0.74848
IL-Yat	Pinus halepensis	2012	240	SLA	4.95655	10	0.409872
IL-Yat	Pinus halepensis	2012	240	SLA	4.390085	10	0.378433
IL-Yat	Pinus halepensis	2012	240	SLA	4.419098	10	0.860665
IL-Yat	Pinus halepensis	2012	240	SLA	4.730624	10	0.763003
IL-Yat	Pinus halepensis	2012	240	SLA	4.251974	10	0.492401
IL-Yat	Pinus halepensis	2012	240	SLA	4.199263	10	0.483183
IL-Yat	Pinus halepensis	2012	240	leaf_P_area	0.158528	5	0.027022
IL-Yat	Pinus halepensis	2012	240	leaf_P_area	0.179846	5	0.01587

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IL-Yat	Pinus halepensis	2012	240	leaf_P_area	0.193771	3	0.022402
IL-Yat	Pinus halepensis	2012	240	leaf_N_P	12.18762	5	1.829421
IL-Yat	Pinus halepensis	2012	240	leaf_N_P	12.61577	3	4.845295
IL-Yat	Pinus halepensis	2012	240	leaf_P_area	0.216306	3	0.077073
IL-Yat	Pinus halepensis	2012	240	leaf_N_P	14.07163	5	1.5303
IL-Yat	Pinus halepensis	2012	240	leaf_N_P	17.03576	3	2.795379
IT-Lav	Fagus sylvatica	2012	221	leaf_P_area	0.013383	4	0.004176
IT-Lav	Fagus sylvatica	2012	221	leaf_P_area	0.028141	4	0.003364
IT-Lav	Fagus sylvatica	2012	221	leaf_P_dry	0.561444	4	0.141649
IT-Lav	Fagus sylvatica	2012	221	leaf_P_dry	0.773917	4	0.041236
IT-Lav	Picea abies	2012	221	leaf_P_dry	0.845426	1	NA
IT-Lav	Abies alba	2012	221	leaf_P_dry	0.895386	3	0.162724
IT-Lav	Abies alba	2012	221	leaf_N_P	7.777646	3	5.367041
IT-Lav	Picea abies	2012	221	leaf_P_area	0.127968	1	NA
IT-Lav	Abies alba	2012	221	leaf_P_area	0.131848	3	0.008733
IT-Lav	Abies alba	2012	221	C_N	49.67154	3	7.217192
IT-Lav	Abies alba	2012	221	C_N	52.75927	3	3.850159
IT-Lav	Abies alba	2012	221	leaf_C_concentration	498.9216		5.55198
IT-Lav	Abies alba	2012	221	leaf_C_concentration	505.3762		5.995015
IT-Lav	Abies alba	2012	221	d13c	-26.5465	3	0.083459
IT-Lav	Abies alba	2012	221	d13c	-29.0223	3	0.258126
IT-Lav	Abies alba	2012	221	LMA	223.1894	3	14.35224
IT-Lav	Abies alba	2012	221	LMA	149.3656	3	17.54708
IT-Lav	Abies alba	2012	221	leaf_N_area	2.268854	3	0.316182
IT-Lav	Abies alba	2012	221	leaf_N_area	1.435813	3	0.206209
IT-Lav	Abies alba	2012	221	Nmass	10.18782	3	1.480473
IT-Lav	Abies alba	2012	221	Nmass	9.615794	3	0.760515
IT-Lav	Abies alba	2012	221	SLA	4.492975	3	0.291191

IT-Lav	Abies alba	2012	221	SLA	6.759885	3	0.829886
IT-Lav	Fagus sylvatica	2012	221	C_N	17.58935	4	0.604138
IT-Lav	Fagus sylvatica	2012	221	C_N	18.04781	4	0.330986
IT-Lav	Fagus sylvatica	2012	221	leaf_C_concentration	468.6951		1.252225
IT-Lav	Fagus sylvatica	2012	221	leaf_C_concentration	462.8703		1.542358
IT-Lav	Fagus sylvatica	2012	221	d13c	-31.0121	4	0.124944
IT-Lav	Fagus sylvatica	2012	221	d13c	-32.1015	4	0.254101
IT-Lav	Fagus sylvatica	2012	221	LMA	36.26767	4	2.456081
IT-Lav	Fagus sylvatica	2012	221	LMA	23.61575	4	1.277319
IT-Lav	Fagus sylvatica	2012	221	leaf_N_area	0.966473	4	0.059023
IT-Lav	Fagus sylvatica	2012	221	leaf_N_area	0.605632	4	0.029769
IT-Lav	Fagus sylvatica	2012	221	Nmass	26.66904	4	0.877458
IT-Lav	Fagus sylvatica	2012	221	Nmass	25.65262	4	0.420934
IT-Lav	Fagus sylvatica	2012	221	SLA	27.66724	4	1.860811
IT-Lav	Fagus sylvatica	2012	221	SLA	42.43539	4	2.239191
IT-Lav	Picea abies	2012	221	C_N	35.32067	1	NA
IT-Lav	Picea abies	2012	221	C_N	43.70655	1	NA
IT-Lav	Picea abies	2012	221	leaf_C_concentration	487.9866		NA
IT-Lav	Picea abies	2012	221	leaf_C_concentration	482.6443		NA
IT-Lav	Picea abies	2012	221	d13c	-25.1697	1	NA
IT-Lav	Picea abies	2012	221	d13c	-28.2588	1	NA
IT-Lav	Picea abies	2012	221	LMA	295.0658	1	NA
IT-Lav	Picea abies	2012	221	LMA	151.3648	1	NA
IT-Lav	Picea abies	2012	221	leaf_N_area	4.076597	1	NA
IT-Lav	Picea abies	2012	221	leaf_N_area	1.671496	1	NA
IT-Lav	Picea abies	2012	221	Nmass	13.81589	1	NA
IT-Lav	Picea abies	2012	221	Nmass	11.04284	1	NA
IT-Lav	Picea abies	2012	221	SLA	3.389075	1	NA
IT-Lav	Picea abies	2012	221	SLA	6.606557	1	NA
IT-Lav	Picea abies	2012	221	leaf_N_P	10.55419	1	NA
IT-Lav	Picea abies	2012	221	leaf_P_dry	1.309044	1	NA
IT-Lav	Abies alba	2012	221	leaf_N_P	10.99405	3	2.36892
IT-Lav	Abies alba	2012	221	leaf_P_dry	1.626049	3	0.689069
IT-Lav	Picea abies	2012	221	leaf_N_P	13.06186	1	NA

IT-Lav	Abies alba	2012	221	leaf_P_area	0.363764	3	0.161602
IT-Lav	Picea abies	2012	221	leaf_P_area	0.386254	1	NA
IT-Lav	Fagus sylvatica	2012	221	leaf_N_P	34.56317	4	2.713617
IT-Lav	Fagus sylvatica	2012	221	leaf_N_P	47.53823	4	9.79918
IT-MBo	Dactylis glomerata	2012	225	leaf_N_P	5.878446		NA
IT-MBo	Avenella flexuosa	2012	225	leaf_P_area	0.048763		NA
IT-MBo	Trifolium pratense	2012	225	leaf_P_area	0.085351		NA
IT-MBo	Festuca rubra	2012	225	leaf_N_P	7.319414		NA
IT-MBo	Alchemilla vulgaris	2012	225	leaf_P_area	0.089478		NA
IT-MBo	Nardus stricta	2012	225	leaf_P_area	0.10367		NA
IT-MBo	Koeleria pyrmidata	2012	225	leaf_P_area	0.106469		NA
IT-MBo	Nardus stricta	2012	225	leaf_P_dry	1.199493		NA
IT-MBo	Avenella flexuosa	2012	225	leaf_P_dry	1.202384		NA
IT-MBo	Festuca rubra	2012	225	leaf_P_area	0.12453		NA
IT-MBo	Trifolium montanum	2012	225	leaf_P_area	0.127281		NA
IT-MBo	Brachypodium pinnatum	2012	225	leaf_P_area	0.133025		NA
IT-MBo	Alchemilla vulgaris	2012	225	C_N	17.33774	1	NA
IT-MBo	Alchemilla vulgaris	2012	225	leaf_C_concentration	453.7294	1	NA
IT-MBo	Alchemilla vulgaris	2012	225	d13c	-28.3539		NA
IT-MBo	Alchemilla vulgaris	2012	225	LMA	45.19961	1	NA
IT-MBo	Alchemilla vulgaris	2012	225	leaf_N_area	1.182876	1	NA
IT-MBo	Alchemilla vulgaris	2012	225	Nmass	26.17004	1	NA
IT-MBo	Alchemilla vulgaris	2012	225	SLA	22.12409	1	NA
IT-MBo	Avenella flexuosa	2012	225	C_N	18.58186	1	NA
IT-MBo	Avenella flexuosa	2012	225	leaf_C_concentration	447.1464	1	NA
IT-MBo	Avenella flexuosa	2012	225	d13c	-30.1134		NA
IT-MBo	Avenella flexuosa	2012	225	LMA	40.555	1	NA
IT-MBo	Avenella flexuosa	2012	225	Nmass	24.0636	1	NA
IT-	Avenella flexuosa	2012	225	SLA	24.65787	1	NA

MBo							
IT-MBo	Avenella flexuosa	2012	225	leaf_N_area	0.975899	1	NA
IT-MBo	Brachypodium pinnatum	2012	225	C_N	22.35766	1	NA
IT-MBo	Brachypodium pinnatum	2012	225	leaf_C_concentration	462.1043	1	NA
IT-MBo	Brachypodium pinnatum	2012	225	d13c	-26.3607		NA
IT-MBo	Brachypodium pinnatum	2012	225	LMA	93.61063	1	NA
IT-MBo	Brachypodium pinnatum	2012	225	Nmass	20.66873	1	NA
IT-MBo	Brachypodium pinnatum	2012	225	leaf_P_dry	1.42105		NA
IT-MBo	Brachypodium pinnatum	2012	225	SLA	10.68255	1	NA
IT-MBo	Brachypodium pinnatum	2012	225	leaf_N_area	1.934812	1	NA
IT-MBo	Dactylis glomerata	2012	225	C_N	23.76758	1	NA
IT-MBo	Dactylis glomerata	2012	225	leaf_C_concentration	453.4915	1	NA
IT-MBo	Dactylis glomerata	2012	225	d13c	-26.3921		NA
IT-MBo	Dactylis glomerata	2012	225	LMA	58.35604	1	NA
IT-MBo	Dactylis glomerata	2012	225	leaf_N_area	1.113448	1	NA
IT-MBo	Dactylis glomerata	2012	225	Nmass	19.08026	1	NA
IT-MBo	Dactylis glomerata	2012	225	SLA	17.13619	1	NA
IT-MBo	Festuca rubra	2012	225	C_N	28.11506	1	NA
IT-MBo	Festuca rubra	2012	225	leaf_C_concentration	449.0038	1	NA
IT-MBo	Festuca rubra	2012	225	d13c	-27.0118		NA
IT-MBo	Festuca rubra	2012	225	LMA	57.07421	1	NA
IT-MBo	Festuca rubra	2012	225	leaf_N_area	0.911488	1	NA
IT-MBo	Festuca rubra	2012	225	Nmass	15.97022	1	NA
IT-MBo	Festuca rubra	2012	225	SLA	17.52105	1	NA
IT-MBo	Koeleria pyrmidata	2012	225	C_N	22.87974	1	NA
IT-MBo	Koeleria pyrmidata	2012	225	leaf_C_concentration	436.898	1	NA
IT-MBo	Koeleria pyrmidata	2012	225	d13c	-27.4037		NA
IT-MBo	Koeleria pyrmidata	2012	225	LMA	68.49126	1	NA

IT-MBo	Koeleria pyrmidata	2012	225	leaf_N_area	1.307869	1	NA
IT-MBo	Koeleria pyrmidata	2012	225	Nmass	19.09541	1	NA
IT-MBo	Koeleria pyrmidata	2012	225	SLA	14.6004	1	NA
IT-MBo	Nardus stricta	2012	225	C_N	31.93367	1	NA
IT-MBo	Nardus stricta	2012	225	leaf_C_concentration	450.8717	1	NA
IT-MBo	Nardus stricta	2012	225	d13c	-27.5588		NA
IT-MBo	Nardus stricta	2012	225	LMA	86.4278	1	NA
IT-MBo	Nardus stricta	2012	225	leaf_N_area	1.220274	1	NA
IT-MBo	Nardus stricta	2012	225	Nmass	14.119	1	NA
IT-MBo	Nardus stricta	2012	225	SLA	11.57035	1	NA
IT-MBo	Trifolium montanum	2012	225	C_N	12.41203	1	NA
IT-MBo	Trifolium montanum	2012	225	leaf_C_concentration	449.548	1	NA
IT-MBo	Trifolium montanum	2012	225	d13c	-27.6723		NA
IT-MBo	Trifolium montanum	2012	225	LMA	54.87337	1	NA
IT-MBo	Nardus stricta	2012	225	leaf_N_P	11.77081		NA
IT-MBo	Trifolium montanum	2012	225	leaf_N_area	1.987443	1	NA
IT-MBo	Trifolium montanum	2012	225	Nmass	36.21872	1	NA
IT-MBo	Trifolium montanum	2012	225	SLA	18.22378	1	NA
IT-MBo	Trifolium pratense	2012	225	C_N	13.06386	1	NA
IT-MBo	Trifolium pratense	2012	225	leaf_C_concentration	451.9691	1	NA
IT-MBo	Trifolium pratense	2012	225	d13c	-29.2325		NA
IT-MBo	Trifolium pratense	2012	225	LMA	38.7919	1	NA
IT-MBo	Trifolium pratense	2012	225	leaf_N_area	1.342079	1	NA
IT-MBo	Trifolium pratense	2012	225	Nmass	34.5969	1	NA
IT-MBo	Trifolium pratense	2012	225	SLA	25.77858	1	NA
IT-MBo	Dactylis glomerata	2012	225	leaf_P_area	0.189412		NA
IT-MBo	Koeleria pyrmidata	2012	225	leaf_P_dry	1.554495		NA
IT-MBo	Koeleria pyrmidata	2012	225	leaf_N_P	12.284		NA

IT-MBo	Alchemilla vulgaris	2012	225	leaf_N_P	13.21968		NA
IT-MBo	Brachypodium pinnatum	2012	225	leaf_N_P	14.54468		NA
IT-MBo	Alchemilla vulgaris	2012	225	leaf_P_dry	1.979628		NA
IT-MBo	Trifolium montanum	2012	225	leaf_N_P	15.61458		NA
IT-MBo	Trifolium pratense	2012	225	leaf_N_P	15.72424		NA
IT-MBo	Festuca rubra	2012	225	leaf_P_dry	2.181899		NA
IT-MBo	Trifolium pratense	2012	225	leaf_P_dry	2.200226		NA
IT-MBo	Trifolium montanum	2012	225	leaf_P_dry	2.319545		NA
IT-MBo	Avenella flexuosa	2012	225	leaf_N_P	20.01325		NA
IT-MBo	Dactylis glomerata	2012	225	leaf_P_dry	3.2458		NA
IT-Ren	Picea abies	2012	191	leaf_P_dry	0.522569	3	0.034286
IT-Ren	Picea abies	2012	191	leaf_P_dry	0.572007	3	0.060675
IT-Ren	Picea abies	2012	191	leaf_P_dry	0.605693	4	0.139091
IT-Ren	Picea abies	2012	191	leaf_P_dry	0.634434	4	0.102433
IT-Ren	Picea abies	2012	191	leaf_P_dry	0.664557	3	0.120413
IT-Ren	grass	2012	191	leaf_P_area	0.075794		NA
IT-Ren	Deschampsia	2012	191	leaf_P_dry	1.131133		NA
IT-Ren	Vaccinium	2012	191	leaf_P_area	0.102922		NA
IT-Ren	Deschampsia	2012	191	leaf_P_area	0.117045		NA
IT-Ren	Picea abies	2012	191	leaf_P_area	0.181885	3	0.044184
IT-Ren	Picea abies	2012	191	leaf_P_area	0.187694	3	0.037225
IT-Ren	Picea abies	2012	191	leaf_P_area	0.194069	4	0.059616
IT-Ren	Vaccinium	2012	191	leaf_P_dry	1.565743		NA
IT-Ren	Deschampsia	2012	191	C_N	30.30378		NA
IT-Ren	Deschampsia	2012	191	leaf_C_concentration	458.3641		NA
IT-Ren	Deschampsia	2012	191	d13c	-28.4067		NA
IT-Ren	Deschampsia	2012	191	LMA	103.4762	1	NA
IT-Ren	Deschampsia	2012	191	leaf_N_area	1.565143		NA
IT-Ren	Deschampsia	2012	191	Nmass	15.12564		NA
IT-Ren	Deschampsia	2012	191	SLA	15.21295		NA
IT-Ren	grass	2012	191	C_N	19.57793		NA
IT-Ren	grass	2012	191	leaf_C_concentration	428.9437		NA

IT-Ren	grass	2012	191	d13c	-29.7191		NA
IT-Ren	grass	2012	191	LMA	46.28807	1	NA
IT-Ren	grass	2012	191	leaf_N_area	1.014151		NA
IT-Ren	grass	2012	191	Nmass	21.90955		NA
IT-Ren	grass	2012	191	SLA	21.60384		NA
IT-Ren	Picea abies	2012	191	C_N	46.22324	4	1.73465
IT-Ren	Picea abies	2012	191	C_N	44.18709	4	7.72227
IT-Ren	Picea abies	2012	191	C_N	53.40814	3	0.375917
IT-Ren	Picea abies	2012	191	C_N	43.53305	3	0.909058
IT-Ren	Picea abies	2012	191	C_N	46.44815	3	1.217623
IT-Ren	Picea abies	2012	191	leaf_C_concentration	481.826	4	2.556701
IT-Ren	Picea abies	2012	191	leaf_C_concentration	483.7967	4	4.995957
IT-Ren	Picea abies	2012	191	leaf_C_concentration	489.1784	2	8.57719
IT-Ren	Picea abies	2012	191	leaf_C_concentration	493.477	2	9.034471
IT-Ren	Picea abies	2012	191	leaf_C_concentration	493.3898	2	6.554652
IT-Ren	Picea abies	2012	191	d13c	-28.1723	4	0.928785
IT-Ren	Picea abies	2012	191	d13c	-27.2784	4	0.712961
IT-Ren	Picea abies	2012	191	d13c	-27.5926	3	1.882072
IT-Ren	Picea abies	2012	191	d13c	-27.3351	3	1.799821
IT-Ren	Picea abies	2012	191	d13c	-27.6142	3	1.755502
IT-Ren	Picea abies	2012	191	LMA	300.6406	16	56.8294
IT-Ren	Picea abies	2012	191	LMA	377.3542	2	65.98434
IT-Ren	Picea abies	2012	191	LMA	380.4009	2	61.51028
IT-Ren	Picea abies	2012	191	LMA	411.3898	2	25.87685
IT-Ren	Picea abies	2012	191	LMA	364.9413	16	51.29338
IT-Ren	Picea abies	2012	191	leaf_N_area	3.124353	4	0.50323
IT-Ren	Picea abies	2012	191	leaf_N_area	3.447925	2	0.497257
IT-Ren	Picea abies	2012	191	leaf_N_area	4.444892	2	0.737923
IT-Ren	Picea abies	2012	191	leaf_N_area	4.670145	2	0.229223
IT-Ren	Picea abies	2012	191	leaf_N_area	4.060162	4	0.556578
IT-Ren	Picea abies	2012	191	Nmass	10.43458	4	0.383878

IT-Ren	Picea abies	2012	191	Nmass	9.161963	2	0.284318
IT-Ren	Picea abies	2012	191	Nmass	11.68062	2	0.051116
IT-Ren	Picea abies	2012	191	Nmass	11.35706	2	0.157179
IT-Ren	Picea abies	2012	191	Nmass	11.24312	4	2.259711
IT-Ren	grass	2012	191	leaf_P_dry	1.637435		NA
IT-Ren	Picea abies	2012	191	SLA	3.439816	16	0.651288
IT-Ren	Picea abies	2012	191	SLA	2.691173	2	0.47058
IT-Ren	Picea abies	2012	191	SLA	2.663628	2	0.430705
IT-Ren	Picea abies	2012	191	SLA	2.435603	2	0.153202
IT-Ren	Picea abies	2012	191	SLA	2.791599	16	0.393803
IT-Ren	Vaccinium	2012	191	C_N	21.94829		NA
IT-Ren	Vaccinium	2012	191	leaf_C_concentration	480.9318		NA
IT-Ren	Vaccinium	2012	191	d13c	-33.0829		NA
IT-Ren	Vaccinium	2012	191	LMA	65.73348	1	NA
IT-Ren	Vaccinium	2012	191	leaf_N_area	1.440355		NA
IT-Ren	Vaccinium	2012	191	Nmass	21.91205		NA
IT-Ren	Vaccinium	2012	191	SLA	9.664063		NA
IT-Ren	Picea abies	2012	191	leaf_P_area	0.222542	3	0.109595
IT-Ren	Picea abies	2012	191	leaf_P_area	0.223703	4	0.067785
IT-SRo	Pinus pinaster	2012	166	leaf_P_dry	0.452694	10	0.714296
IT-SRo	Pinus pinaster	2012	166	leaf_P_dry	0.47278	10	0.790883
IT-SRo	Pinus pinaster	2012	166	leaf_P_area	0.184398	10	0.220557
IT-SRo	Pinus pinaster	2012	166	leaf_P_area	0.201818	10	0.404677
IT-SRo	Pinus pinaster	2012	166	C_N	60.43087	10	8.572048
IT-SRo	Pinus pinaster	2012	166	C_N	56.3068	10	5.542537
IT-SRo	Pinus pinaster	2012	166	leaf_C_concentration	506.0563	10	5.552087
IT-SRo	Pinus pinaster	2012	166	leaf_C_concentration	507.291	10	5.798889
IT-SRo	Pinus pinaster	2012	166	d13c	-28.6	10	5.71
IT-SRo	Pinus pinaster	2012	166	d13c	-28.5	10	6.002052
IT-SRo	Pinus pinaster	2012	166	LMA	424.8308	16	33.90392
IT-SRo	Pinus pinaster	2012	166	LMA	410.7077	16	36.69111

IT-SRo	Pinus pinaster	2012	166	leaf_N_area	3.47738	10	0.370952
IT-SRo	Pinus pinaster	2012	166	leaf_N_area	3.887291	10	0.619176
IT-SRo	Pinus pinaster	2012	166	Nmass	8.536741	10	1.284114
IT-SRo	Pinus pinaster	2012	166	Nmass	9.092644	10	0.946718
IT-SRo	Pinus pinaster	2012	166	SLA	2.367815	16	0.18754
IT-SRo	Pinus pinaster	2012	166	SLA	2.451635	16	0.201668
IT-SRo	Pinus pinaster	2012	166	leaf_P_dry	2.051928	5	0.663717
IT-SRo	Pinus pinaster	2012	166	leaf_N_P	19.16959	10	34.80671
IT-SRo	Pinus pinaster	2012	166	leaf_N_P	19.63791	10	33.23432
NL-Loo	Pinus sylvestris	2012	170	leaf_P_dry	1.132905	5	0.217344
NL-Loo	Pinus sylvestris	2012	170	leaf_P_dry	1.207223	2	0.052774
NL-Loo	Pinus sylvestris	2012	170	leaf_P_dry	1.281703	4	0.406783
NL-Loo	Pinus sylvestris	2012	170	leaf_P_area	0.180893	5	0.049957
NL-Loo	Pinus sylvestris	2012	170	leaf_N_P	11.75219	5	5.250428
NL-Loo	Pinus sylvestris	2012	170	leaf_N_P	11.96218	5	3.582416
NL-Loo	Pinus sylvestris	2012	170	C_N	23.40466	5	4.283281
NL-Loo	Pinus sylvestris	2012	170	C_N	27.67421	5	3.73839
NL-Loo	Pinus sylvestris	2012	170	C_N	26.93005	2	0.9587
NL-Loo	Pinus sylvestris	2012	170	C_N	24.31474	5	1.233109
NL-Loo	Pinus sylvestris	2012	170	C_N	24.63668	5	4.168991
NL-Loo	Pinus sylvestris	2012	170	C_N	26.70306	4	3.635554
NL-Loo	Pinus sylvestris	2012	170	leaf_C_concentration	487.6206	5	3.755449
NL-Loo	Pinus sylvestris	2012	170	leaf_C_concentration	503.1883	5	4.225278
NL-Loo	Pinus sylvestris	2012	170	leaf_C_concentration	508.7569	2	7.136834
NL-Loo	Pinus sylvestris	2012	170	leaf_C_concentration	491.313	5	4.068811
NL-Loo	Pinus sylvestris	2012	170	leaf_C_concentration	504.6724	5	5.650663
NL-Loo	Pinus sylvestris	2012	170	leaf_C_concentration	510.6433	4	5.676618
NL-Loo	Pinus sylvestris	2012	170	d13c	-28.9683	5	0.987401
NL-Loo	Pinus sylvestris	2012	170	d13c	-28.7778	5	1.037772

NL-Loo	Pinus sylvestris	2012	170	d13c	-29.3752	2	0.768859
NL-Loo	Pinus sylvestris	2012	170	d13c	-28.1314	5	0.900453
NL-Loo	Pinus sylvestris	2012	170	d13c	-28.0292	5	1.368856
NL-Loo	Pinus sylvestris	2012	170	d13c	-27.8348	4	0.939151
NL-Loo	Pinus sylvestris	2012	170	LMA	92.11406	5	25.56808
NL-Loo	Pinus sylvestris	2012	170	LMA	194.7485	5	9.753237
NL-Loo	Pinus sylvestris	2012	170	LMA	235.0207	2	9.459692
NL-Loo	Pinus sylvestris	2012	170	LMA	138.3203	5	23.35071
NL-Loo	Pinus sylvestris	2012	170	LMA	250.1312	5	40.6899
NL-Loo	Pinus sylvestris	2012	170	LMA	268.8469	4	47.30372
NL-Loo	Pinus sylvestris	2012	170	leaf_N_area	2.008357	5	0.744419
NL-Loo	Pinus sylvestris	2012	170	leaf_N_area	3.618525	5	0.733569
NL-Loo	Pinus sylvestris	2012	170	leaf_N_area	4.448326	2	0.399353
NL-Loo	Pinus sylvestris	2012	170	leaf_N_area	2.80341	5	0.514686
NL-Loo	Pinus sylvestris	2012	170	leaf_N_area	5.372924	5	1.884723
NL-Loo	Pinus sylvestris	2012	170	leaf_N_area	5.264053	4	1.375962
NL-Loo	Pinus sylvestris	2012	170	Nmass	21.45334	5	4.258665
NL-Loo	Pinus sylvestris	2012	170	Nmass	18.48678	5	2.843169
NL-Loo	Pinus sylvestris	2012	170	Nmass	18.90849	2	0.938149
NL-Loo	Pinus sylvestris	2012	170	Nmass	20.24282	5	0.90085
NL-Loo	Pinus sylvestris	2012	170	Nmass	21.00602	5	3.888921
NL-Loo	Pinus sylvestris	2012	170	Nmass	19.40099	4	2.723026
NL-Loo	Pinus sylvestris	2012	170	SLA	11.61349	5	3.564677
NL-Loo	Pinus sylvestris	2012	170	SLA	5.145164	5	0.258314
NL-Loo	Pinus sylvestris	2012	170	SLA	4.258393	2	0.171402
NL-Loo	Pinus sylvestris	2012	170	SLA	7.403966	5	1.301776
NL-Loo	Pinus sylvestris	2012	170	SLA	4.08511	5	0.680367
NL-Loo	Pinus sylvestris	2012	170	SLA	3.819652	4	0.762319
NL-Loo	Pinus sylvestris	2012	170	leaf_N_P	13.60262	5	8.36702

NL-Loo	Pinus sylvestris	2012	170	leaf_P_area	0.252264	5	0.090298
NL-Loo	Pinus sylvestris	2012	170	leaf_P_dry	1.803783	5	0.470765
NL-Loo	Pinus sylvestris	2012	170	leaf_P_area	0.283473	2	0.000983
NL-Loo	Pinus sylvestris	2012	170	leaf_P_area	0.283703	5	0.072998
NL-Loo	Pinus sylvestris	2012	170	leaf_P_dry	1.983034	5	1.555639
NL-Loo	Pinus sylvestris	2012	170	leaf_N_P	15.69478	2	1.463219
NL-Loo	Pinus sylvestris	2012	170	leaf_N_P	16.13041	4	4.534162
NL-Loo	Pinus sylvestris	2012	170	leaf_P_area	0.355513	4	0.164842
NL-Loo	Pinus sylvestris	2012	170	leaf_N_P	19.10358	5	4.949518
NL-Loo	Pinus sylvestris	2012	170	leaf_P_area	0.392508	5	0.32774
RU-Fyo	Picea abies	2012	199	leaf_N_P	5.742728	3	0.838753
RU-Fyo	Picea abies	2012	199	leaf_P_dry	0.672726	1	NA
RU-Fyo	Picea abies	2012	199	leaf_P_dry	0.768148	1	NA
RU-Fyo	Picea abies	2012	199	leaf_P_dry	0.856813	2	0.041191
RU-Fyo	Picea abies	2012	199	leaf_P_dry	0.864604	2	0.060047
RU-Fyo	Picea abies	2012	199	leaf_P_dry	0.878255	2	0.06807
RU-Fyo	Picea abies	2012	199	leaf_N_P	6.559917	4	0.685639
RU-Fyo	Picea abies	2012	199	leaf_P_dry	0.916691	2	0.176122
RU-Fyo	Picea abies	2012	199	leaf_P_dry	1.014447	2	0.28415
RU-Fyo	Picea abies	2012	199	leaf_N_P	7.725312	3	0.185642
RU-Fyo	Picea abies	2012	199	leaf_P_dry	1.0658	3	0.023276
RU-Fyo	Picea abies	2012	199	leaf_N_P	8.398903	2	0.275118
RU-Fyo	Picea abies	2012	199	leaf_N_P	8.50014	2	1.103139
RU-Fyo	Picea abies	2012	199	leaf_N_P	8.958465	2	2.733287
RU-Fyo	Picea abies	2012	199	leaf_N_P	9.099289	2	1.394017
RU-Fyo	Picea abies	2012	199	leaf_N_P	9.537501	2	0.567612
RU-Fyo	Picea abies	2012	199	leaf_N_P	9.892897	1	NA
RU-Fyo	Picea abies	2012	199	leaf_N_P	10.47402	1	NA
RU-Fyo	Picea abies	2012	199	leaf_P_area	0.164151	2	0.007056
RU-Fyo	Picea abies	2012	199	leaf_P_area	0.175958	2	0.004835
RU-Fyo	Picea abies	2012	199	leaf_P_area	0.186279	1	NA

RU-Fyo	Picea abies	2012	199	leaf_P_dry	1.467729	4	0.103753
RU-Fyo	Picea abies	2012	199	leaf_P_area	0.197516	2	0.026869
RU-Fyo	Picea abies	2012	199	leaf_P_area	0.219576	1	NA
RU-Fyo	Picea abies	2012	199	C_N	46.4809	3	2.04493
RU-Fyo	Picea abies	2012	199	C_N	57.1229	2	1.149134
RU-Fyo	Picea abies	2012	199	C_N	60.21972	2	2.762019
RU-Fyo	Picea abies	2012	199	C_N	65.25335	1	NA
RU-Fyo	Picea abies	2012	199	C_N	59.96741	2	0.634036
RU-Fyo	Picea abies	2012	199	C_N	52.23105	4	2.731713
RU-Fyo	Picea abies	2012	199	C_N	60.84204	3	0.744405
RU-Fyo	Picea abies	2012	199	C_N	68.28839	2	2.702697
RU-Fyo	Picea abies	2012	199	C_N	69.50078	2	4.604667
RU-Fyo	Picea abies	2012	199	C_N	70.44758	1	NA
RU-Fyo	Picea abies	2012	199	leaf_C_concentration	493.9005	3	1.058692
RU-Fyo	Picea abies	2012	199	leaf_C_concentration	496.8134	2	2.98308
RU-Fyo	Picea abies	2012	199	leaf_C_concentration	494.466	2	3.146109
RU-Fyo	Picea abies	2012	199	leaf_C_concentration	495.8739	1	NA
RU-Fyo	Picea abies	2012	199	leaf_C_concentration	493.4529	2	0.303867
RU-Fyo	Picea abies	2012	199	leaf_C_concentration	499.5279	4	5.405395
RU-Fyo	Picea abies	2012	199	leaf_C_concentration	500.7742	3	6.193141
RU-Fyo	Picea abies	2012	199	leaf_C_concentration	502.6356	2	2.630572
RU-Fyo	Picea abies	2012	199	leaf_C_concentration	503.2275	2	7.92551
RU-Fyo	Picea abies	2012	199	leaf_C_concentration	496.3837	1	0
RU-Fyo	Picea abies	2012	199	d13c	-29.461	3	0.639075
RU-Fyo	Picea abies	2012	199	d13c	-29.9135	2	1.40119
RU-Fyo	Picea abies	2012	199	d13c	-30.5905	2	0.404822
RU-Fyo	Picea abies	2012	199	d13c	-28.5738	1	NA
RU-Fyo	Picea abies	2012	199	d13c	-29.4589	2	0.832412
RU-Fyo	Picea abies	2012	199	d13c	-28.0881	4	0.558979
RU-Fyo	Picea abies	2012	199	d13c	-28.7483	3	0.442964

RU-Fyo	Picea abies	2012	199	d13c	-26.3319	2	4.112542
RU-Fyo	Picea abies	2012	199	d13c	-28.4677	2	0.991935
RU-Fyo	Picea abies	2012	199	d13c	-28.466	1	NA
RU-Fyo	Picea abies	2012	199	LMA	166.1769	3	39.88659
RU-Fyo	Picea abies	2012	199	LMA	210.7181	3	29.20474
RU-Fyo	Picea abies	2012	199	LMA	196.7841	3	32.46995
RU-Fyo	Picea abies	2012	199	LMA	208.849	3	16.33611
RU-Fyo	Picea abies	2012	199	LMA	222.3997	3	20.39354
RU-Fyo	Picea abies	2012	199	LMA	204.1996	2	19.77384
RU-Fyo	Picea abies	2012	199	LMA	223.7667	4	45.17229
RU-Fyo	Picea abies	2012	199	LMA	276.5832	4	31.44567
RU-Fyo	Picea abies	2012	199	LMA	285.7069	4	17.79849
RU-Fyo	Picea abies	2012	199	LMA	306.7822	3	29.6744
RU-Fyo	Picea abies	2012	199	LMA	339.8792	1	NA
RU-Fyo	Picea abies	2012	199	LMA	326.3974	1	NA
RU-Fyo	Picea abies	2012	199	leaf_N_area	1.767223	3	0.42905
RU-Fyo	Picea abies	2012	199	leaf_N_area	1.732715	2	0.299158
RU-Fyo	Picea abies	2012	199	leaf_N_area	1.488741	2	0.164628
RU-Fyo	Picea abies	2012	199	leaf_N_area	1.842842	1	0.223991
RU-Fyo	Picea abies	2012	199	leaf_N_area	1.679572	2	0.145989
RU-Fyo	Picea abies	2012	199	leaf_N_area	2.133648	4	0.351935
RU-Fyo	Picea abies	2012	199	leaf_N_area	2.199785	3	0.222553
RU-Fyo	Picea abies	2012	199	leaf_N_area	2.204312	2	0.08401
RU-Fyo	Picea abies	2012	199	leaf_N_area	2.128167	2	0.033603
RU-Fyo	Picea abies	2012	199	leaf_N_area	2.299843	1	NA
RU-Fyo	Picea abies	2012	199	Nmass	10.63968	3	0.471599
RU-Fyo	Picea abies	2012	199	Nmass	8.699557	2	0.22723
RU-Fyo	Picea abies	2012	199	Nmass	8.218477	2	0.324702
RU-Fyo	Picea abies	2012	199	Nmass	7.59921	1	0
RU-Fyo	Picea abies	2012	199	Nmass	8.229117	2	0.081939
RU-Fyo	Picea abies	2012	199	Nmass	9.584525	4	0.538345

RU-Fyo	Picea abies	2012	199	Nmass	8.231746	3	0.160131
RU-Fyo	Picea abies	2012	199	Nmass	7.367016	2	0.330091
RU-Fyo	Picea abies	2012	199	Nmass	7.260314	2	0.595056
RU-Fyo	Picea abies	2012	199	Nmass	7.046143	1	0
RU-Fyo	Picea abies	2012	199	leaf_P_area	0.252754	2	0.036755
RU-Fyo	Picea abies	2012	199	leaf_P_area	0.262757	2	0.018609
RU-Fyo	Picea abies	2012	199	leaf_P_dry	1.873475	3	0.227753
RU-Fyo	Picea abies	2012	199	SLA	6.298512	3	1.754995
RU-Fyo	Picea abies	2012	199	SLA	4.81119	3	0.710064
RU-Fyo	Picea abies	2012	199	SLA	5.179528	3	0.892619
RU-Fyo	Picea abies	2012	199	SLA	4.807857	3	0.378351
RU-Fyo	Picea abies	2012	199	SLA	4.521926	3	0.417978
RU-Fyo	Picea abies	2012	199	SLA	4.920238	2	0.476455
RU-Fyo	Picea abies	2012	199	SLA	4.588234	4	0.790547
RU-Fyo	Picea abies	2012	199	SLA	3.653225	4	0.442792
RU-Fyo	Picea abies	2012	199	SLA	3.51065	4	0.226149
RU-Fyo	Picea abies	2012	199	SLA	3.280903	3	0.329993
RU-Fyo	Picea abies	2012	199	SLA	3.318111	2	0.531587
RU-Fyo	Picea abies	2012	199	SLA	3.694	1	NA
RU-Fyo	Picea abies	2012	199	leaf_P_area	0.285246	3	0.034995
RU-Fyo	Picea abies	2012	199	leaf_P_area	0.305784	3	0.048119
RU-Fyo	Picea abies	2012	199	leaf_P_area	0.32788	4	0.065988
UK-Ham	Fraxinus excelsior	2012	204	leaf_N_P	6.183614	5	0.843946
UK-Ham	Fraxinus excelsior	2012	204	leaf_N_P	6.592848	5	0.79122
UK-Ham	Quercus robur	2012	204	leaf_N_P	10.94649	5	1.806957
UK-Ham	Quercus robur	2012	204	leaf_P_area	0.186168	3	0.076439
UK-Ham	Quercus robur	2012	204	leaf_N_P	11.87318	3	0.325575
UK-Ham	Fraxinus excelsior	2012	204	leaf_P_area	0.209102	5	0.036912
UK-	Quercus robur	2012	204	leaf_P_area	0.210539	5	0.04627

Ham							7
UK-Ham	Fraxinus excelsior	2012	204	C_N	21.32052	5	2.533408
UK-Ham	Fraxinus excelsior	2012	204	C_N	23.3893	5	2.369981
UK-Ham	Fraxinus excelsior	2012	204	leaf_C_concentration	450.6306	5	6.440926
UK-Ham	Fraxinus excelsior	2012	204	leaf_C_concentration	454.495	5	4.865597
UK-Ham	Fraxinus excelsior	2012	204	d13c	-30.3037	5	0.525767
UK-Ham	Fraxinus excelsior	2012	204	d13c	-28.892	5	0.441723
UK-Ham	Fraxinus excelsior	2012	204	LMA	63.81359	5	4.519437
UK-Ham	Fraxinus excelsior	2012	204	LMA	90.02749	5	4.666031
UK-Ham	Fraxinus excelsior	2012	204	leaf_N_area	1.357962	5	0.118935
UK-Ham	Fraxinus excelsior	2012	204	leaf_N_area	1.759898	5	0.148183
UK-Ham	Fraxinus excelsior	2012	204	Nmass	21.38338	5	2.604818
UK-Ham	Fraxinus excelsior	2012	204	Nmass	19.60162	5	2.120255
UK-Ham	Fraxinus excelsior	2012	204	leaf_P_area	0.288222	5	0.041863
UK-Ham	Fraxinus excelsior	2012	204	SLA	15.7314	5	1.073958
UK-Ham	Fraxinus excelsior	2012	204	SLA	11.13175	5	0.579831
UK-Ham	Quercus robur	2012	204	C_N	19.19204	5	1.063486
UK-Ham	Quercus robur	2012	204	C_N	19.4291	3	1.103747
UK-Ham	Quercus robur	2012	204	leaf_C_concentration	488.1354	5	2.693715
UK-Ham	Quercus robur	2012	204	leaf_C_concentration	486.3977	3	10.45437
UK-Ham	Quercus robur	2012	204	d13c	-29.173	5	0.800337
UK-Ham	Quercus robur	2012	204	d13c	-28.4124	3	0.426657
UK-Ham	Quercus robur	2012	204	LMA	89.40843	5	20.70156
UK-Ham	Quercus robur	2012	204	LMA	86.52053	3	30.08991
UK-Ham	Quercus robur	2012	204	leaf_N_area	2.277554	5	0.544564
UK-Ham	Quercus robur	2012	204	leaf_N_area	2.196213	3	0.858877
UK-Ham	Quercus robur	2012	204	Nmass	25.49651	5	1.410661
UK-Ham	Quercus robur	2012	204	Nmass	25.10668	3	1.905866

UK-Ham	Quercus robur	2012	204	SLA	11.6208	5	2.37532
UK-Ham	Quercus robur	2012	204	SLA	12.46475	3	3.968897
UK-Ham	Quercus robur	2012	204	leaf_P_dry	2.118436	3	0.214221
UK-Ham	Quercus robur	2012	204	leaf_P_dry	2.410773	5	0.627533
UK-Ham	Fraxinus excelsior	2012	204	leaf_P_dry	3.205565	5	0.453997
UK-Ham	Fraxinus excelsior	2012	204	leaf_P_dry	3.278123	5	0.542952
US-NC2	Pinus taeda	2012	206	leaf_N_P	9.483735	6	2.645856
US-NC2	Pinus taeda	2012	206	leaf_P_dry	1.746361	6	0.724834
US-NC2	Pinus taeda	2012	206	C_N	33.49981	6	4.093513
US-NC2	Pinus taeda	2012	206	leaf_C_concentration	498.6707	6	2.645804
US-NC2	Pinus taeda	2012	206	d13c	-29.5226	6	0.818744
US-NC2	Pinus taeda	2012	206	LMA	204.9509	6	25.55206
US-NC2	Pinus taeda	2012	206	leaf_N_area	3.120751	6	0.690903
US-NC2	Pinus taeda	2012	206	Nmass	15.05672	6	1.685069
US-NC2	Pinus taeda	2012	206	SLA	4.949423	6	0.678484
US-NC2	Pinus taeda	2012	206	leaf_P_area	0.368445	6	0.184532
US-So2	Ceanothus greggii	2012	294	leaf_P_dry	0.497259	3	0.096677
US-So2	Ceanothus greggii	2012	294	leaf_P_dry	0.699451	3	0.127001
US-So2	Adenostoma sparsifolium	2012	294	leaf_P_dry	0.898524	3	0.351337
US-So2	Cercocarpus	2012	294	leaf_P_dry	0.902074	3	0.143106
US-So2	Adenostoma fasciculatum	2012	294	leaf_N_P	7.183044	3	1.711751
US-So2	Adenostoma sparsifolium	2012	294	leaf_P_dry	1.058957	3	0.441742
US-So2	Adenostoma fasciculatum	2012	294	leaf_P_dry	1.060086	3	0.373865
US-So2	Adenostoma fasciculatum	2012	294	leaf_N_P	9.148914	3	2.962816
US-So2	Adenostoma sparsifolium	2012	294	leaf_N_P	9.499999	3	3.572516
US-So2	Cercocarpus	2012	294	leaf_P_area	0.161432	3	0.003066
US-So2	Adenostoma fasciculatum	2012	294	leaf_P_dry	1.330557	3	0.413559
US-So2	Adenostoma sparsifolium	2012	294	leaf_N_P	11.31701	3	5.268747

US-So2	Cercocarpus	2012	294	leaf_P_dry	1.424934	4	1.319113
US-So2	Ceanothus greggii	2012	294	leaf_P_area	0.195439	3	0.027618
US-So2	Adenostoma sparsifolium	2012	294	leaf_P_area	0.200241	3	0.074574
US-So2	Adenostoma sparsifolium	2012	294	leaf_P_area	0.201185	3	0.088729
US-So2	Ceanothus greggii	2012	294	leaf_P_area	0.249597	3	0.053015
US-So2	Ceanothus greggii	2012	294	leaf_N_P	14.83909	3	6.135897
US-So2	Cercocarpus	2012	294	leaf_N_P	15.14508	4	6.647793
US-So2	Cercocarpus	2012	294	leaf_P_area	0.302116	4	0.235767
US-So2	Adenostoma fasciculatum	2012	294	leaf_P_area	0.304825	3	0.102894
US-So2	Adenostoma fasciculatum	2012	294	Nmass	8.995554	3	1.317671
US-So2	Adenostoma fasciculatum	2012	294	Nmass	9.096633	3	1.30238
US-So2	Adenostoma fasciculatum	2012	294	SLA	3.501378	10	0.33103
US-So2	Adenostoma fasciculatum	2012	294	SLA	3.71371	10	0.727929
US-So2	Adenostoma fasciculatum	2012	294	d13c	-25.9514	3	1.039897
US-So2	Adenostoma fasciculatum	2012	294	d13c	-28.1458	3	0.543212
US-So2	Adenostoma fasciculatum	2012	294	LMA	287.8023	10	25.98419
US-So2	Adenostoma fasciculatum	2012	294	LMA	277.1251	10	45.84112
US-So2	Adenostoma fasciculatum	2012	294	leaf_N_area	2.606112	3	0.530279
US-So2	Adenostoma fasciculatum	2012	294	leaf_N_area	2.528133	3	0.340042
US-So2	Adenostoma sparsifolium	2012	294	Nmass	9.038025	3	1.25204
US-So2	Adenostoma sparsifolium	2012	294	Nmass	9.037554	3	1.880322
US-So2	Adenostoma sparsifolium	2012	294	SLA	4.496465	7	0.171676
US-So2	Adenostoma sparsifolium	2012	294	SLA	5.510283	7	1.195205
US-So2	Adenostoma sparsifolium	2012	294	d13c	-24.7026	3	0.530258
US-So2	Adenostoma sparsifolium	2012	294	d13c	-25.9537	3	0.289519
US-So2	Adenostoma sparsifolium	2012	294	LMA	222.6803	7	8.665329
US-So2	Adenostoma sparsifolium	2012	294	LMA	188.0962	7	36.579
US-So2	Cercocarpus	2012	294	leaf_N_P	18.01879	2	6.046254

US-So2	Adenostoma sparsifolium	2012	294	leaf_N_area	2.016969	3	0.211228
US-So2	Adenostoma sparsifolium	2012	294	leaf_N_area	1.71101	3	0.454345
US-So2	Ceanothus greggii	2012	294	d13c	-25.2657	3	0.487809
US-So2	Ceanothus greggii	2012	294	d13c	-26.4876	3	0.399975
US-So2	Ceanothus greggii	2012	294	LMA	358.7738	5	33.87424
US-So2	Ceanothus greggii	2012	294	LMA	397.5284	5	59.25122
US-So2	Adenostoma fasciculatum	2012	294	leaf_P_area	0.371321	3	0.122071
US-So2	Ceanothus greggii	2012	294	Nmass	9.86033	3	2.623221
US-So2	Ceanothus greggii	2012	294	Nmass	10.50792	3	1.852064
US-So2	Ceanothus greggii	2012	294	SLA	2.806714	5	0.258184
US-So2	Ceanothus greggii	2012	294	SLA	2.570244	5	0.460203
US-So2	Ceanothus greggii	2012	294	leaf_N_area	3.487174	3	0.838181
US-So2	Ceanothus greggii	2012	294	leaf_N_area	4.138814	3	0.565918
US-So2	Cercocarpus	2012	294	d13c	-26.6809	4	1.087968
US-So2	Cercocarpus	2012	294	d13c	-27.6655	3	0.303811
US-So2	Cercocarpus	2012	294	LMA	227.6793	4	29.2486
US-So2	Cercocarpus	2012	294	LMA	170.9545	4	32.09329
US-So2	Cercocarpus	2012	294	Nmass	15.37308	4	3.505566
US-So2	Cercocarpus	2012	294	Nmass	17.52244	4	1.43557
US-So2	Cercocarpus	2012	294	leaf_N_area	3.460988	4	0.416749
US-So2	Cercocarpus	2012	294	leaf_N_area	2.989693	4	0.365211
US-So2	Cercocarpus	2012	294	SLA	4.44844	4	0.585343
US-So2	Cercocarpus	2012	294	SLA	6.006985	4	1.133201
US-So2	Ceanothus greggii	2012	294	leaf_N_P	21.2044	3	0.890161

Table 2 - 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. Due to size limitation, the table is presented in three pieces.

site.code	**AT-Neu**	**BR-Sa1**	**CA-Qfo**	**CZ-BK1**	**DE-Hai**	**ES-ES2**	**FI-Hyy**
CWM_C_N	16.19793	22.63714	71.95308	44.38642	21.08715	13.10593	41.48681
CWM_leaf_C_concentration	443.5932	469.0275	526.7932	501.7527	475.8013	415.3668	520.7857
CWM_d13c	-28.4746	-30.9599	NA	-28.5002	-30.2697	-27.8135	-29.115
CWM_LMA	41.75546	106.9187	291.6528	246.1367	63.70397	179.358	202.2797
CWM_leaf_N_area	1.200615	2.347107	2.18286	2.957086	1.417043	5.820197	2.532181
CWM_Nmass	2.906181	2.219488	0.738779	1.146627	2.316771	3.234508	1.257758
CWM_SLA	24.75197	10.97657	3.461288	4.26538	22.17926	6.379126	4.945452
CWM_leaf_P_area	0.07965	0.085426	0.582239	0.305184	0.077782	0.521963	0.281051
CWM_leaf_P_dry	1.896433	0.817839	1.86438	1.260958	1.352765	2.977446	1.363887
CWM_leaf_N_P	16.50778	27.41131	3.975643	10.34384	17.89954	13.0811	9.752842
CWMT_C_N	18.45474	NA	41.19889	40.64825	19.72856	NA	33.11182
CWMT_leaf_C_concentration	453.3631	488.0218	NA	495.7241	466.233	NA	505.159
CWMT_d13c	1.30E-12	NA	NA	NA	NA	NA	NA
CWMT_LMA	43.69435	93.15758	298.6678	235.1035	69.34987	51.17785	213.6171
CWMT_leaf_N_area	1.13142	2.032582	3.31493	3.159912	1.418148	1.327431	2.731557
CWMT_Nmass	2.368113	2.113338	0.868903	1.237445	2.268228	1.867262	1.287184
CWMT_SLA	22.88625	10.7345	3.348202	4.253446	14.41964	19.5397	4.681272
CWMT_leaf_P_area	0.102099	0.071089	NA	0.488557	0.084195	NA	0.274121
CWMT_leaf_P_dry	2.336196	0.81626	1.053435	1.412725	1.556374	4.6	1.31916
CWMT_leaf_N_P	9.228068	28.2249	8.301142	8.556704	13.78539	3.756522	9.477867
GPPsat-insitu	36.99937	35.5024	14.89893	30.66649	31.93329	49.22434	27.03431
GPPsat-lathuile	37.71878	34.10709	14.0246	32.77801	32.67662	44.50069	22.93803
GPPsat.structure-insitu	41.09735	39.36204	17.08235	36.89685	39.16647	63.9199	30.12201
GPPsat.structure-lathuile	42.56153	37.48434	15.63961	37.22347	37.48299	50.81578	26.94393
site.code	**FR-Hes**	**FR-Lq1**	**FR-Lq2**	**IL-Yat**	**IT-Lav**	**IT-MBo**	**IT-Ren**
CWM_C_N	NA	11.39143	18.12147	51.92673	46.56886	23.56202	43.19979
CWM_leaf_C_concentration	NA	436.8895	441.8809	501.299	495.6982	451.0995	485.2103
CWM_d13c	NA	-29.3364	-28.3502	-23.3617	-27.496	-27.6771	-28.2041
CWM_LMA	NA	39.71881	51.24906	229.2007	195.7096	60.67202	322.2576
CWM_leaf_N_area	NA	1.515371	1.296343	2.211249	2.17839	1.219707	3.564986
CWM_Nmass	2.50303	3.888944	2.633798	0.973834	1.108636	2.138845	1.226266
CWM_SLA	NA	27.08265	21.66885	4.491266	6.001199	17.81801	4.305512
CWM_leaf_P_area	0.074692	0.136823	0.120917	0.177572	0.246429	0.112108	0.186769
CWM_leaf_P_dry	1.289436	3.437713	2.499344	0.78515	1.186473	1.927631	0.734937
CWM_leaf_N_P	19.41181	11.44937	10.70635	13.07472	10.84268	11.66273	17.33482
CWMT_C_N	20.80927	13.92256	18.33537	NA	30.19025	20.96134	40.64825
CWMT_leaf_C_concentration	480.3819	452.8137	450.8655	523.162	499.6981	453.8033	496.9908
CWMT_d13c	NA	7.71E-13	1.54E-12	NA	NA	1.78E-12	NA
CWMT_LMA	67.18751	40.63683	45.16111	228.8153	190.3769	57.5865	203.4818

CWMT_leaf_N_area	1.218922	1.179075	1.088849	2.612694	2.39061	1.343492	2.770824
CWMT_Nmass	2.259025	2.730732	2.228978	1.17461	1.285157	2.252715	1.275562
CWMT_SLA	14.88372	24.60822	22.14295	4.370337	5.252738	17.36518	4.914444
CWMT_leaf_P_area	0.067263	0.086625	0.086077	0.210311	0.276058	0.103338	0.488557
CWMT_leaf_P_dry	1.402929	2.048156	1.924127	0.797866	1.45043	1.455547	1.396644
CWMT_leaf_N_P	15.94407	12.43191	10.6464	12.07733	8.919921	9.238589	8.745714
GPPsat-insitu	34.47593	32.48059	24.37614	15.20294	29.02556	33.47582	21.25927
GPPsat-lathuile	33.68055	30.4956	26.06604	14.95366	30.14579	29.56173	24.82192
GPPsat.structure-insitu	36.36888	34.54528	27.71349	23.37873	35.90655	35.65721	34.91334
GPPsat.structure-lathuile	35.33168	34.55264	27.83678	22.08196	37.93645	31.34069	34.206

site.code	**NL-Loo**	**RU-Fyo**	**UK-Ham**	**US-NC2**	**US-So2**
CWM_C_N	25.61057	61.03541	19.64883	33.49981	NA
CWM_leaf_C_concentration	501.0324	497.7056	483.4106	498.6707	NA
CWM_d13c	-28.5194	-28.81	-28.8821	-29.5226	-26.8697
CWM_LMA	196.5303	247.3536	86.73738	204.9509	275.0303
CWM_leaf_N_area	3.919266	1.947685	2.161555	3.120751	2.516855
CWM_Nmass	1.991641	0.828758	2.476725	1.505672	0.9129
CWM_SLA	6.054296	4.382031	12.19708	4.949423	3.751264
CWM_leaf_P_area	0.291393	0.23779	0.203943	0.368445	0.322431
CWM_leaf_P_dry	1.48173	1.037869	2.373187	1.746361	1.167923
CWM_leaf_N_P	14.70763	8.488917	10.85188	9.483735	8.564969
CWMT_C_N	31.78128	40.64825	19.58326	42	NA
CWMT_leaf_C_concentration	507.0674	495.7241	482.6146	NA	NA
CWMT_d13c	NA	NA	NA	NA	NA
CWMT_LMA	209.5615	235.1035	72.81771	184.4365	233.2807
CWMT_leaf_N_area	2.653123	3.159912	1.778991	1.900725	2.332533
CWMT_Nmass	1.297369	1.237445	2.196016	1.058254	1.023403
CWMT_SLA	4.771869	4.253446	13.73292	5.42192	4.286681
CWMT_leaf_P_area	0.244202	0.488557	0.11276	NA	0.331017
CWMT_leaf_P_dry	1.301205	1.412725	1.785371	1.15879	1.192206
CWMT_leaf_N_P	9.673673	8.556704	12.6941	9.782396	8.817993
GPPsat-insitu	28.4188	25.58003	43.97018	31.51059	10.50983
GPPsat-lathuile	31.45719	24.80549	43.22431	39.98528	6.445735
GPPsat.structure-insitu	34.19777	28.03949	53.56655	37.81442	13.512
GPPsat.structure-lathuile	37.93532	28.67609	49.6671	43.71556	8.454755

Table 3 – Species Composition

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

site.code	Species	abundace
AT-Neu	Dactylis glomerata	19
AT-Neu	Phleum pratense	19
AT-Neu	Ranunculus acris	3
AT-Neu	Taraxacum officinale	5
AT-Neu	Trifolium pratense	1
AT-Neu	Trifolium repens	3
BR-Sa1	Abuta rufescens	5
BR-Sa1	Anomalocalyx uleanus	5
BR-Sa1	Arrabidea prancei	5
BR-Sa1	Combretum	5
BR-Sa1	Copaifera duckei	5
BR-Sa1	Cordia bicolor	5
BR-Sa1	Duguetia cadaverica	5
BR-Sa1	Faramea platyneura	5
BR-Sa1	Lecythis lurida	5
BR-Sa1	Lecythis	5
BR-Sa1	Manilkara huberi	5
BR-Sa1	Memora tanaeciicarpa	5
BR-Sa1	Miconia acinodendron	5
BR-Sa1	Micropholis	5
BR-Sa1	Prinostemma af. aspera	5
BR-Sa1	Protium puncticulatum	5
BR-Sa1	Rinorea neglecta	5
BR-Sa1	Sclerolobium paraense	5
BR-Sa1	Tachigali myrmecophila	5
BR-Sa1	Tetrapterys	5
CA-Qfo	Picea mariana	90
CA-Qfo	Pinus banksiana	10
CZ-BK1	Picea abies	100
DE-Hai	Acer pseudoplatanus	10.6
DE-Hai	Fagus sylvatica	66.5
DE-Hai	Fraxinus excelsior	21.9
ES-ES2	Oryza sativa	100
FI-Hyy	Picea abies	
FI-Hyy	Pinus sylvestris	
FR-Hes	Fagus sylvatica	100
FR-Lq1	Agrostis capillaris	11.61

FR-Lq1	Dactylis glomerata	25.376
FR-Lq1	Festuca rubra	4.673
FR-Lq1	Lolium perenne	12.447
FR-Lq1	Poa pratensis	5.58
FR-Lq1	Poa trivialis	8.003
FR-Lq1	Trifolium repens	23.195
FR-Lq2	Agrostis capillaris	18.756
FR-Lq2	Anthoxanthum odoratum	5.134
FR-Lq2	Dactylis glomerata	17.229
FR-Lq2	Festuca rubra	10.278
FR-Lq2	Holcus mollis	4.775
FR-Lq2	Phleum pratense	4.248
FR-Lq2	Poa pratensis	12.142
FR-Lq2	Trifolium repens	6.776
FR-Lq2	Trisetum flavescens	4.601
FR-Lq2	Veronica chamaes	4.236
IL-Yat	Pinus halepensis	100
IT-Lav	Abies alba	64
IT-Lav	Fagus sylvatica	2
IT-Lav	Picea abies	34
IT-MBo	Alchemilla vulgaris	5
IT-MBo	Avenella flexuosa	5.6
IT-MBo	Brachypodium pinnatum	5.3
IT-MBo	Dactylis glomerata	3.6
IT-MBo	Festuca rubra	25
IT-MBo	Koeleria pyramidata	6.2
IT-MBo	Nardus stricta	12.8
IT-MBo	Trifolium montanum	6.3
IT-MBo	Trifolium pratense	8.2
IT-Ren	Deschampsia	2.7
IT-Ren	grass	2.7
IT-Ren	Picea abies	85
IT-Ren	Vaccinium	9.6
IT-SRo	Pinus pinaster	100
NL-Loo	Pinus sylvestris	100
RU-Fyo	Picea abies	100
UK-Gri	Picea sitchensis	100
UK-Ham	Fraxinus excelsior	10
UK-Ham	Quercus robur	80
US-Fuf	Pinus ponderosa	100
US-Ha1	Acer rubrum	38
US-Ha1	Acer rubrum	13
US-Ha1	Quercus rubra	21

US-NC2	Pinus taeda	100
US-So2	Adenostoma fasciculatum	90
US-So2	Adenostoma sparsifolium	10
US-So2	Ceanothus greggii	1
US-So2	Cercocarpus	1

3.3 Paper 3

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Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity

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Abstract

The total uptake of carbon dioxide by ecosystems via photosynthesis (gross primary productivity, GPP) is the largest flux in the global carbon cycle. A key ecosystem functional property determining GPP is the photosynthetic capacity at light saturation (GPPsat), and its interannual variability (IAV) is propagated to the net land–atmosphere exchange of CO_2. Given the importance of understanding the IAV in CO_2 fluxes for improving the predictability of the global carbon cycle, we have tested a range of alternative hypotheses to identify potential drivers of the magnitude of IAV in GPPsat in forest ecosystems. Our results show that while the IAV in GPPsat within sites is closely related to air temperature and soil water availability fluctuations,

the magnitude of IAV in GPPsat is related to stand age and biodiversity ($R^2 = 0.55$, $P < 0.0001$). We find that the IAV of GPPsat is greatly reduced in older and more diverse forests, and is higher in younger forests with few dominant species. Older and more diverse forests seem to dampen the effect of climate variability on the carbon cycle irrespective of forest type. Preserving old forests and their diversity would therefore be beneficial in reducing the effect of climate variability on Earth's forest ecosystems.

Introduction

Interannual variability (IAV) of the net carbon dioxide exchange over land is globally the main determinant of the variability of atmospheric CO_2 growth rate[1,2]. So understanding the factors controlling the IAV in CO_2 fluxes is essential to improve the predictability of the global carbon cycle[3]. Ecosystem biotic properties — such as soil and canopy nutrient status, rates of change in physiological properties of the vegetation, or the sensitivity of these properties to environmental factors — influence ecosystem CO_2 exchange. Recent studies have shown that the IAV of the carbon budget can be better explained by variation in biotic properties of ecosystems such as photosynthetic capacity (GPPsat) than directly by environmental and climatic drivers[4–6]. GPPsat is defined as the value of gross primary productivity (GPP) at saturating light under non-stressed conditions, minimizing the influence of anomalous hydrometeorological conditions (for example, droughts and heatwaves), which potentially affect photosynthesis. A robustly retrieved characterization of GPPsat can be regarded as an ecosystem functional property reflecting the physiological response of the ecosystem to the environment. Given that IAV of GPPsat must propagate to observed GPP, this quantity is thought to be a key variable in understanding IAV of carbon fluxes[7]. In fact, recent studies demonstrated that GPPsat correlates more strongly than any climatic variable with annual GPP[8], but also correlates with net ecosystem CO2 exchange[5]. The magnitude of IAV in GPPsat has been shown to exhibit considerable variation across ecosystems[9], yet no obvious explanation for this pattern has been reported in the literature. However, the consequences are important: a low IAV in GPPsat would suggest that ecosystem functioning is not very sensitive to climatic variability, and that it preserves its functionality under the influence of that variability — and, likewise, high IAV is a consequence of high sensitivity. The capability of an ecosystem to preserve its functioning and structure over time (after external disturbances or climate extremes), is often defined as ecosystem stability and is linked to ecosystem resilience[10]. Using this terminology, low values of IAV in GPPsat can be understood as a characterization of high ecosystem functional stability.

The relation of ecosystem functionality, structure and stability has been a matter of debate for many decades in the field of ecology. In particular, the diversity of vascular plants has been investigated as a stabilizing factor with respect to variations in productivity, for example by buffering the ecosystem's sensitivity to climate extremes[11]. However, it is also well known that plant diversity is co-limited by soil properties[12], ecosystem management, and climate conditions. Another variable to consider is stand age (the mean age of the forest stand or the number of years after a major stand replacement after disturbance), which may affect ecosystem stability through adaptation, particularly of trees to their environment — hence increasing ecosystem resilience to climate variability[13]. Moreover, structural parameters such as canopy cover, rooting depth, canopy height or leaf area index (LAI), which also depend on tree species diversity and stand age[14], have an important effect on the ecosystem response to variation in environmental drivers since they define the capacity of trees to access resources such as water and light[15]. For instance, a regional study in the Amazon basin has shown that GPP, derived from the remotely sensed enhanced vegetation index, is less sensitive to environmental influences in regions with high canopy cover[16]. Despite this growing body of ecological knowledge, it remains largely uncertain which factors stabilize ecosystem functional properties at the global scale. In particular, we do not understand the causes of variability of specific ecosystem functional properties, such as photosynthetic capacity across ecosystem types, which ultimately controls ecosystem productivity. Here we hypothesize that stand age and species diversity play an important role in stabilizing ecosystem photosynthetic capacity. We test this hypothesis while also considering other factors related to climate, water availability, forest structure and soil properties that might have direct or indirect effects on ecosystem photosynthetic capacity. In this study, we used measurements of ecosystem-level fluxes, and climate variables (temperature, precipitation, and water availability), species richness, stand age, forest structure (canopy cover, height, and LAI), and soil properties (nutrient availability[17]) derived from satellite data, in situ observations and the literature (see the Methods). We used half-hourly ecosystem-level GPP fluxes estimated by the means of the eddy-covariance technique at 50 FLUXNET sites[18] with at least 4 years of measured fluxes, and with different vegetation types across different climatic regions. We included data from evergreen forest (EF) as well as deciduous broadleaved and mixed forest

(DBMF) located in temperate, boreal, mediterranean, tropical and dry climate regions (Supplementary Fig. 1 and Table 1).

All 50 sites have information on stand age (referred to simply as ‘age’ in Figs 1–3) and species richness in addition to the CO_2 flux data. Species richness (‘sp. no.’ in Figs 1–3) is the number of dominant plant species (for example tree or herb) that account for a cumulative abundance of 90 percent at a given site. We collected additional information on (i) canopy cover, (ii) canopy height, (iii) LAI, (iv) temperature and precipitation, and (v) soil water availability index (WAI) for a subset of 44 sites; and (vi) an index of nutrient availability for 36 sites compiled from the literature[17] (see Methods). We characterized the response of half-hourly GPP estimates to incoming shortwave radiation by fitting ecosystem-level light response curves yielding daily estimates of GPPsat (see Methods). The site-level estimates of annual GPPsat (that is, GPP at saturating light conditions) were then determined by extracting the 90th percentile of the daily estimates of GPPsat. The magnitude of the IAV in GPPsat was computed as the coefficient of variation of annual estimates of GPPsat ($cvGPPsat = \sigma\ (GPPsat(t))/\mu\ (GPPsat(t))$), where GPPsat(t) is the annual GPPsat for year t, and σ and μ are the standard deviation and mean of GPPsat(t), respectively. Two variable selection methods based on (i) relative importance of regressors[19], and (ii) multivariate generalized regression models and a stepwise algorithm based on Akaike Information Criteria (stepAIC) were used to select the most relevant predictors of the IAV of GPPsat (see Methods).

Results

Results from the variable selection and relative importance methods (see Methods) conducted over the 44 sites with all variables are consistent with our hypothesis that stand age and species richness of the sites are the most important predictors of cvGPPsat, with stand age being statistically the dominant factor (Fig. 1a). We further tested the performance of a multiple linear model, where cvGPPsat is a function of stand age and species richness, using all sites with data available for these two predictors (50 sites). The model suggests a clear relationship between cvGPPsat and the logarithm of stand age and the species richness (Table 2, $R^2 = 0.55$, $P < 0.0001$). Stand age, which is negatively correlated with cvGPPsat, is the most important predictor (from the 55% explained variance by both variables, the relative contribution to the explained variance by stand age and species richness is 74.5% and 25.5%, respectively; Fig. 1b and Supplementary Fig. 2).

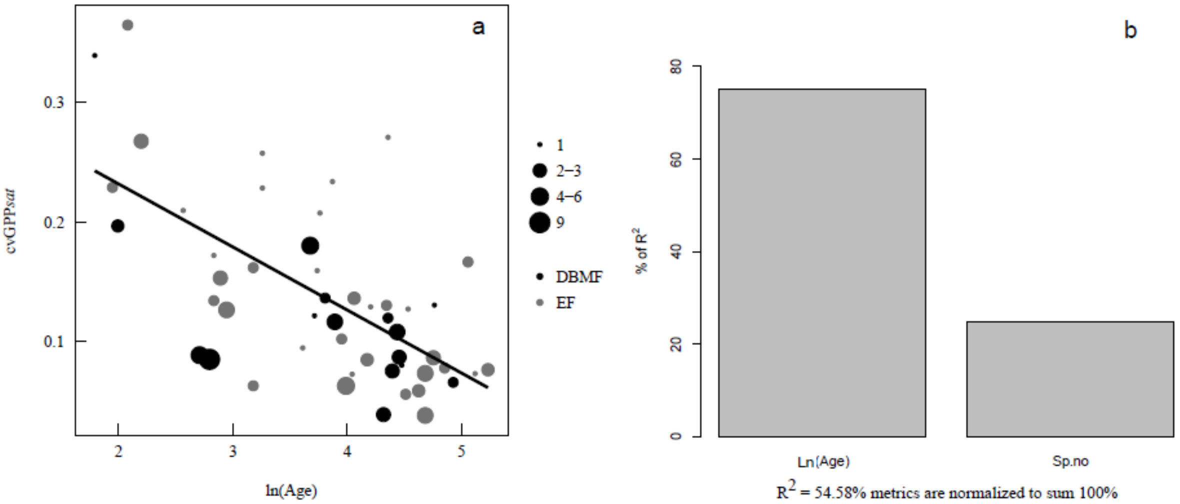

Figure 1 | Relationship of cvGPPsat with stand age and species richness. a, The relationship between the interannual variability of ecosystem photosynthetic capacity (cvGPPsat) computed for each FLUXNET site and stand age (which is transformed using the natural logarithm, ln(age)): (R^2 = 0.39, $P < 0.0001$, n = 50). *The number of plant species at the sites that account for 90% of the total species abundances (sp. no.) is indicated with the size of the points. DBMF, deciduous broad leaf and mixed forests (n = 16; black); EF, evergreen needleleaf and broadleaf forests (n = 34; grey).* **b, Relative importance metrics of ln(age) and sp. no. as predictors of cvGPPsat.** *For a version of this figure using age without logarithm transformation, see Supplementary Fig. 11.*

Model structure	**R^2**	**adj.R^2**	**predictors**	**coefficients**	***p***
cvGPP*sat* ~ Sp.no	0.12	0.10	Intercept	0.18 ± 0.02	0.01
			Sp.no	-0.01 ± 0.00	
cvGPP*sat* ~ Age	0.25	0.24	Intercept	0.19 ± 0.01	0.0002
			Age	-0.00 ± 0.00	
cvGPP*sat* ~ ln(Age)	0.39	0.38	Intercept	0.33 ± 0.04	<0.0001
			Ln(Age)	-0.05 ± 0.01	
cvGPP*sat* ~ln(Age) + Sp.no	0.55	0.53	Intercept	0.39 ± 0.03	<0.0001
			Ln(Age)	-0.05 ± 0.01	
			Sp.no	-0.02 ± 0.00	
cvGPP*sat* ~ ln(Age) + Sp.no + Age:Sp.no	0.55	0.52	Intercept	0.42 ± 0.06	<0.0001
			Ln(Age)	-0.06 ± 0.01	
			Sp.no	-0.03 ± 0.02	
			Ln(Age):Sp.no	0.00 ± 0.00	

Table 1 | Summary of the linear models fitted for cvGPPsat (the interannual variability of ecosystem photosynthetic capacity computed for each FLUXNET site) with the chosen predictors for the different groups of sites classified according to vegetation type. *PFT, plant functional types; s.e., standard error; d.f., degree of freedom; DBMF, deciduous broad leaf and mixed forests; EF, evergreen forests. ln(Age) is the natural logarithm of the average stand age, and sp. no. is the number of dominant plant species that have a cumulative abundance of 90% at the sites.*

Sites PFT	R^2	adj. R^2	predictors	coefficients	SE	d.f.	*p*
DBMF	0.65	0.60	Intercept	0.38	0.05	13	<0.0001
			ln(Age)	-0.06	0.01		0.0004
			Sp.no	-0.01	0.00		0.02
DBMF	0.46	0.42	Intercept	0.31	0.05	14	<0.0001
			ln(Age)	-0.05	0.01		0.004
EF	0.49	0.46	Intercept	0.38	0.04	31	<0.0001
			ln(Age)	-0.05	0.01		<0.0001
			Sp.no	-0.02	0.007		0.02
EF	0.40	0.38	Intercept	0.35	0.05	32	<0.0001
			ln(Age)	-0.05	0.01		<0.0001

Table 2 | Comparison of different models computed using the set of predictors chosen by both stepwise model selection according to AIC and relative importance methods. *cvGPPsat is the IAV magnitude of ecosystem photosynthetic capacity, and sp. no. is the number of dominant plant species that have a cumulative abundance of 90% at the sites. ln(Age) is the natural logarithm of the average stand age. The number of sites is n = 50.*

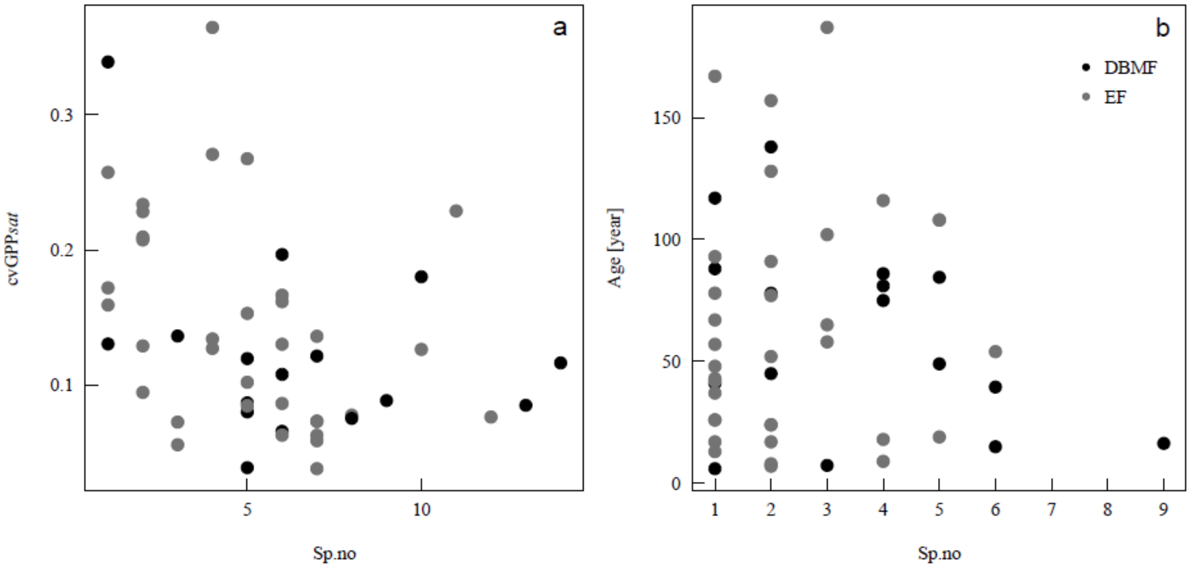

Figure 2 | Relationship of species richness with stand age and cvGPPsat. a, The relationship between cvGPPsat computed for each FLUXNET site and species richness (sp. no.) (R2 = 0.12, P = 0.01, n = 50). b, The relationship between species richness and stand age (R2 = 0, P = 0.68, n = 50). *DBMF are deciduous broad leaf and mixed forests (n = 16; black) and EF are evergreen needleleaf and broadleaf forests (n = 34; grey).*

The relationship between cvGPPsat and stand age also holds across the different forest types (ENF and DBMF) (Fig. 1a and Table 1). Species richness has a complementary effect: for the same age class, higher values of species richness yield lower IAVs of GPPsat (Table 2 and Fig. 1a). While species richness has a negative relation with cvGPPsat (Fig. 2a and Table 2), it is not correlated with stand age (R^2 = 0, Fig. 2b). Furthermore, Fig. 1 shows that the slope of cvGPPsat versus stand age is similar for the two different forest types, which suggests that the relationship between cvGPPsat and stand age is independent of forest type (Table 1). The relationship is also independent of LAImax of the sites (Supplementary Fig. 3).

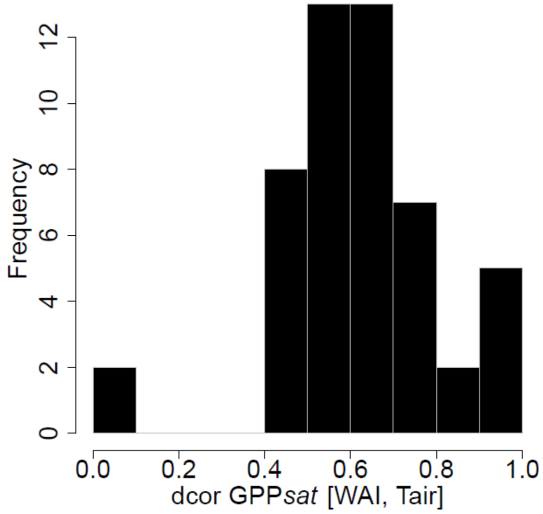

Figure 3 | Frequency distribution of the distance correlation coefficients computed between the annual ecosystem photosynthetic capacity (GPPsat) and the environmental variables WAI and T_{air} (n = 50). *WAI, average water availability index; and* T_{air}*, temperature (both during the growing season). Using the distance correlation coefficient (dcor)*[32]*, we show the strength of the correlation of GPPsat with WAI and* T_{air} *jointly (see the Methods).*

In young forests, cvGPPsat might depend also on the expected trend in annual growth and GPP, as young stands are expected to rapidly increase their biomass and LAI in the first years of establishment[20]. Thus, young stands could have a higher variability of GPPsat — but this does not necessarily reflect instability. To remove this potentially confounding factor, we tested whether there is a temporal trend in our data of annual GPPsat at the sites (Methods). Using a Mann-Kendall test, we found only five sites had a significant trend, two of which were old sites (> 80 years). The results of the model selection and the relationship between cvGPPsat, stand age and species richness remains the same regardless of whether the trend in GPPsat from these sites is removed (see Supplementary Information). While there is a strong relationship between the annual GPPsat and mean growing season temperature and WAI (Fig. 3 and Supplementary Figs 4–7) across all sites, the magnitude of the

IAV of GPPsat is best explained by stand age differences, and not by the differences in the IAV of climate and environmental factors (that is, standard deviation of annual growing season temperature and WAI). The distance correlation coefficient between GPPsat and climate variables, which can account for nonlinearity in statistical relations, is also not linked to stand age, species richness or cvGPPsat (Supplementary Fig. 8). Pairwise relationships between cvGPPsat, environmental variables and ecosystem structural variables were also tested. Soil nutrient availability has no effect on the cvGPPsat (Supplementary Fig. 9), and neither do the other variables (Supplementary Fig. 10).

Discussion

Previous studies have shown that vegetation responses to climate variability can explain the IAV of ecosystem fluxes better than climate variables themselves on longer timescales[4,6,21]. Here we show further that the magnitude of IAV in GPPsat (ecosystem photosynthetic capacity) is best explained by vegetation properties of the sites. We identify a joint control of stand age and biodiversity on the magnitude of the IAV of ecosystem photosynthetic capacity (that is, cvGPPsat). Part of the unexplained variance in cvGPPsat by stand age and species richness could be also associated with management and disturbances that were not included in the ancillary database of the sites, and can therefore not be formally investigated. Accurately simulating GPP in terrestrial biosphere models depends crucially on parameters related to GPPsat[22]. These parameters are typically assumed to be constant over time, but may vary spatially according to forest types[23]. Our findings suggest that stand age and species richness should be accounted for to dynamically adjust parameters related to photosynthetic capacity. Stand age can influence GPPsat stability in different ways by enhancing soil conditions over time (for example, a thicker humus layer with favourable microbial communities, increased water storage capacity, and access to deeper water with a tap root system[13]). Also, a forest may develop a more diverse canopy and rooting structure, allowing for more complementary use of nutrients and water.

In addition, older forests are more resilient to environmental changes because with time species selection leads to a better adaptation to the environment[24]. Site fertility can also improve with stand age, following the nutrient losses occurring during major disturbances (such as fire or harvest). In fact, the ecosystem internal cycle of macronutrients is particularly relevant[25,26] and leads to a progressive accumulation of nutrients in the living biomass with age[27].

Although species diversity is generally assumed to increase ecosystem resilience, exceptions have been reported[28]. For example, species diversity can enhance forest resistance to drought only if the system is prone to drought[28]. This is considering the gradual adaptation of the ecosystem to its environment by changing species composition to track environmental changes.

Facilitation (specie interactions that results in the species benefitting from each other) and complementary functioning of plant species can explain why species richness is important for ecosystem stability and how the interaction of species modulates the climate effect on ecosystem functioning[29]. In addition, mixed forests are able to buffer the effect of climate IAV through competition and facilitation in normal and stressful years, respectively[29]. Facilitation and complementary effects are clearly related to the functional richness of the species pool (that is, species with different functional traits), which is linked to stand age as shown by a regional study in the tropics[30]. Diverse ecosystems with a higher number of plant species respond less dramatically in their functioning (compared to ecosystems with single or few species) to climate and environmental stresses. The Earth's forest cover is essential to remove CO_2 from the atmosphere, and afforestation is important to compensate for forest loss due to land use changes (such as agriculture). While young forests established on former agricultural lands, or burned and harvested forests for several years cannot compensate for the initial carbon loss nor contribute to CO_2 sequestration from the atmosphere, old forest stands retain their capacity to sequester CO_2 for long periods[31,32]. We show that the photosynthetic capacity and therefore the gross primary production of old growth forests are more resilient to climate variability than young forests. In addition, our study suggests that species-rich forest stands offer a larger potential for maintaining a stable photosynthetic capacity across time than species-poorer stands. Therefore, preserving our current forest (with old forests covering 15% of Earth's surface[32]) and their species diversity may attenuate the annual fluctuations of global forest–atmosphere CO_2 exchange.

Methods

Data: In this study we brought together a wide range of data: ecosystem–atmosphere CO_2 fluxes measured at eddy covariance flux sites, information about climate (temperature, precipitation, and water availability index (WAI)), species richness, stand age, and plant traits, derived from field campaigns, and information about forest structure derived from satellite data for each of the selected sites; finally, data about nutrient availability was derived from the literature[17]. Sites were selected according to the availability of eddy covariance flux measurements for at least 4 years, information about stand age, canopy cover, canopy height, and species abundance. This led to a global dataset of 50 sites with different vegetation types across different climatic regions. We included data from evergreen forest (EF) and deciduous broadleaved and mixed forest (DBMF) located in temperate, boreal, tropical, Mediterranean and dry climate regions.

CO_2 fluxes and meteorological data: From the global eddy covariance flux database[18] we downloaded half-hourly ecosystem-level gross primary productivity (GPP) fluxes estimated from net ecosystem exchange (NEE) data[34]. Half-hourly shortwave incoming global radiation, temperature, and precipitation were also downloaded. From the dataset WAI was computed according to ref. 35. Here the WAI is the ratio between soil water storage and plant available water storage capacity at lower layer (100 mm)[35].

Average stand age: These data were obtained from the Biological, Ancillary, Disturbance and Metadata (BADM) of the FLUXNET database[36]. Stand age (expressed in years) reported in the BADM is the average tree age of the stand or the age of the stand since the last major disturbance that caused stand replacement. Stand age was reported for different years at the sites, and so we normalized the data by using the age of all sites at the year 2007 (which is the year of the release of FLUXNET LaThuile Database used in this study).

Species richness: Species identity and abundances from the BADM data and literature search were collected. Because these data come from diverse sources and are collected with different protocols, they can have variable level of details. Therefore, we developed a strategy to guarantee comparability of the plant species richness computed across sites. For each site we sorted the plant species according to their abundance, from the one with highest abundance to the lowest. Then we considered only the number of species that add up to 90% of the total site abundance.

Canopy structure: For the selected sites we extracted satellite products to characterize canopy structure: canopy cover, plant height and Leaf Area Index (LAI). Canopy cover was extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation products continuous field version 4[37] (http://glcf.umd.edu/data/vcf/). Plant height was derived for each site from the estimates reported in ref. 38 (http://lidarradar.jpl.nasa.gov/). We used estimates of LAI derived at 1 km (0.01°) spatial resolution by the JRC-TIP[39] from the MODIS broadband visible and near-infrared surface albedo products[40]. The processing for the gap filling and the extraction of the time series from MODIS-TIP LAI products is described in ref. 9. Annual maximum LAI values were derived at each site by extracting for each year the 90th percentile of the 16-day LAI time series. Finally for each site the maximum LAI (LAImax) and the coefficient of variation of the annual maximum LAI (cvLAImax) were estimated. In this study we did not use site level LAI data reported in the FLUXNET database for the following reasons:

1. LAI data have been collected with a variety of different methods, from direct (that is, harvesting and litter fall) to indirect (for example, hemispherical photography or LAI-2000) methods. Site-level method intercomparisons of various techniques always reveal large and non-systematic differences among LAI methodologies, rendering the LAI information reported in the FLUXNET database not always suited for network synthesis studies. Efforts toward the standardization of the collection of these measurements are ongoing in the context of the Integrated Carbon Observation System (ICOS) and National Ecological Observatory Network (NEON), but these data are not yet available.

2. The availability of data in regular annual measurement is very different among sites. For some sites the LAI is available for each measurement year (and sometimes even seasonally), but for many sites only one estimate during the whole measurement period is available.

Considering the limitations of site-level LAI data, we selected the MODIS-TIP LAI product. MODIS-TIP LAI is recognized as one of the most effective LAI products available and it was successfully evaluated at a FLUXNET site included in this study[41].

Nutrient availability: Part of the dataset (36 sites) was complemented with soil nutrient availability classes derived from literature[17]. For each site, nutrient availability was computed using site-level specific information about the following variables: carbon, nitrogen and phosphorus concentrations of soil and/or leaves, soil type, soil texture, soil C/N ratio, and soil pH. These data were derived for each site from the literature and in some cases provided by the site principal investigator. The sites were eventually classified in three classes: low, medium and high nutrient availability. Afterwards the classification was approved by the site principal investigators[17].

Estimation of photosynthetic capacity and its interannual variability magnitude: Site-level estimates of the annual photosynthetic capacity (GPPsat) were determined from half-hourly GPP estimates and global solar radiation (Rg)[9].

In summary, we fit a non-rectangular hyperbolic light response curve (NHLRC) to GPP and Rg data[42]. The NHLRC was fit to 5 days of data selected with a moving window approach. The parameters of the NHLRC were estimated and we computed the GPP at 1,000 W m^{-2} of Rg (GPP1,000), which represents the GPP at saturating light (that is, ecosystem photosynthetic capacity in the selected 5-day window). The estimated parameters and the GPP1,000 values were assigned to the day in the middle of the 5-day window. Parameters estimated with R^2 of the fitting lower than 0.6 were removed. To estimate the annual GPPsat, for each year from the daily GPP1,000 time series, we calculated the 90th percentile. The interannual variability (IAV) of the annual estimates of GPPsat was computed as the coefficient of variation of GPPsat, that is, cvGPPsat calculated by dividing the standard deviation by the mean($\frac{standard\ deviation}{mean}$). In young stands cvGPPsat might depend on the trend in annual growth and GPP that can lead to high cvGPPsat values that are not related to interannual variability in photosynthetic capacity. To remove this confounding factor we first tested the presence of a significant trend in GPPsat time series at each site with the Mann-Kendall non-parametric trend test. Finally, for the sites with a significant trend ($P < 0.1$) we recomputed the cvGPPsat by detrending the GPPsat time series (that is, the standard deviation of detrended GPPsat divided by the mean of the GPPsat, hereafter referred as detrended cvGPPsat).

Aggregation of environmental variables: For the estimation of year-to-year variability of climate we used temperature and precipitation measured, and the WAI[35] estimated at the flux sites. To aggregate temperature and precipitation we used only daily values with more than 70% of original half-hourly data (gaps in the half-hourly data are filled using ERA-Interim climate data downscaled at the FLUXNET, http://www.bgc-jena.mpg.de/~MDIwork/meteo/index.php). Average temperature, WAI, and cumulative precipitation over the active growing season were computed. Active growing season was considered as the days with daily GPP higher than the annual median GPP. From these annual estimates we derived the standard deviation (s.d.) of annual mean temperature, WAI and precipitation during the growing season as a measure of their IAV.

Statistical analysis: We used a variable selection method and relative importance method to select and quantify the contribution of each predictor (for example, average stand age (age), ln(age), species richness (sp. no.), canopy cover, canopy height, and nutrient availability, temperature, WAI) to the cvGPPsat; precipitation was once used in the calculation instead of WAI. The stepwise algorithm based on the Akaike Information Criteria (AIC) algorithm with generalized linear regression models was used[43]. The independent variable was cvGPPsat, while the predictors were stand age (referred to in the figures simply as ‘age’), species abundance (sp. no.), ln(age), s.d. of temperature and of WAI, canopy cover, canopy height, LAI, and so on; interactions of age and sp. no., s.d. of temperature and s.d. of WAI and canopy height and LAImax were also included (cumulative precipitation was also used in place of WAI with similar results; data not shown). The algorithm was set up with the possibility to account for model pairwise interactions, and imposing a selection only if the model is statistical significant ($P < 0.01$). Although the sites used in this study have at least 4 years of flux data, the number of years (no.years) with available data at each site was different. Therefore, we used $\frac{1}{\sqrt{no.years}}$ to weight the model selection, weighting more the sites with higher numbers of years. A stepwise selection without the weighting was used as well. The distribution of the residuals of the best model was tested for normality using the Shapiro and Kolmogorov-Smirnov test. The results showed that the residuals were normally distributed; therefore the weighting was not strictly necessary, but was used for a comprehensive evaluation. In order to assess the uncertainty introduced by the potential trend in GPPsat in young stands, we repeated the analysis using the detrended cvGPPsat dataset, and the cvGPPsat for the sites without a significant trend in GPPsat.

To disentangle the importance of each predictor in determining cvGPPsat we used the Lindeman-Merenda-Gold (LMG) relative importance method[19]. This method allows the assessment of the importance of correlated predictors in a multiple linear regression model. Moreover, the pairwise linear regression and correlation between the different predictors and cvGPPsat, and between the predictors themselves, was tested. Both stepwise AIC and the LMG identified ln(age) and sp. no. as the most important variables controlling the cvGPPsat. We used a generalized linear model to fit the coefficients of the multiple linear model. To test differences of cvGPPsat between the age and nutrient availability classes, we used the Kruskal-Wallis rank sum test. Sites were divided by age class (young, middle aged and mature stands) according to the 33rd and 66th percentiles of the distribution of age. Nutrient availability classes were defined according to ref. 17 (low, medium and high). The correlation between GPPsat and climate variables was tested with distance correlation[33]. Distance correlation is a measure of statistical dependence between random variables and here we tested the dependence between GPPsat and temperature and WAI jointly.

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640176. This work used eddy covariance data acquired and shared by the FLUXNET community, including these networks: AmeriFlux, AfriFlux, AsiaFlux, CarboAfrica, CarboEuropeIP, CarboItaly, CarboMont, ChinaFlux, Fluxnet- Canada, GreenGrass, ICOS, KoFlux, LBA, NECC, OzFlux-TERN, TCOS-Siberia and USCCC. The ERA-Interim reanalysis data are provided by ECMWF and processed by LSCE. The FLUXNET eddy covariance data processing and harmonization was carried out by the European Fluxes Database Cluster, AmeriFlux Management Project, and Fluxdata project of FLUXNET, with the support of CDIAC and ICOS Ecosystem Thematic Center, and the OzFlux, ChinaFlux and AsiaFlux offices. T.M. acknowledges the International Max Planck Research School for global biogeochemical cycles.

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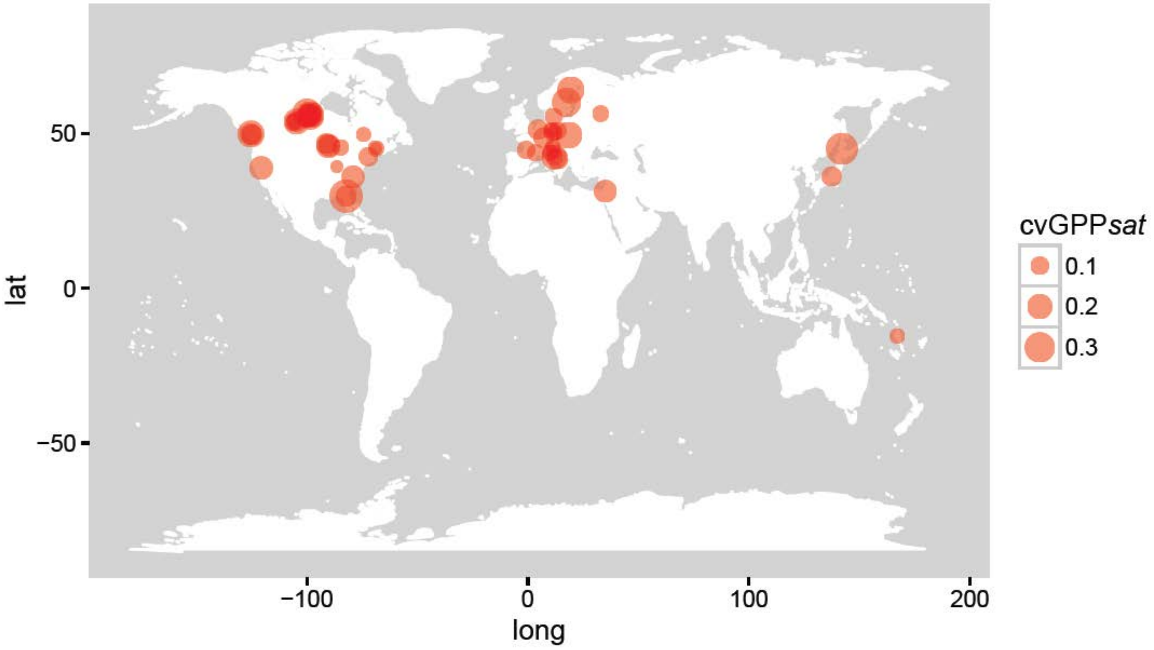
Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity – SUPPLEMENTARY INFORMATION

Figure 1 | Global map with the location of the FLUXNET sites used in the analysis (n=50). The size of the points is proportional to interannual variability of ecosystem photosynthetic capacity computed for each FLUXNET site (cvGPP*sat*).



Supplementary Figure 2 | The boxplot of the cvGPP*sat* i.e. the interannual variability of ecosystem photosynthetic capacity computed for each FLUXNET site, which indicates the stability of the ecosystems. The sites are split among 3 different age classes using the 33rd, 66th quantile as follows: Young (=< 37 years), Intermediate (38-78 years old) and Mature (older than 78 years) sites. The numbers on the boxplot indicates the number of sites in age class group. We evidence differences in cvGPP*sat* for the different age classes (Kruskal-Wallis rank sum test, chi-squared=15.43, p<0.001), with older forest showing the lowest variability.

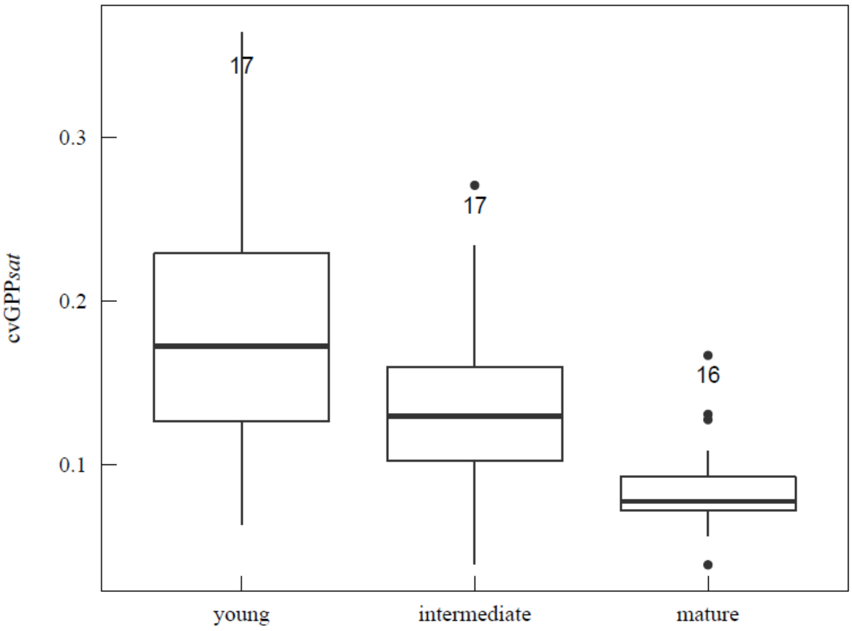
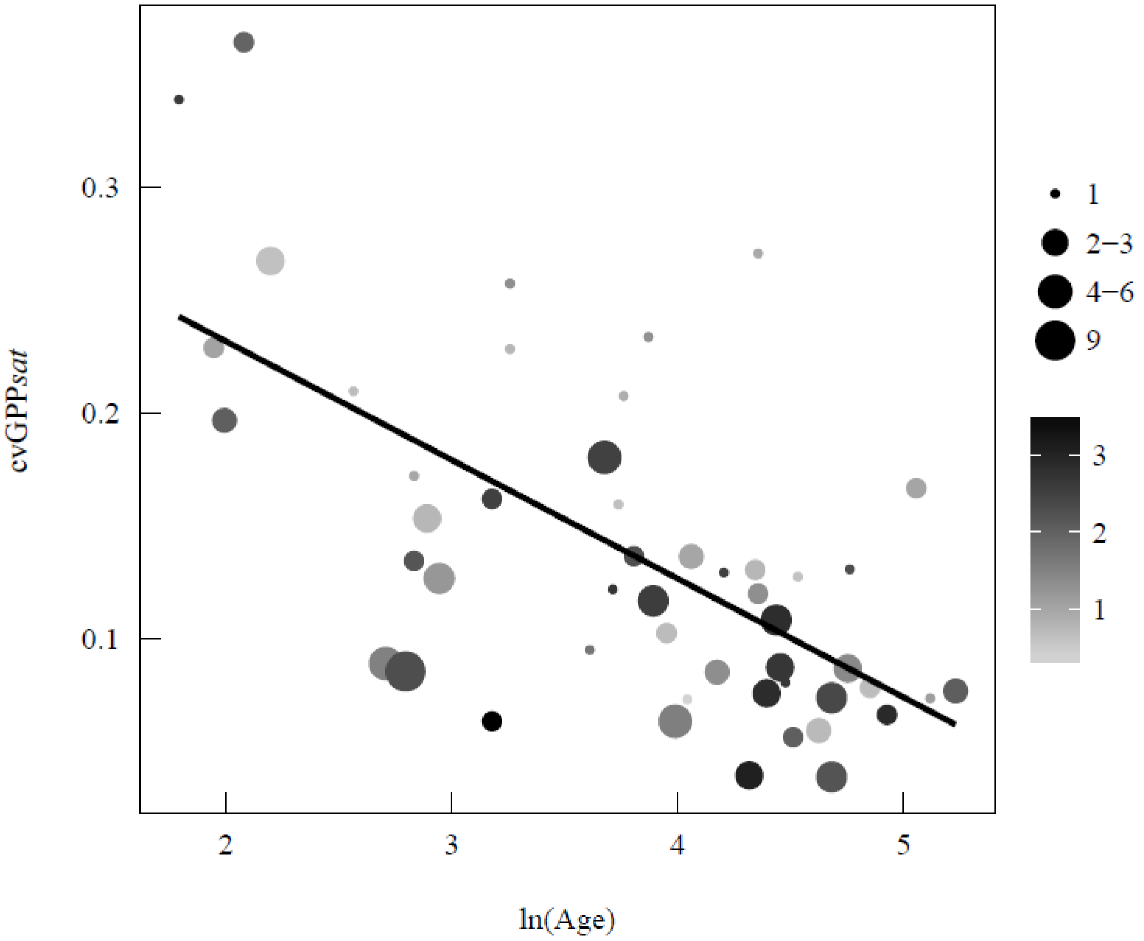
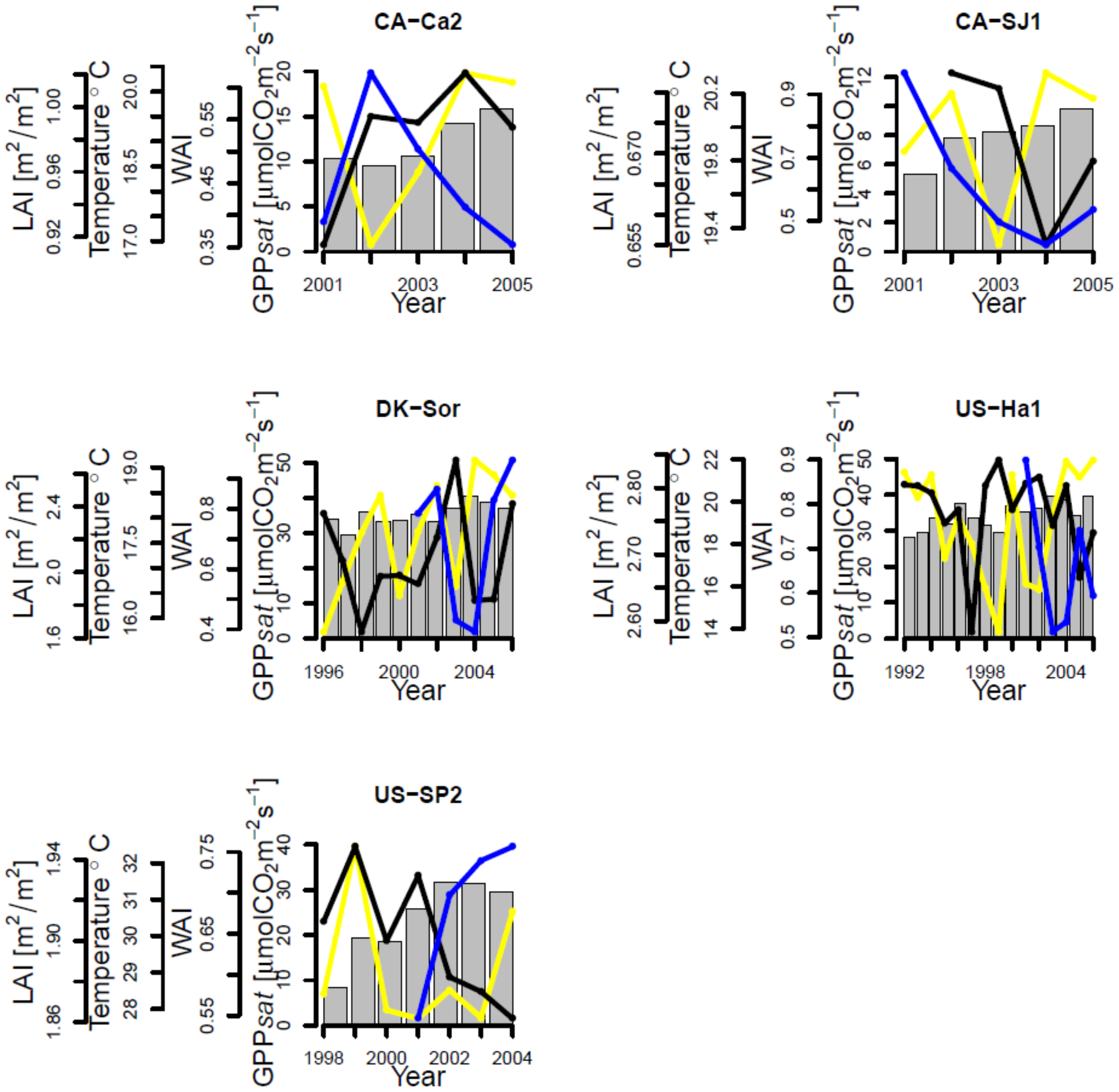


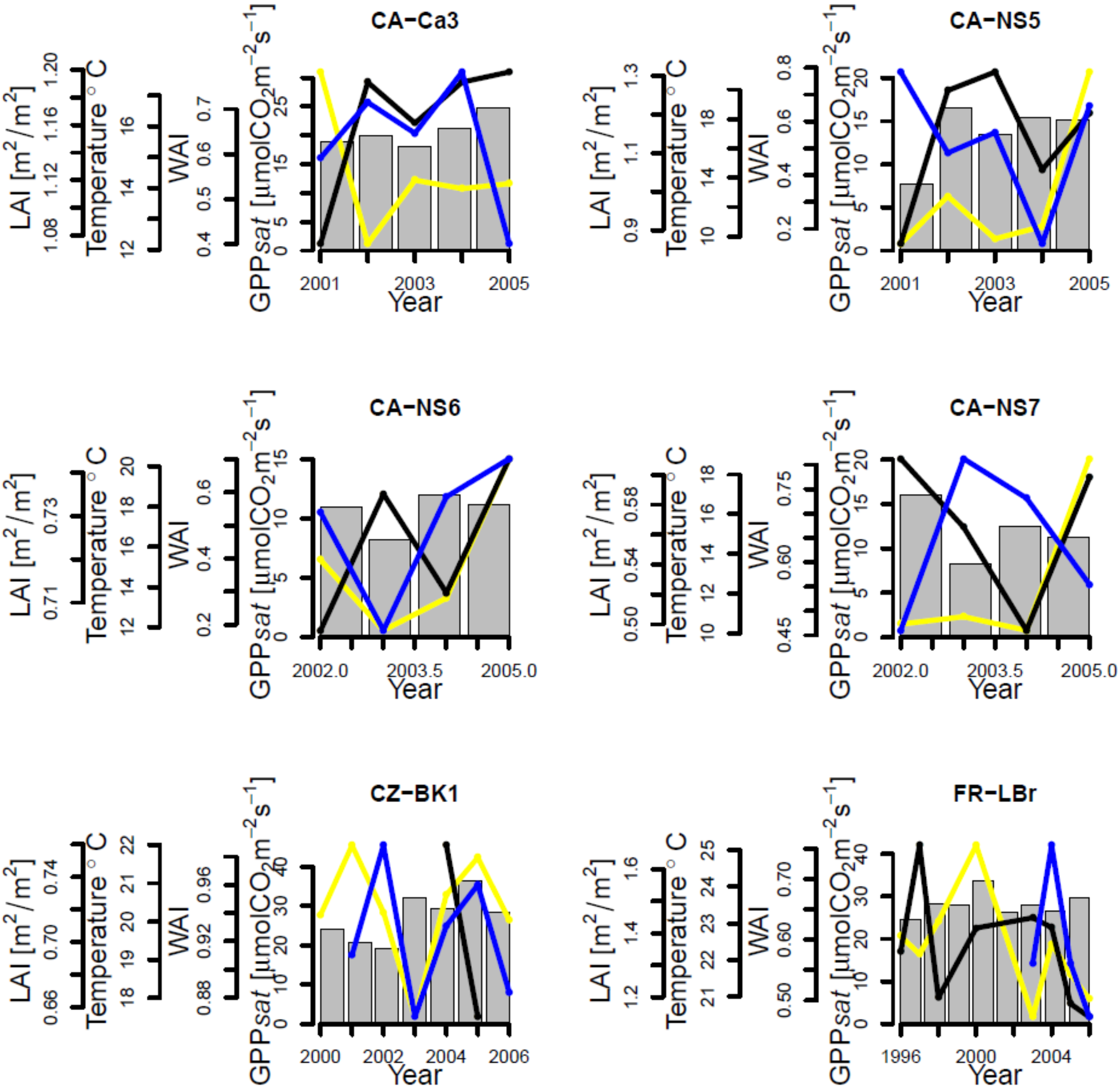
Figure 3 | Relationship between the interannual variability (IAV) of ecosystem photosynthetic capacity (cvGPP*sat*) computed for each FLUXNET site and stand age (Age – log transformed) (R^2=0.39, *p*<0.0001, n=50). The number of plant species at the sites that account for 90% of the total species abundances (Sp.no) is indicated with the size of the points. DBMF are deciduous broad leaf and mixed forests (n=16), EF are evergreen needleleaf and broadleaf forests (n=34). The LAImax of the sites (i.e. maximum of leaf area index at each site) is used to color code the points. Each point indicates a site.

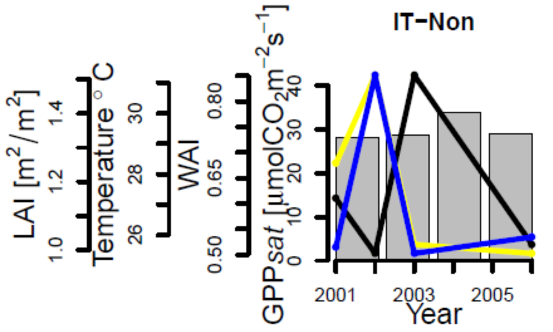


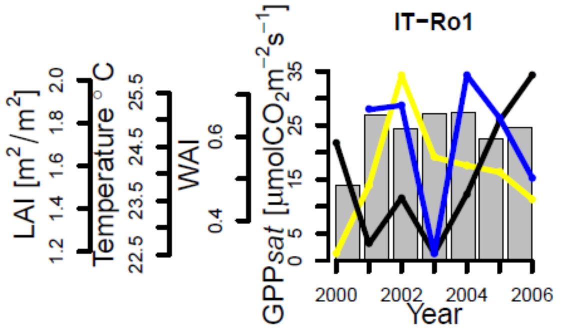
Supplementary Figure 4 | Ecosystem photosynthetic capacity computed for each FLUXNET site (GPP*sat*) (grey bars), growing season water availability index (WAI, yellow lines), growing season temperature (black lines) and leaf area index (LAI, blue lines) for the five sites where a trend in GPP*sat* was detected with the Mann-Kendall's non parametric trend test.

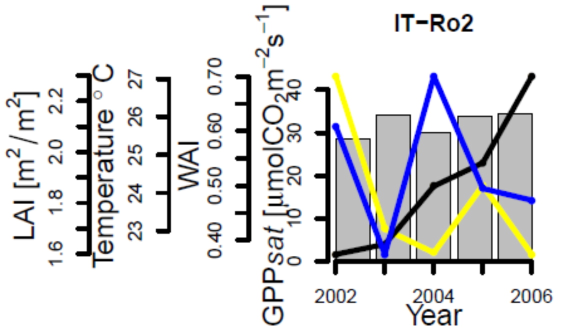


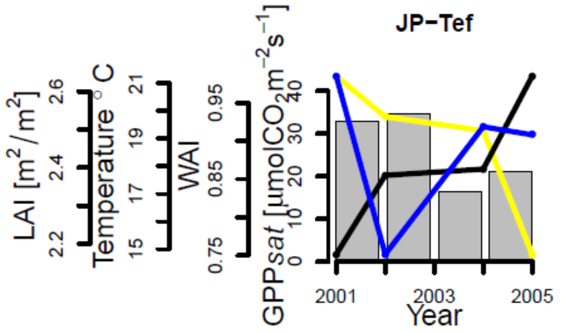
Supplementary Figure 5 | Ecosystem photosynthetic capacity computed for each FLUXNET site (GPP*sat*) (grey bars), growing season water availability index (WAI, yellow lines), growing season temperature (black lines) and leaf area index (LAI, blue lines) for sites with stand age =< 37 years.

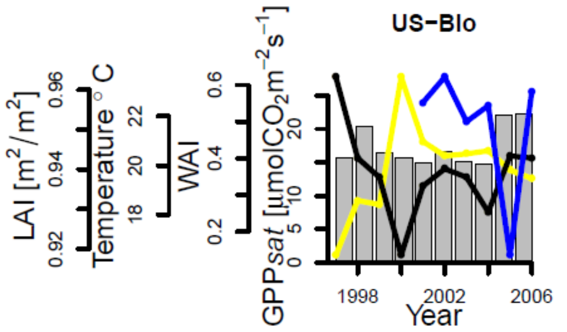


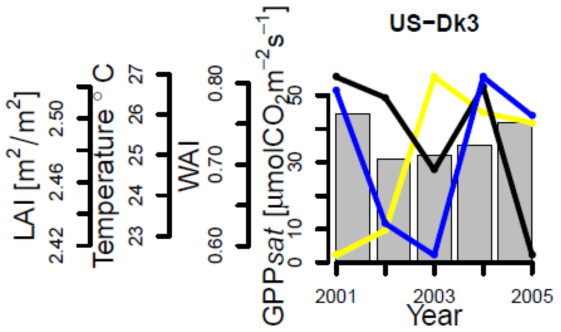

IT−Non
LAI [m2/m2]
1.0 1.2 1.4
Temperature °C
26 28 30
WAI
0.50 0.65 0.80
GPPsat [μmolCO2m−2s−1]
0 10 20 30 40
2001 2003 2005
Year

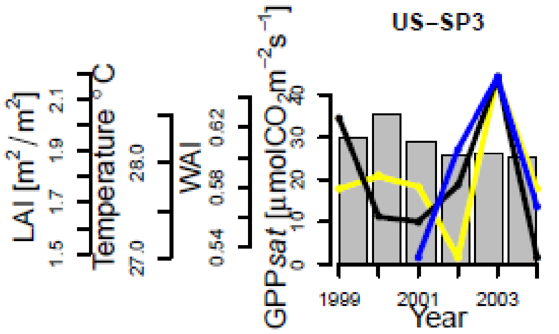

IT−Ro1
LAI [m2/m2]
1.2 1.4 1.6 1.8 2.0
Temperature °C
22.5 23.5 24.5 25.5
WAI
0.4 0.6
GPPsat [μmolCO2m−2s−1]
0 5 15 25 35
2000 2002 2004 2006
Year

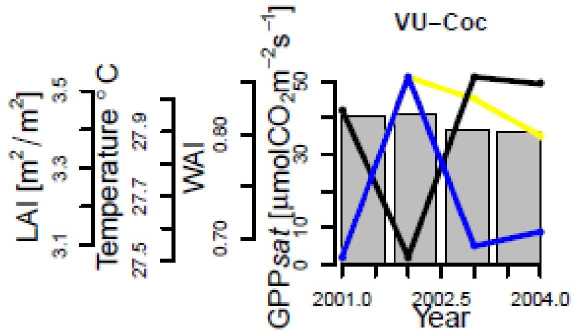

IT−Ro2
LAI [m2/m2]
1.6 1.8 2.0 2.2
Temperature °C
23 24 25 26 27
WAI
0.40 0.50 0.60 0.70
GPPsat [μmolCO2m−2s−1]
0 10 20 30 40
2002 2004 2006
Year


JP−Tef
LAI [m2/m2]
2.2 2.4 2.6
Temperature °C
15 17 19 21
WAI
0.75 0.85 0.95
GPPsat [μmolCO2m−2s−1]
0 10 20 30 40
2001 2003 2005
Year

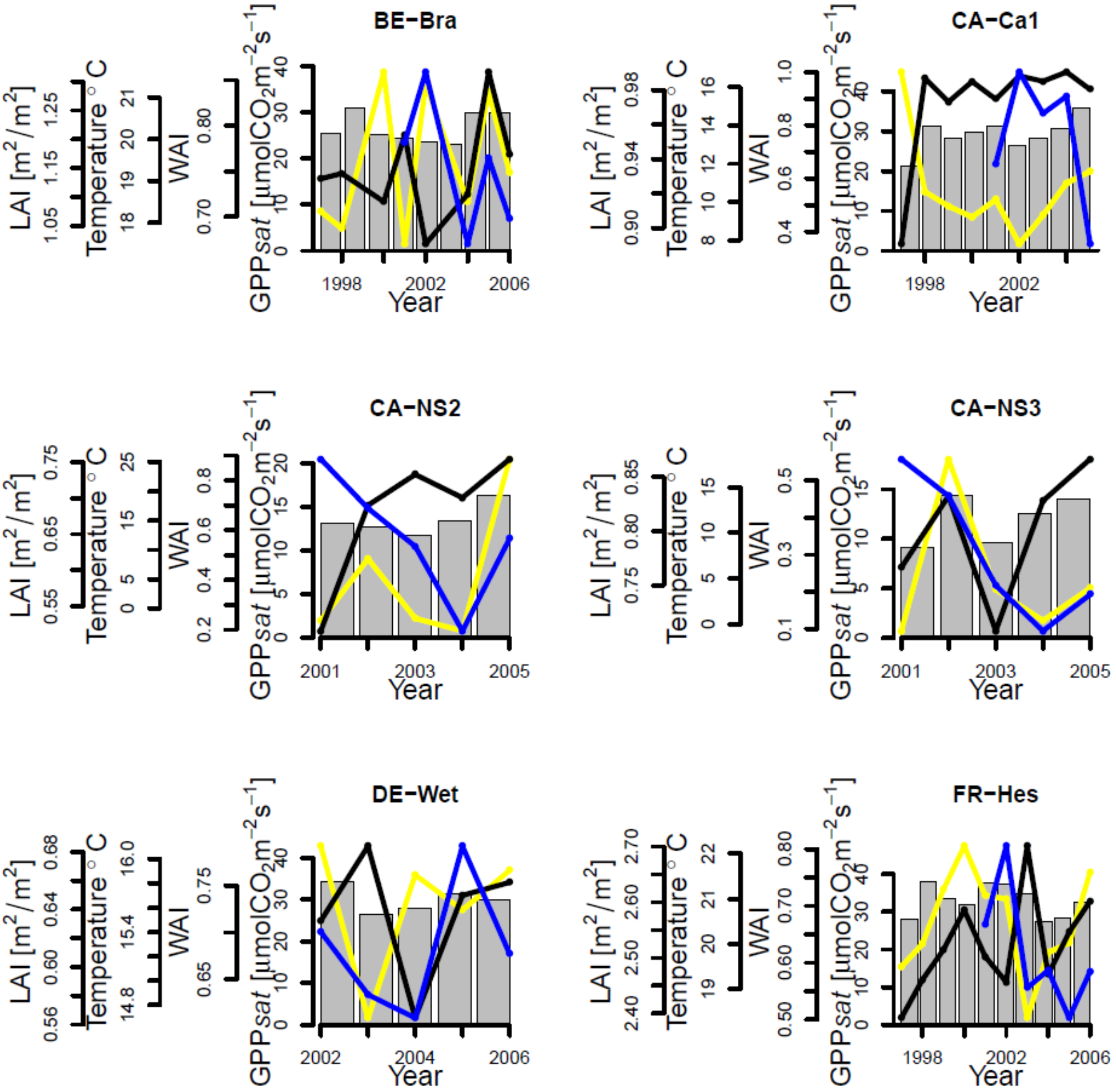

US−Blo
LAI [m2/m2]
0.92 0.94 0.96
Temperature °C
18 20 22
WAI
0.2 0.4 0.6
GPPsat [μmolCO2m−2s−1]
0 5 10 20
1998 2002 2006
Year

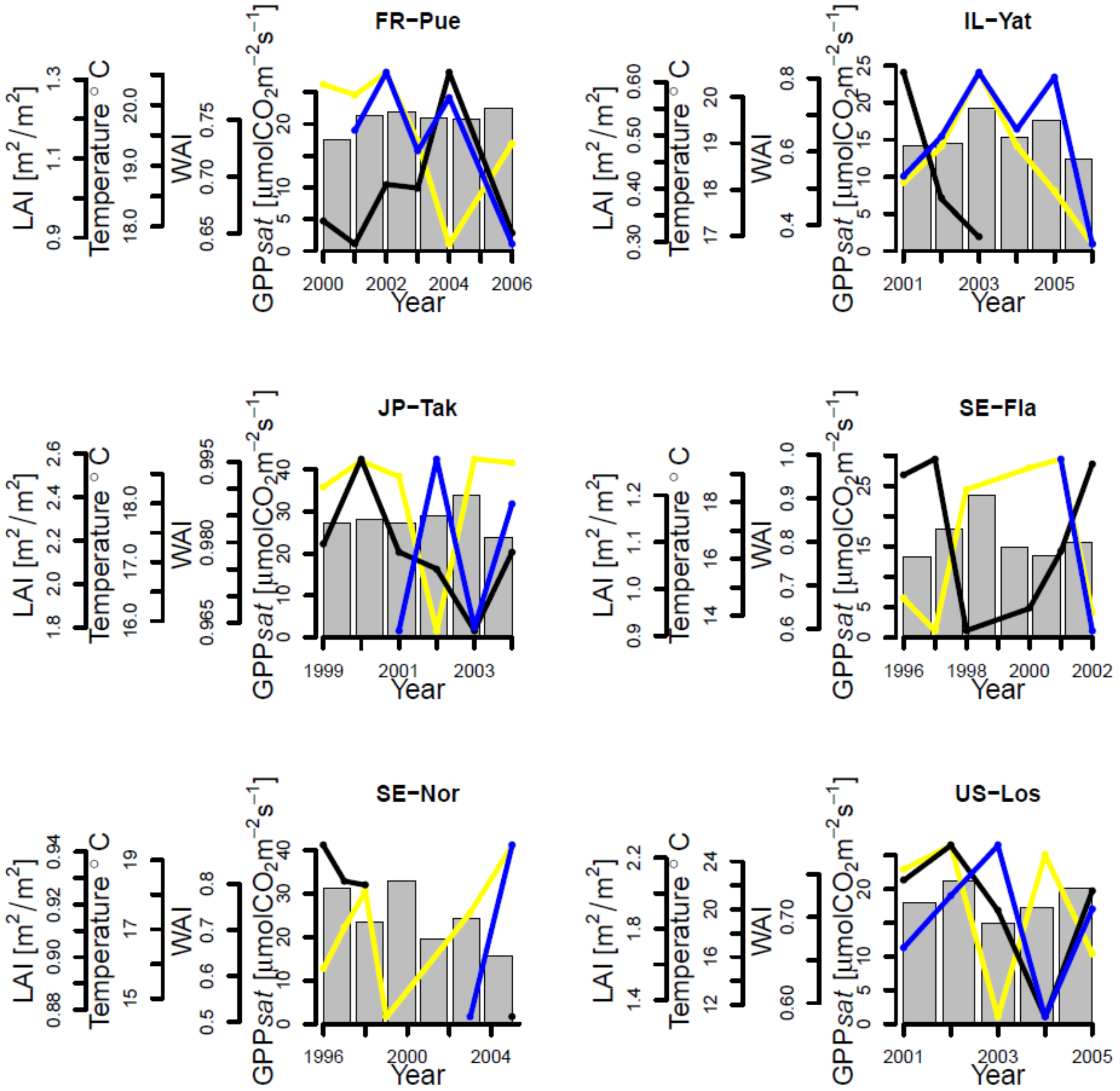

US−Dk3
LAI [m2/m2]
2.42 2.46 2.50
Temperature °C
23 24 25 26 27
WAI
0.60 0.70 0.80
GPPsat [μmolCO2m−2s−1]
0 10 30 50
2001 2003 2005
Year

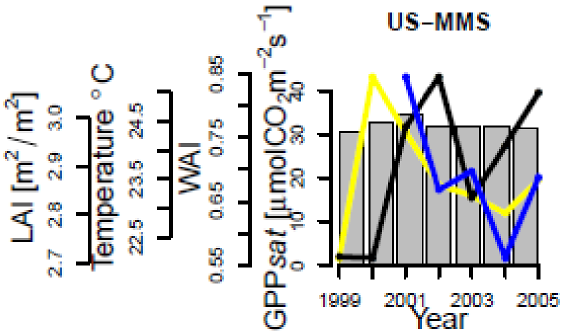

US−SP3
LAI [m2/m2]
1.5 1.7 1.9 2.1
Temperature °C
27.0 28.0
WAI
0.54 0.58 0.62
GPPsat [μmolCO2m−2s−1]
0 10 20 30 40
1999 2001 2003
Year

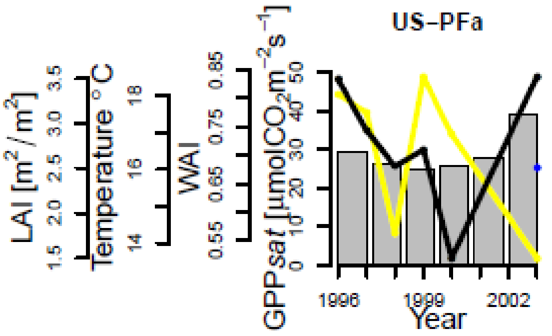

VU−Coc
LAI [m2/m2]
3.1 3.3 3.5
Temperature °C
27.5 27.7 27.9
WAI
0.70 0.80
GPPsat [μmolCO2m−2s−1]
0 10 30 50
2001.0 2002.5 2004.0
Year

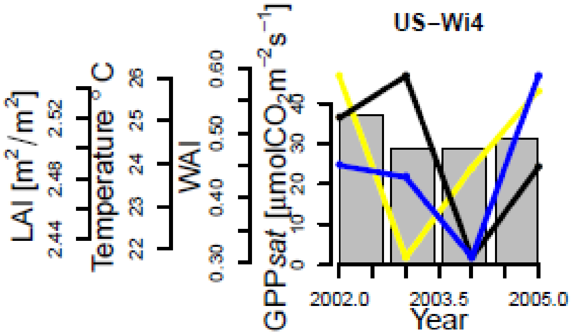
Supplementary Figure 6 | Ecosystem photosynthetic capacity computed for each FLUXNET site (GPP*sat*) (grey bars), growing season water availability index (WAI, yellow lines), growing season temperature (black lines) and leaf area index (LAI, blue lines) for sites with stand age > 37 and <78 years.



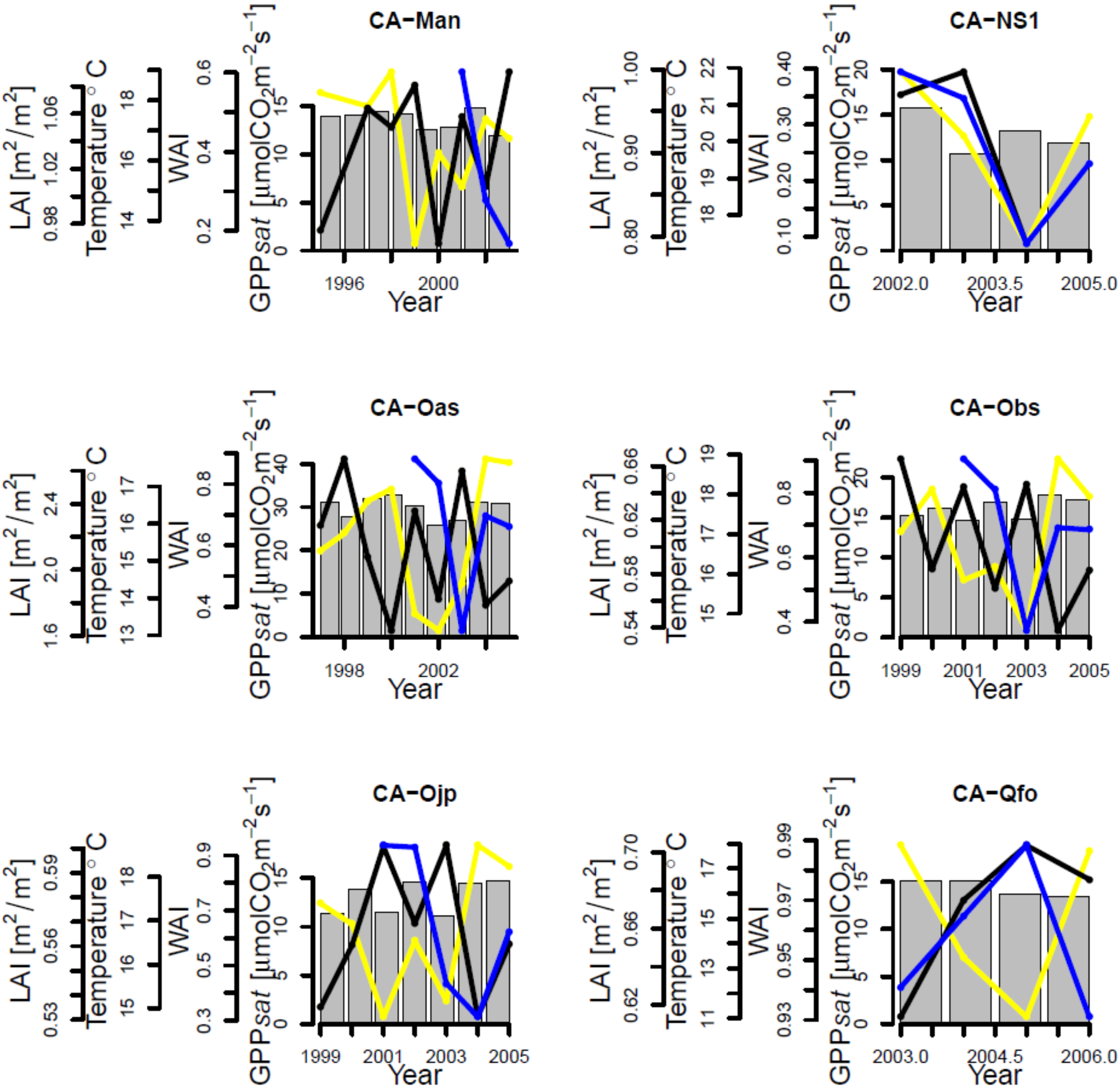

FR−Pue
IL−Yat
JP−Tak
SE−Fla
SE−Nor
US−Los
LAI [m^2/m^2]
Temperature °C
WAI
GPPsat [µmolCO2m^-2s^-1]
Year
2000
2002
2004
2006
2001
2003
2005
1999
1996
1998

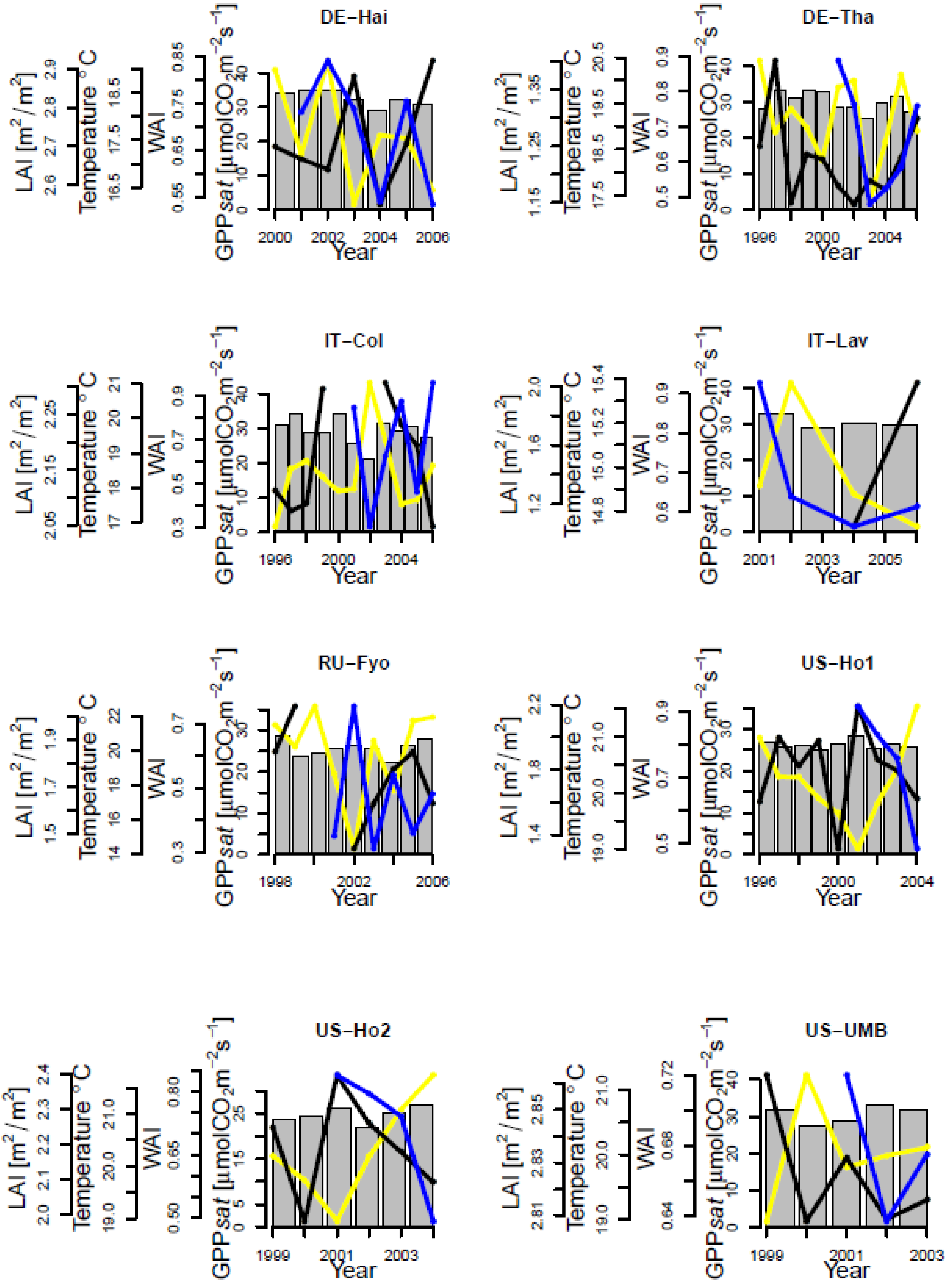

US−MMS


US−PFa

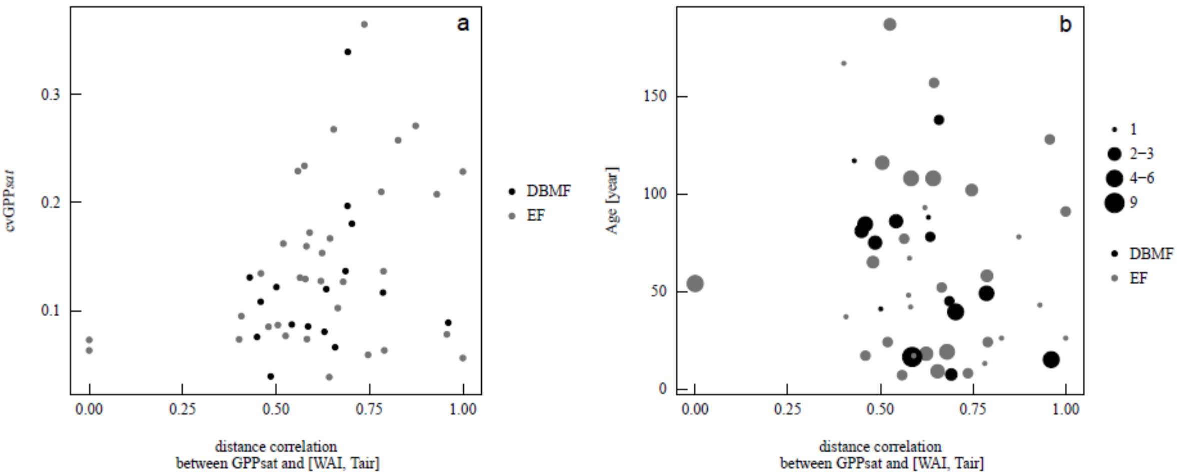

US−Wi4

Supplementary Figure 7 | Ecosystem photosynthetic capacity computed for each FLUXNET site (GPPsat) (grey bars), growing season water availability index (WAI, yellow lines), growing season temperature (black lines) and leaf area index (LAI, blue lines) for sites with stand age >78 years.

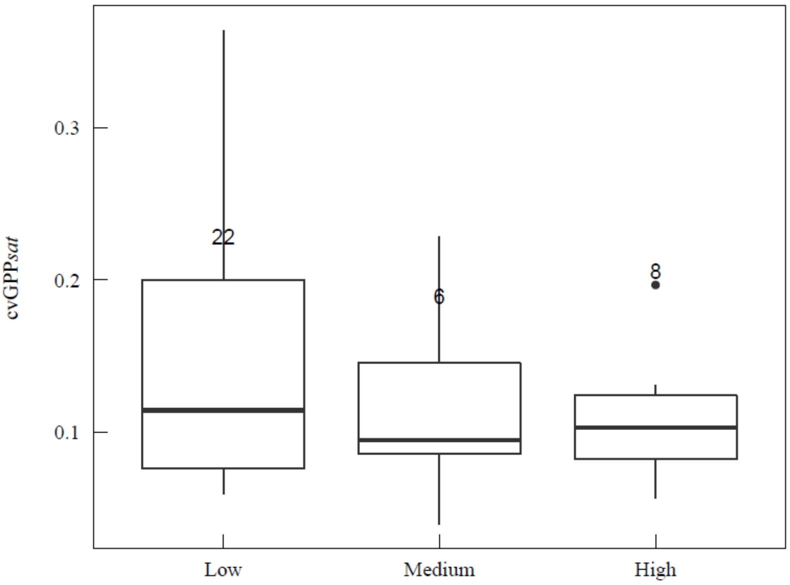



DE−Hai
DE−Tha
IT−Col
IT−Lav
RU−Fyo
US−Ho1
US−Ho2
US−UMB
LAI [m^2/m^2]
Temperature °C
WAI
GPPsat [µmolCO$_2$m^{-2}s^{-1}]
Year
2000
2002
2004
2006
1996
2000
2004
2001
2003
2005
1998
2002
2006
1996
2000
2004
1999
2001
2003
1999
2001
2003

Supplementary Figure 8 | Distance correlation of ecosystem photosynthetic capacity (GPP*sat*) with the two environmental variable water availability index (WAI) and temperature in relation to a) Interannual variability of ecosystem photosynthetic capacity computed for each FLUXNET site (cvGPP*sat*) (R^2=0.09, *p*=0.03, n=50), and b) stand age (R^2=0, *p*=0.32, n=50). DBMF are deciduous broadleaf and mixed forests (n=16), EF are evergreen needleleaf and broadleaf forests (n=34). In the Fig 8b, the size of the points is proportional to the number of species at the sites that account for up to 90% of the total species abundances.



Supplementary Figure 9 | IAV magnitude of ecosystem photosynthetic capacity (cvGPP*sat*) at FLUXNET sites within different nutrient availability classes. High, medium and low refer to the soil nutrient availability of the sites. A non-parametric Kruskal-Wallis rank sum test indicated non-significant differences between the three nutrient availability groups (χ^2=0.47, *p*=0.79). The numbers on the boxplot indicates the number of sites in age class group.



Supplementary Figure 10 | Scatterplot of the interannual variability of ecosystem photosynthetic capacity computed for each FLUXNET site (cvGPP*sat*) with environmental and ecosystem structural variables tested in the analysis (sdTair, standard deviation of average growing season temperature (n=50); sdWAI is the standard deviation of the average growing season water availability index (n=48); LAI*max* is the maximum LAI observed at the site (n=49); cvLAI*max* is the coefficient of variation of LAI (n=48); canopy height (n=50); canopy cover (n=47)) . The number in the upper right corner of the graphs is the R^2 of the linear regression model between the two variables. None of the relationships has a *p*<0.01. Only the relationship of cvGPP*sat* with Tair, LAI*max* and Canopy cover has *p*<0.1.

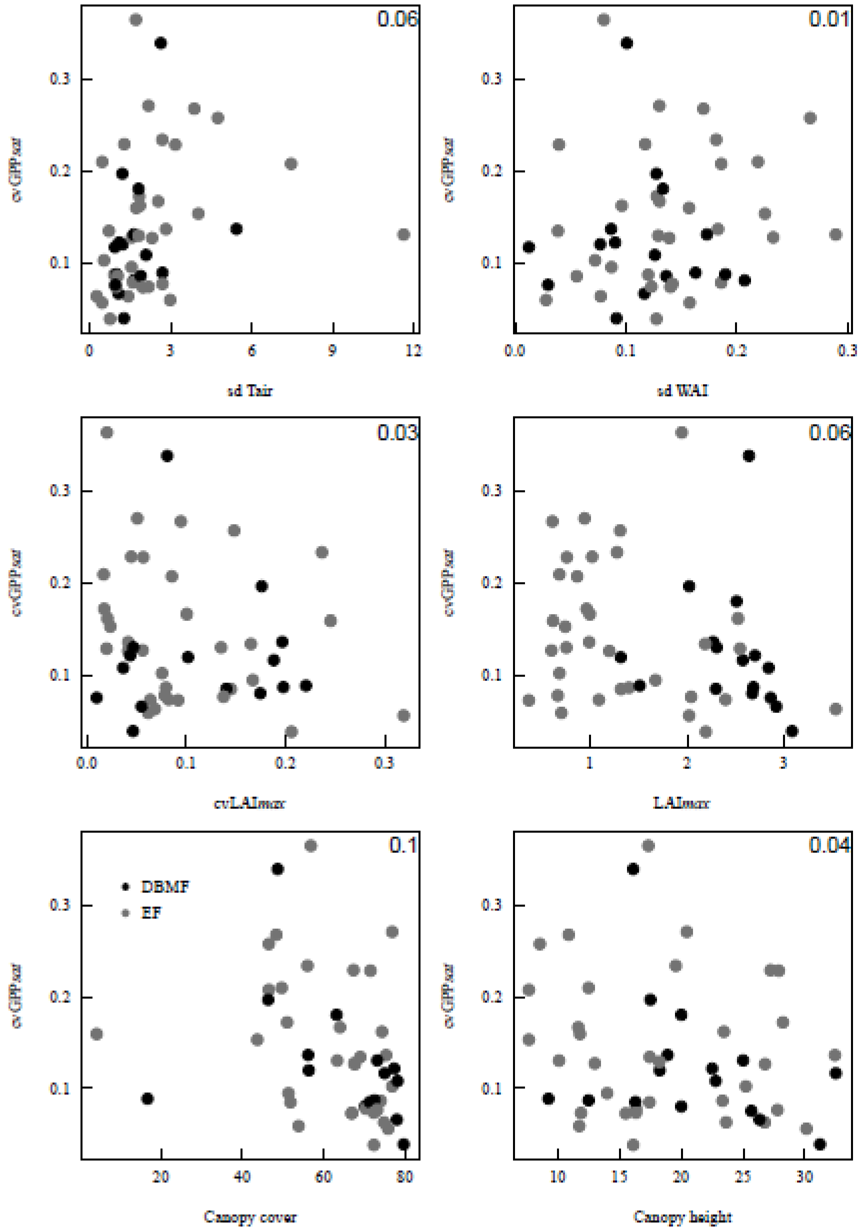


Figure 9 | Relationship between the interannual variability (IAV) of ecosystem photosynthetic capacity (cvGPP*sat*) computed for each FLUXNET site and stand age (Age) (R^2=0.25, *p*<0.001, n=50). The number of plant species at the sites that account for 90% of the total species abundances (Sp.no) is indicated with the size of the points. DBMF are deciduous broad leaf and mixed forests (n=16), EF are evergreen needleleaf and broadleaf forests (n=34).

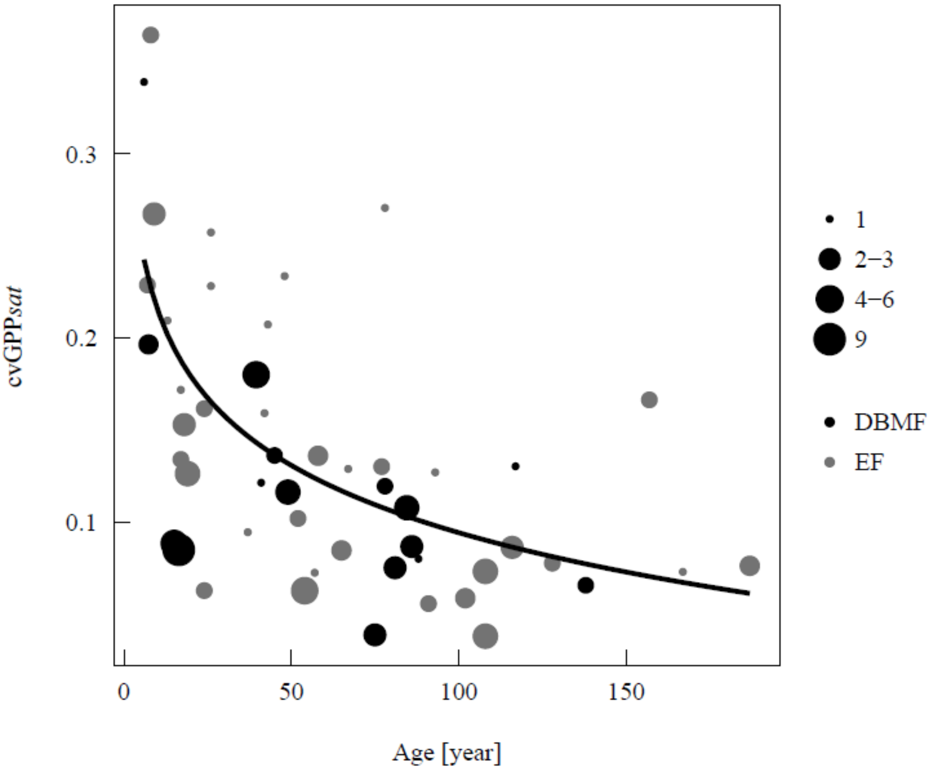


Table 1 | Comparison of the model chosen by stepAIC and relative importance methods once removing the 5 sites that show a trend in GPPsat (gray rows) and once with including the 5 sites that show trend but using detrended cvGPP*sat* for these sites (cf. Methods). Abbreviations: cvGPPsat is the IAV magnitude of ecosystem photosynthetic capacity, Sp.no is the number of dominant plant species that have a cumulative abundance of 90 percent at the sites. ln(Age) is the average stand age. The number of sites used in the upper model (gray rows) equals n=45 and in the lower model n=50.

Model structure	**R^2**	**adj.R^2**	**predictors**	**coefficients**	***p***
cvGPP*sat* ~ ln(Age) + Sp.no	0.49	0.46	Intercept	0.37 ± 0.04	<0.0001
			ln(Age)	-0.05 ± 0.01	
			Sp.no	-0.02 ± 0.00	
cvGPP*sat* ~ln(Age) + Sp.no	0.49	0.46	Intercept	0.37 ± 0.04	<0.0001
			ln(Age)	-0.05 ± 0.01	
			Sp.no	-0.02 ± 0.00	

**** The code R code used for the analysis is available online: https://media.nature.com/original/nature-assets/natecolevol/2017/s41559-016-0048/extref/s41559-016-0048-s2.txt**

SUPPLEMENTARY DATASET 1a,b - Information on the sites used in this study including site identifier (site.code), coefficient of variation of GPPsat (cvGPPsat), Number of years with data (No_years), number of abundant species at the sites (Sp.no90), stand age (Age), plant functional type (PFT), Climate Group, canopy height (Height), canopy cover (these variables are presented in table a and the rest in table b), nutrient availability classes (Nutrient_availability), cv of leaf area index (cvLAI), mean of LAI (mean.LAI), maximum LAI (LAI max), standard deviation of growing season water availability index (sdWAI), sd of growing season air temperature (sdTair), sd of growing season cumulative precipitation (sdPrecip), latitude (LAT), longitude (LONG).

Table 1a

site.code	cvGPPsat	No_years	Sp.no90	Age	PFT	ClimateGroup	Height	CanopyCover
BE-Bra	0.119852	8	2	78	MF	Temperate	18.25	56.33333
CA-Ca1	0.136349	9	3	58	ENF	Temperate	32.4286	75.33333
CA-Ca2	0.228963	5	2	7	ENF	Temperate	27.2222	67.33333
CA-Ca3	0.126649	5	5	19	ENF	Temperate	26.7778	67.66667
CA-Man	0.07341	8	1	167	ENF	Boreal	11.8889	67
CA-NS1	0.166682	4	2	157	ENF	Boreal	11.6667	64
CA-NS2	0.130454	5	2	77	ENF	Boreal	10.1111	63.33333
CA-NS3	0.207524	5	1	43	ENF	Boreal	7.6667	46.5
CA-NS5	0.257481	5	1	26	ENF	Boreal	8.5556	46.5
CA-NS6	0.153258	4	4	18	ENF	Boreal	7.6667	43.66667
CA-NS7	0.267508	4	4	9	ENF	Boreal	10.8889	48.33333
CA-Oas	0.080465	9	1	88	DBF	Boreal	20	70.16667
CA-Obs	0.078103	7	2	128	ENF	Boreal	16.3333	70.33333
CA-Ojp	0.127358	7	1	93	ENF	Boreal	13	67.5
CA-Qfo	0.059142	4	3	102	ENF	Boreal	11.75	53.83333
CA-SJ1	0.20969	5	1	13	ENF	Boreal	12.5	49.66667
CZ-BK1	0.228408	7	1	26	ENF	Temperate-Continental with hot or warm summers	27.8889	71.5
DE-Bay	0.063199	4	6	54	ENF	Temperate	26.75	74.83333
DE-Hai	0.06612	7	2	138	DBF	Temperate	26.3333	78
DE-Tha	0.08668	11	4	116	ENF	Temperate	23.3333	74

DE-Wet	0.102364	5	2	52	ENF	Temperate	25.2222	76.83333
DK-Sor	0.087169	11	4	86	DBF	Temperate	12.5	72.5
FR-Hes	0.12175	10	1	41	DBF	Temperate	22.5	77.33333
FR-LBr	0.094906	8	1	37	ENF	Temperate	14	51.33333
FR-Pue	0.085038	6	3	65	EBF	SubTropical-Mediterranean	17.4286	51.83333
IL-Yat	0.159462	6	1	42	ENF	Dry (arid and semi arid)	11.8	4.166667
IT-Col	0.130653	11	1	117	DBF	SubTropical-Mediterranean	25	73.16667
IT-Lav	0.056177	4	2	91	ENF	Temperate	30.125	75.83333
IT-Non	0.088855	4	6	15	DBF	SubTropical-Mediterranean	9.25	16.66667
IT-Ro1	0.196748	7	3	7.34	DBF	SubTropical-Mediterranean	17.5	46.33333
IT-Ro2	0.085346	5	9	16.37	DBF	SubTropical-Mediterranean	16.2857	71.33333
IT-SRo	0.072931	8	1	57	ENF	SubTropical-Mediterranean	15.5	66.83333
JP-Tak	0.116673	6	5	49	DBF	Temperate-Continental with hot or warm summers	32.5	75
JP-Tef	0.339062	4	1	6	MF	Temperate-Continental with hot or warm summers	16.1111	48.66667
RU-Fyo	0.076683	9	3	187	ENF	Temperate-Continental with hot or warm summers	27.7778	73.16667
SE-Fla	0.233784	6	1	48	ENF	Boreal	19.5556	56
SE-Nor	0.270773	6	1	78	ENF	Temperate-Continental with hot or warm summers	20.4444	76.83333
US-Blo	0.172105	10	1	17	ENF	SubTropical-Mediterranean	28.2222	51
US-Dk3	0.161907	5	2	24	ENF	SubTropical-Mediterranean	23.4444	74.33333
US-Ha1	0.108196	15	5	84.5	DBF	Temperate-Continental with hot or warm summers	22.7778	78.16667
US-Ho1	0.038529	9	5	108	ENF	Temperate-Continental with hot or warm summers	16.1111	72.33333
US-Ho2	0.073664	6	5	108	ENF	Temperate-Continental with hot or warm summers	16.3333	72.33333
US-Los	0.136529	5	2	45	DBF	Temperate-Continental with hot or warm summers	18.8889	56.16667
US-MMS	0.039225	7	4	75	DBF	SubTropical-Mediterranean	31.2222	79.66667
US-PFa	0.180321	6	6	39.5	MF	Temperate-Continental with hot or	20	63.16667

						warm summers		
US-SP2	0.364531	7	2	8	ENF	SubTropical-Mediterranean	17.3333	56.83333
US-SP3	0.134369	6	2	17	ENF	SubTropical-Mediterranean	17.4444	69
US-UMB	0.075635	5	4	81	DBF	Temperate-Continental with hot or warm summers	25.6667	NA
US-Wi4	0.129222	4	1	67	ENF	Temperate-Continental with hot or warm summers	18.2222	NA
VU-Coc	0.06325	4	2	24	EBF	Tropical	23.625	NA

Table 1b

site.code	**Nutrient_availability**	**cvLAI**	**mean.LAI**	**LAImax**	**sdWAI**	**sdTair**	**sdPrecip**	**LAT**	**LONG**
BE-Bra	L	0.101745	1.151875	1.3164	0.076805	1.223766	85.08243	51.3092	4.52056
CA-Ca1	L	0.041482	0.952242	0.9904	0.18287	2.825004	69.25976	49.8672	-125.334
CA-Ca2	L	0.044509	0.95542	1.0208	0.117275	1.283872	147.9933	49.8705	-125.291
CA-Ca3	L	0.041326	1.147784	1.1984	0.138988	2.311307	78.73928	49.5346	-124.9
CA-Man	L	0.063825	1.0176	1.0904	0.139961	2.182313	71.4518	55.8796	-98.4808
CA-NS1	NA	0.100562	0.9104	0.9968	0.13021	2.538087	73.86583	55.8792	-98.4839
CA-NS2	NA	0.135084	0.64664	0.7544	0.289089	11.62735	83.4768	55.9058	-98.5247
CA-NS3	NA	0.085483	0.77968	0.8664	0.185883	7.460557	102.2947	55.9117	-98.3822
CA-NS5	NA	0.148247	1.13	1.31	0.266012	4.747232	124.7902	55.8631	-98.485
CA-NS6	NA	0.023462	0.728	0.7432	0.225222	4.024822	95.22952	55.9167	-98.9644
CA-NS7	NA	0.094591	0.5545	0.6108	0.169818	3.875502	84.12844	56.6358	-99.9483
CA-Oas	L	0.174596	2.28472	2.6736	0.20693	1.634073	129.413	53.6289	-106.198
CA-Obs	L	0.078218	0.614622	0.6656	0.185794	1.612093	107.1161	53.9872	-105.118
CA-Ojp	L	0.055977	0.568699	0.6012	0.232669	1.564342	135.1115	53.9163	-104.692
CA-Qfo	L	0.061609	0.6532	0.7036	0.027991	2.982089	254.8924	49.6925	-74.3421
CA-SJ1	L	0.016687	0.665093	0.6832	0.218926	0.466343	101.7295	53.908	-104.656
CZ-BK1	M	0.056645	0.703312	0.75945	0.039601	3.175402	788.047	49.5026	18.5384
DE-Bay	L	NA	NA	NA	NA	1.426195	202.7926	50.1419	11.8669

DE-Hai	H	0.054849	2.738382	2.921729	0.116549	1.071064	55.30874	51.0793	10.452
DE-Tha	M	0.079475	1.263344	1.401151	0.120014	0.911309	74.85467	50.9636	13.5669
DE-Wet	M	0.075576	0.612561	0.684	0.072173	0.532689	48.7759	50.4535	11.4575
DK-Sor	H	0.197815	2.222711	2.6848	0.189526	1.001642	190.318	55.4869	11.6458
FR-Hes	H	0.043362	2.508933	2.7008	0.09021	1.092532	108.2019	48.6742	7.06462
FR-LBr	L	0.167079	1.3564	1.6748	0.086907	1.550938	94.26417	44.7171	-0.7693
FR-Pue	M	0.145019	1.14912	1.3176	0.055527	1.033285	56.59512	43.7414	3.59583
IL-Yat	M	0.245483	0.492312	0.6176	0.156867	1.727242	61.57762	31.345	35.0515
IT-Col	H	0.046676	2.195467	2.3064	0.172894	1.632596	119.302	41.8494	13.5881
IT-Lav	H	0.319135	1.3758	2.022	0.157379	0.460243	81.31727	45.9553	11.2812
IT-Non	H	0.2206	1.137173	1.512294	0.162669	2.698462	275.833	44.6898	11.0887
IT-Ro1	H	0.176041	1.721533	2.0232	0.127397	1.211355	129.7241	42.4081	11.93
IT-Ro2	NA	0.14032	1.932496	2.298	0.13622	1.890787	113.2363	42.3903	11.9209
IT-SRo	L	0.091807	0.338473	0.3676	NA	1.971645	59.91229	43.72786	10.28444
JP-Tak	H	0.188244	2.132676	2.5756	0.012466	0.937222	NA	36.1462	137.423
JP-Tef	L	0.080808	2.4514	2.64	0.100754	2.637301	100.6045	45.05634	142.1062
RU-Fyo	L	0.137584	1.648494	2.0428	0.141902	2.696584	141.9796	56.46167	32.92389
SE-Fla	L	0.236736	1.0944	1.2776	0.181317	2.690867	86.47471	64.1128	19.4569
SE-Nor	L	0.050674	0.9098	0.9424	0.130088	2.18242	10.39261	60.0865	17.4795
US-Blo	L	0.017248	0.951	0.9632	0.127649	1.837421	67.51007	38.8952	-120.633
US-Dk3	NA	0.020612	2.478592	2.526	0.096197	1.863259	43.77057	35.9782	-79.0942
US-Ha1	L	0.036442	2.684584	2.842	0.12599	2.089296	129.1505	42.5378	-72.1715
US-Ho1	NA	0.206056	1.8465	2.194	0.127412	0.756678	97.23358	45.2041	-68.7402
US-Ho2	L	0.082243	2.250934	2.397336	0.122931	0.971983	62.06781	45.2091	-68.747
US-Los	NA	0.196744	1.832871	2.2696	0.086604	5.437735	84.72113	46.0827	-89.9792
US-MMS	M	0.046368	2.88288	3.0848	0.091367	1.270342	105.6314	39.3231	-86.4131
US-PFa	NA	NA	2.5116	2.5116	0.133305	1.813024	144.007	45.9459	-90.2723
US-SP2	L	0.020039	1.917499	1.946251	0.079995	1.712366	231.3287	29.7648	-82.2448
US-SP3	NA	0.165174	1.816091	2.1864	0.038632	0.717104	102.9947	29.7548	-82.1633
US-UMB	L	0.009748	2.8348	2.8632	0.029775	0.948186	83.73883	45.5598	-84.7138

US-Wi4	NA		0.019694	2.4863	2.5476	0.129124	1.82006	74.55053	46.7393	-91.1663
VU-Coc	NA		0.068376	3.209371	3.536106	0.077204	0.263491	409.6292	-15.4427	167.192

SUPPLEMENTARY DATASET 2 - Annual information on the GPPsat, leaf area index (LAI), mean growing season air temperature (avgTair), mean growing season cumulative precipitation (avgPrecip), mean growing season water availability index (avgWAI). site.code is the identifier of the sites.

site.code	YEAR	GPPsat	LAI	avgTair	avgPrecip	avgWAI
BE-Bra	1997	25.40863	NA	19.05522	208.1	0.705888
BE-Bra	1998	31.00332	NA	19.18014	399.1	0.687184
BE-Bra	2000	25.14053	NA	18.50444	328.2863	0.85893
BE-Bra	2001	24.55767	1.194282	20.10189	371.3	0.670236
BE-Bra	2002	23.52138	1.3164	17.49041	256.4	0.845067
BE-Bra	2004	23.02275	1.018695	18.68473	187.2	0.716218
BE-Bra	2005	29.92095	1.168	21.61484	174.4519	0.837151
BE-Bra	2006	29.83949	1.062	19.65079	250.625	0.748745
CA-Ca1	1997	21.31579	NA	7.799439	68.7786	1
CA-Ca1	1998	31.22706	NA	16.46755	220.1992	0.55016
CA-Ca1	1999	28.33714	NA	15.24221	216.7444	0.495943
CA-Ca1	2000	29.6433	NA	16.30021	164.2068	0.454778
CA-Ca1	2001	31.39731	0.937209	15.37924	192.7959	0.520368
CA-Ca1	2002	26.43072	0.9904	16.59679	99.994	0.353981
CA-Ca1	2003	28.27223	0.9664	16.3179	213.8354	0.461148
CA-Ca1	2004	30.72226	0.9764	16.79885	225.8538	0.582977
CA-Ca1	2005	35.85841	0.8908	15.88469	296.9496	0.62595
CA-Ca2	2001	10.28122	0.929101	16.93072	511.68	0.601708
CA-Ca2	2002	9.497282	1.0208	19.50636	163.5731	0.353725

CA-Ca2	2003	10.60472	0.974	19.37702	143.76	0.466632
CA-Ca2	2004	14.18731	0.938	20.37047	316.17	0.623044
CA-Ca2	2005	15.83232	0.9152	19.27843	310.3781	0.608283
CA-Ca3	2001	18.85298	1.136122	12.20292	182.2	0.782673
CA-Ca3	2002	19.96921	1.1764	17.41888	154.7564	0.400636
CA-Ca3	2003	18.14786	1.154	16.09863	346.7518	0.541985
CA-Ca3	2004	21.21392	1.1984	17.42142	253.764	0.523049
CA-Ca3	2005	24.76672	1.074	17.75127	292.824	0.534298
CA-Man	1995	13.89331	NA	13.67035	267.2185	0.54873
CA-Man	1997	14.02676	NA	17.74346	195.7563	0.515045
CA-Man	1998	14.39575	NA	17.10816	232.0169	0.601634
CA-Man	1999	14.14815	NA	18.50247	85.32674	0.167789
CA-Man	2000	12.61605	NA	13.23451	192.8091	0.396774
CA-Man	2001	12.81149	1.0904	17.44242	210.7967	0.312687
CA-Man	2002	14.81475	0.9968	15.12422	335.1077	0.482385
CA-Man	2003	11.95838	0.9656	18.94273	190.2174	0.434031
CA-NS1	2002	15.75141	0.9968	21.27421	80.93898	0.394148
CA-NS1	2003	10.73432	0.9656	21.88932	160.6323	0.280401
CA-NS1	2004	13.16397	0.7916	17.21807	13.05813	0.087098
CA-NS1	2005	11.91869	0.8876	NA	NA	0.31354
CA-NS2	2001	13.12065	0.7544	-3.80965	12.92987	0.236782
CA-NS2	2002	12.64546	0.686	17.61766	230.4597	0.485316
CA-NS2	2003	11.68445	0.6332	22.8739	120.0387	0.246306
CA-NS2	2004	13.37508	0.5156	18.91797	172.0234	0.195583
CA-NS2	2005	16.34998	0.644	25.49833	80.58973	0.885229
CA-NS3	2001	9.077855	0.8664	6.211872	42.65345	0.094286

CA-NS3	2002	14.4313	0.8324	14.02486	269.0458	0.557782
CA-NS3	2003	9.628732	0.75	-0.7331	18.40948	0.205949
CA-NS3	2004	12.61405	0.708	13.49138	172.744	0.121942
CA-NS3	2005	14.04932	0.7416	18.05745	96.39385	0.20973
CA-NS5	2001	7.705969	1.31	9.500296	0	0.144849
CA-NS5	2002	16.53816	1.1004	19.94706	94.40733	0.321328
CA-NS5	2003	13.39346	1.1532	21.20643	95.56236	0.162956
CA-NS5	2004	15.48843	0.8652	14.54646	185.194	0.209175
CA-NS5	2005	15.20007	1.2212	18.37967	331.3188	0.784247
CA-NS6	2002	10.99927	0.7308	11.84331	192.6804	0.395749
CA-NS6	2003	8.270848	0.7036	18.62868	116.9346	0.183042
CA-NS6	2004	12.02594	0.7344	13.71092	189.3182	0.280469
CA-NS6	2005	11.17072	0.7432	20.38761	343.4862	0.701952
CA-NS7	2002	16.05872	0.496	18.79513	115.5847	0.472874
CA-NS7	2003	8.282513	0.6108	15.34651	166.7811	0.488194
CA-NS7	2004	12.43948	0.5844	10.13826	174.8031	0.460122
CA-NS7	2005	11.28407	0.5268	17.83064	312.2592	0.81259
CA-Oas	1997	31.01244	NA	15.94909	209.7156	0.582383
CA-Oas	1998	27.79837	NA	17.7467	210	0.638693
CA-Oas	1999	31.92855	NA	15.0899	331	0.745114
CA-Oas	2000	32.87654	NA	13.13211	264	0.783582
CA-Oas	2001	30.14386	2.6736	16.33131	151	0.376604
CA-Oas	2002	25.84301	2.5268	13.97613	189.8435	0.322618
CA-Oas	2003	27.03124	1.6332	17.41543	192	0.476646
CA-Oas	2004	31.20463	2.3264	13.81687	473	0.882631
CA-Oas	2005	30.96555	2.2636	14.44924	507	0.869481
CA-Obs	1999	15.20269	NA	18.88386	191	0.678139
CA-Obs	2000	16.18342	NA	16.12405	368	0.810327
CA-Obs	2001	14.67087	0.6656	18.16312	296	0.528959
CA-Obs	2002	16.86126	0.6424	15.6208	307	0.569619
CA-Obs	2003	14.78593	0.538	18.2474	189	0.373556
CA-Obs	2004	17.86573	0.614312	14.57951	487	0.905685

CA-Obs	2005	17.20546	0.6128	16.07828	384.4	0.788899
CA-Ojp	1999	11.40585	NA	15.01622	61	0.725218
CA-Ojp	2000	13.90127	NA	16.43741	236	0.650152
CA-Ojp	2001	11.52807	0.6012	18.69266	223	0.312699
CA-Ojp	2002	14.57974	0.6004	16.94026	326	0.58895
CA-Ojp	2003	11.07973	0.5448	18.72034	158	0.372818
CA-Ojp	2004	14.4921	0.531097	14.79926	463	0.936649
CA-Ojp	2005	14.6802	0.566	16.45567	369.8	0.860189
CA-Qfo	2003	15.03362	0.6292	11.05572	149.4497	0.988338
CA-Qfo	2004	15.05166	0.6664	15.7322	484.1385	0.950907
CA-Qfo	2005	13.71496	0.7036	17.92507	748.0863	0.930961
CA-Qfo	2006	13.45992	0.6136	16.56024	601.4766	0.986255
CA-SJ1	2001	5.291651	0.6832	NA	NA	0.719285
CA-SJ1	2002	7.799839	0.6676	20.32067	2.59999	0.90441
CA-SJ1	2003	8.256081	0.6588	20.23067	85.2	0.424798
CA-SJ1	2004	8.668371	0.655067	19.30266	246.4145	0.96775
CA-SJ1	2005	9.810311	0.6608	19.79983	131.2	0.885506
CZ-BK1	2000	24.01262	NA	NA	NA	0.938744
CZ-BK1	2001	20.596	0.692024	NA	NA	0.987957
CZ-BK1	2002	19.22405	0.75945	NA	NA	0.940644
CZ-BK1	2003	32.11813	0.654	NA	NA	0.866275
CZ-BK1	2004	29.23157	0.710001	21.99185	250.6	0.952981
CZ-BK1	2005	36.32444	0.7352	17.50115	1365.067	0.979266
CZ-BK1	2006	28.512	0.6692	NA	NA	0.935062
DE-Bay	1996	26.37468	NA	13.82062	58.13704	NA
DE-Bay	1997	22.75551	NA	17.29463	159.8	NA
DE-Bay	1998	24.22308	NA	15.80816	427.5	NA

DE-Bay	1999	25.40077	NA	15.82686	474.8	NA
DE-Hai	2000	34.17627	NA	17.35269	402.0525	0.821159
DE-Hai	2001	34.92254	2.786961	17.10108	346.28	0.641784
DE-Hai	2002	34.86263	2.921729	16.8845	444.5	0.842744
DE-Hai	2003	32.33778	2.7948	18.82872	281.3	0.536604
DE-Hai	2004	29.08469	2.558	16.16337	375.8	0.683534
DE-Hai	2005	32.35399	2.8172	17.42746	399.4	0.675663
DE-Hai	2006	30.99842	2.5516	19.17103	319.9	0.56579
DE-Tha	1996	28.24911	NA	18.56822	91.3	0.888315
DE-Tha	1997	33.27161	NA	20.43348	146.3959	0.682075
DE-Tha	1998	31.21526	NA	17.32657	290.6211	0.751774
DE-Tha	1999	33.14693	NA	18.38479	259.9895	0.698522
DE-Tha	2000	33.11306	NA	18.29511	264.6644	0.603555
DE-Tha	2001	28.69225	1.401151	17.69908	311.6577	0.811791
DE-Tha	2002	28.67655	1.324799	17.3194	325.6007	0.831776
DE-Tha	2003	25.46562	1.1476	17.81837	192.1	0.480935
DE-Tha	2004	29.70932	1.1728	17.63536	301.1	0.65776
DE-Tha	2005	31.3907	1.212	18.318	289.6858	0.847073
DE-Tha	2006	27.37801	1.321714	19.16038	283.1	0.685705
DE-Wet	2002	34.21268	0.6244	15.49284	295.9	0.791987
DE-Wet	2003	26.41874	0.5808	16.10637	284	0.608898
DE-Wet	2004	27.84321	0.564516	14.69392	339.5	0.761391
DE-Wet	2005	31.55776	0.684	15.70194	230.7	0.723992
DE-Wet	2006	29.85942	0.609087	15.80851	353.7	0.766159
DK-Sor	1996	33.86896	NA	18.08433	77.57727	0.392094
DK-Sor	1997	29.40516	NA	17.14331	239.2	0.55701
DK-Sor	1998	36.06682	NA	15.72728	316.4333	0.719848
DK-Sor	1999	33.30616	NA	16.83569	315.6759	0.845585
DK-Sor	2000	33.71235	NA	16.84284	204.0587	0.510721
DK-Sor	2001	35.22088	2.358712	16.67453	445.787	0.723101
DK-Sor	2002	33.16872	2.506752	17.60763	440.3634	0.875343
DK-Sor	2003	36.97734	1.7072	19.15637	246.0359	0.542704

DK-Sor	2004	40.61516	1.6388	16.34314	751.3632	0.962047
DK-Sor	2005	38.81689	2.44	16.37945	362.3667	0.911121
DK-Sor	2006	36.95251	2.6848	18.26908	604.6829	0.842409
FR-Hes	1997	28.16698	NA	18.36753	215.62	0.592937
FR-Hes	1998	37.88122	NA	19.20879	421.8	0.632814
FR-Hes	1999	33.4528	NA	19.86889	475	0.728656
FR-Hes	2000	31.90932	NA	20.75039	358.6095	0.805398
FR-Hes	2001	37.70153	2.5608	19.72265	483.2	0.718589
FR-Hes	2002	37.29403	2.7008	19.16243	553.6	0.712345
FR-Hes	2003	34.67425	2.446	22.16201	302.8	0.502709
FR-Hes	2004	27.3774	2.478	19.32453	388.8	0.617896
FR-Hes	2005	28.39183	2.392	20.26126	336.2	0.635454
FR-Hes	2006	32.6713	2.476	20.94824	541.4	0.760015
FR-LBr	1996	24.53418	NA	22.22681	141.2	0.605693
FR-LBr	1997	28.20563	NA	25.13088	359	0.576227
FR-LBr	1998	27.90339	NA	20.97396	246.6	0.630335
FR-LBr	2000	33.57249	NA	22.87523	347.7594	0.755286
FR-LBr	2003	26.41214	1.3072	23.15486	130.629	0.472564
FR-LBr	2004	27.97842	1.6748	22.88894	134.601	0.593173
FR-LBr	2005	26.64429	1.3056	20.81021	194.786	0.54347
FR-LBr	2006	29.54445	1.138	20.44697	156.581	0.502058
FR-Pue	2000	17.45321	NA	18.08735	90.4	0.781209
FR-Pue	2001	21.41963	1.1712	17.70638	206.2	0.7721
FR-Pue	2002	21.93963	1.3176	18.69201	153.6	0.791837
FR-Pue	2003	21.02929	1.1188	18.63205	143.8	0.731048
FR-Pue	2004	20.73219	1.254	20.54134	84.408	0.640924
FR-Pue	2006	22.4648	0.884	17.89354	51	0.729435
IL-Yat	2001	14.22269	0.4232	20.53659	9	0.514895
IL-Yat	2002	14.51068	0.497472	17.80057	137	0.61365
IL-Yat	2003	19.24324	0.6176	16.962	36.91695	0.816408
IL-Yat	2004	15.26292	0.5104	NA	NA	0.615814
IL-Yat	2005	17.6287	0.6092	NA	NA	0.491933

IL-Yat	2006	12.41234	0.296	16.81598	116.5351	0.348088
IT-Col	1996	31.08883	NA	17.91826	9.2	0.306291
IT-Col	1997	34.5021	NA	17.33381	77.4	0.568283
IT-Col	1998	28.70382	NA	17.52884	414.1982	0.604098
IT-Col	1999	28.64437	NA	20.86844	179.0451	0.531601
IT-Col	2000	34.16921	NA	NA	NA	0.466705
IT-Col	2001	25.78451	2.2608	NA	NA	0.475071
IT-Col	2002	20.94372	2.048	NA	NA	0.95773
IT-Col	2003	31.5813	2.1744	21.02472	195.8	0.695385
IT-Col	2004	29.52186	2.2744	19.81573	108.8	0.407209
IT-Col	2005	30.66933	2.1088	19.20607	187.0333	0.42861
IT-Col	2006	27.4935	2.3064	16.87804	198.2	0.580764
IT-Lav	2001	33.10424	2.022	NA	NA	0.665667
IT-Lav	2002	29.18438	1.2528	NA	NA	0.926238
IT-Lav	2004	30.47092	1.048	14.7304	313.4	0.644475
IT-Lav	2006	29.82067	1.1804	15.38128	198.4	0.562672
IT-Non	2001	28.10025	1.0084	27.20097	222.4	0.678244
IT-Non	2002	28.73654	1.512294	25.3912	693.7117	0.851283
IT-Non	2003	33.89305	0.99	31.2541	102.2285	0.520069
IT-Non	2006	29.05593	1.038	25.69206	130.4	0.502476
IT-Ro1	2000	14.01261	NA	24.57038	117	0.322144
IT-Ro1	2001	26.84909	1.8624	22.69705	32.36666	0.483636
IT-Ro1	2002	24.47292	1.8824	23.55284	385.1941	0.746477
IT-Ro1	2003	27.27324	1.1916	22.52393	206.96	0.551631
IT-Ro1	2004	27.41111	2.0232	23.62473	380.796	0.531637
IT-Ro1	2005	22.63412	1.8244	24.97555	272.695	0.515672
IT-Ro1	2006	24.55807	1.5452	25.8215	233.724	0.451728
IT-Ro2	2002	28.48346	2.099677	22.38572	479.7255	0.700655
IT-Ro2	2003	34.10516	1.598	22.6509	258.699	0.420743
IT-Ro2	2004	29.98126	2.298	24.17843	307.336	0.377209
IT-Ro2	2005	33.76487	1.8564	24.79391	196.0279	0.50059
IT-Ro2	2006	34.51132	1.8104	27.07352	217.877	0.374292

IT-SRo	1999	28.76489	NA	NA	NA	NA
IT-SRo	2000	28.08307	NA	20.49684	172	NA
IT-SRo	2001	24.11051	0.32888	NA	NA	NA
IT-SRo	2002	23.52651	0.36292	24.31849	154.0192	NA
IT-SRo	2003	25.20579	0.33764	19.41404	86	NA
IT-SRo	2004	25.5317	0.28256	21.38298	173.2	NA
IT-SRo	2005	25.05776	0.3676	18.63815	22.88	NA
IT-SRo	2006	27.29586	0.35124	20.62185	150.2	NA
JP-Tak	1999	27.13042	NA	17.30121	NA	0.99037
JP-Tak	2000	28.16418	NA	18.75595	NA	0.995225
JP-Tak	2001	27.3587	1.785307	17.17423	NA	0.992297
JP-Tak	2002	28.93126	2.5756	16.88523	NA	0.963532
JP-Tak	2003	33.99091	1.800199	15.83577	NA	0.995582
JP-Tak	2004	23.91046	2.3696	17.17211	NA	0.994855
JP-Tef	2001	32.98181	2.64	14.82108	246.8	0.985147
JP-Tef	2002	34.76034	2.1724	17.67966	472.6	0.93194
JP-Tef	2004	16.44147	2.5072	17.90515	351.7092	0.91366
JP-Tef	2005	21.20179	2.486	21.26736	276.8	0.751417
RU-Fyo	1998	28.68522	NA	19.94742	913.2	0.696464
RU-Fyo	1999	23.91324	NA	22.60639	642.7	0.62833
RU-Fyo	2000	24.57255	NA	NA	NA	0.755275
RU-Fyo	2001	25.45813	1.491766	NA	NA	0.541724
RU-Fyo	2002	26.21038	2.0428	14.29257	509.3	0.309585
RU-Fyo	2003	25.54891	1.4352	16.92588	905.8	0.646419
RU-Fyo	2004	22.13492	1.7484	18.90008	732.3	0.490735
RU-Fyo	2005	26.36995	1.5028	19.92699	740.1	0.707484
RU-Fyo	2006	27.71568	1.67	16.98465	711.7	0.720507
SE-Fla	1996	13.29543	NA	18.95925	13.4	0.669887
SE-Fla	1997	17.93879	NA	19.52953	27.76236	0.596351
SE-Fla	1998	23.51732	NA	13.48044	210.1821	0.920375
SE-Fla	2000	14.92038	NA	14.2613	178.2735	0.970051
SE-Fla	2001	13.46096	1.2776	16.262	191.643	0.990751

SE-Fla	2002	15.63556	0.9112	19.35333	157.9645	0.638077
SE-Nor	1996	31.24595	NA	19.4267	87.97748	0.616202
SE-Nor	1997	23.40187	NA	18.39733	112.271	0.704358
SE-Nor	1998	32.8098	NA	18.27959	98.81	0.783856
SE-Nor	1999	19.44153	NA	NA	NA	0.510843
SE-Nor	2003	24.29188	0.8772	NA	NA	0.737609
SE-Nor	2005	15.6571	0.9424	14.45976	93.6	0.883205
US-Blo	1997	15.69029	NA	23.5907	1.663168	0.135826
US-Blo	1998	20.42857	NA	20.30543	74.57	0.28495
US-Blo	1999	16.3376	NA	19.51985	27.178	0.273989
US-Blo	2000	15.6632	NA	16.36083	227.6715	0.621535
US-Blo	2001	14.97685	0.9568	19.16923	35.56	0.446113
US-Blo	2002	16.56786	0.9632	19.86659	26.035	0.406587
US-Blo	2003	15.05513	0.952	19.52644	140.3503	0.412204
US-Blo	2004	14.77307	0.956	18.11211	31.496	0.420582
US-Blo	2005	22.13088	0.9184	20.38931	63.89068	0.368169
US-Blo	2006	22.19135	0.9596	20.3037	76.962	0.34475
US-Dk3	2001	44.36397	2.517359	26.92598	171.293	0.588591
US-Dk3	2002	30.8876	2.434	26.41801	224.1	0.61916
US-Dk3	2003	32.13158	2.414	24.62529	158.44	0.807468
US-Dk3	2004	34.92139	2.526	26.68285	256.129	0.763707
US-Dk3	2005	41.76055	2.5016	22.52212	160.573	0.751423
US-Ha1	1992	28.01109	NA	20.81017	439.2	0.871428
US-Ha1	1993	29.62493	NA	20.76565	233.7	0.813003
US-Ha1	1994	33.60487	NA	20.42823	513	0.865447
US-Ha1	1995	31.94775	NA	18.98674	393.6	0.677438
US-Ha1	1996	37.66202	NA	19.64707	543.1	0.77089
US-Ha1	1997	33.63861	NA	13.87707	240.9	0.710094
US-Ha1	1998	31.55541	NA	20.78775	271.5	0.609868
US-Ha1	1999	29.6298	NA	21.99482	462.4	0.512118
US-Ha1	2000	36.82112	NA	19.64854	470.3	0.86618
US-Ha1	2001	35.1674	2.842	20.86034	340.1	0.620671

US-Ha1	2002	36.11215	2.709902	21.19587	74.05	0.606564
US-Ha1	2003	39.72972	2.584	18.86517	375.0455	0.777487
US-Ha1	2004	38.45775	2.5984	20.76897	525.8	0.896503
US-Ha1	2005	34.16287	2.736	16.41854	389.65	0.859658
US-Ha1	2006	39.60573	2.6372	18.51679	418.751	0.899628
US-Ho1	1996	26.74466	NA	19.83671	553.6668	0.819622
US-Ho1	1997	25.80355	NA	20.98795	311.278	0.70207
US-Ho1	1998	26.01189	NA	20.47923	286.1	0.700533
US-Ho1	1999	24.86608	NA	20.93398	261	0.637394
US-Ho1	2000	26.64025	NA	18.99176	222.9	0.590387
US-Ho1	2001	28.40212	2.194	21.55833	278.867	0.482828
US-Ho1	2002	25.41006	2.012	20.58258	293.238	0.622652
US-Ho1	2003	26.52227	1.868	20.39801	380.5697	0.725014
US-Ho1	2004	25.80196	1.312	19.88215	355.6	0.916842
US-Ho2	1999	23.6101	NA	20.7432	383.9	0.647157
US-Ho2	2000	24.24044	NA	18.95148	220.4	0.589353
US-Ho2	2001	26.20509	2.397336	21.74772	270.056	0.492095
US-Ho2	2002	21.82717	2.344	20.81512	291.938	0.645078
US-Ho2	2003	25.03448	2.2796	20.27188	369.3697	0.757214
US-Ho2	2004	26.81076	1.9828	19.68705	286.139	0.840446
US-Los	2001	17.99381	1.693157	22.41026	387.263	0.75547
US-Los	2002	21.13927	1.9864	25.34941	302.122	0.78324
US-Los	2003	14.84725	2.2696	19.89465	168.13	0.583782
US-Los	2004	17.19594	1.3036	10.97451	229.891	0.772163
US-Los	2005	20.19986	1.9116	21.54461	321.295	0.65732
US-MMS	1999	30.62939	NA	22.16762	326.869	0.561233
US-MMS	2000	32.97086	NA	22.15324	442.5763	0.845453
US-MMS	2001	34.5778	3.0848	24.39551	629.0809	0.758628
US-MMS	2002	32.09942	2.8512	25.25679	606.0966	0.6761

US-MMS	2003	31.75916	2.8904	23.17749	418.6892	0.658928
US-MMS	2004	31.97261	2.7108	24.07916	495.709	0.631184
US-MMS	2005	31.42323	2.8772	24.97723	470.45	0.683149
US-PFa	1996	29.29945	NA	18.43488	268.372	0.807464
US-PFa	1997	26.46502	NA	17.06258	361.5115	0.774916
US-PFa	1998	24.79614	NA	16.08619	242.055	0.561745
US-PFa	1999	25.68095	NA	16.53644	482.37	0.837827
US-PFa	2000	27.97977	NA	13.60124	98.93	0.7366
US-PFa	2003	38.9659	2.5116	18.51338	127.0706	0.519765
US-SP2	1998	8.284076	NA	30.40006	28.17	0.576897
US-SP2	1999	19.45799	NA	32.44898	71.03	0.756319
US-SP2	2000	18.64706	NA	29.86596	300.126	0.556726
US-SP2	2001	25.78257	1.861863	31.65209	562.372	0.546473
US-SP2	2002	31.58403	1.9224	28.87413	422.896	0.581304
US-SP2	2003	31.51594	1.939482	28.47239	237.998	0.547504
US-SP2	2004	29.42969	1.946251	27.73494	632.262	0.676352
US-SP3	1999	29.60609	NA	28.46097	354.3411	0.579168
US-SP3	2000	35.28139	NA	27.4332	111.68	0.587571
US-SP3	2001	28.83059	1.489057	27.38325	407.117	0.580678
US-SP3	2002	25.83585	1.906107	27.76014	285.242	0.533775
US-SP3	2003	26.07121	2.1864	28.90027	322.316	0.653837
US-SP3	2004	24.94062	1.6828	27.01402	241.292	0.578481
US-UMB	1999	31.65117	NA	21.23763	341.8788	0.63708
US-UMB	2000	27.58812	NA	18.97573	556.4179	0.720158
US-UMB	2001	28.54424	2.8632	19.95331	383.25	0.667601
US-UMB	2002	32.95183	2.808	19.00127	386.3778	0.674146
US-	2003	31.78521	2.8332	19.30616	383.6	0.678912

UMB						
US-Wi4	2002	37.37381	2.4888	25.06475	182.6	0.588773
US-Wi4	2003	28.82016	2.4808	26.04254	3.934286	0.307795
US-Wi4	2004	28.71686	2.428	21.80987	102.2667	0.446941
US-Wi4	2005	31.02355	2.5476	23.91261	125.901	0.566401
VU-Coc	2001	40.60159	3.06938	27.96865	163.93	0.682074
VU-Coc	2002	40.91065	3.536106	27.51039	692.08	0.855235
VU-Coc	2003	36.70833	3.0976	28.07115	1109.01	0.833879
VU-Coc	2004	36.36203	3.1344	28.04992	384.85	0.798799

4. GENERAL DISCUSSION

Terrestrial ecosystems play an important role in global biogeochemical cycles and especially the carbon cycle (Heimann & Reichstein, 2008). While their importance is evident, our shortcoming in understanding ecosystem processes, functions and their feedback mechanism to climate introduces large uncertainties in carbon budget estimates (Friedlingstein *et al.*, 2014) and earth system models (Bonan, 2008). Terrestrial biosphere models are just a small component of coupled Earth system models and yet cause the largest uncertainties when it comes to future projections (Friedlingstein *et al.*, 2006, Friedlingstein *et al.*, 2014). The role of vegetation with respect to fluxes of matter and energy between biosphere and atmosphere is often defined by some mathematical descriptions, based on leaf or organism level physiology. These model implementations are not always benchmarked with empirical analysis of relationships between ecosystem functioning and plants (Luo *et al.*, 2013). Empirical studies of ecosystem function with a focus on plant impacts could bear more detailed insight in this regard. Especially studying plant traits in relation to ecosystem functioning can be a promising avenue (Reichstein *et al.*, 2014).

The dissertation here has made a contribution in this framework by developing further the definition of EFPs as proxies for long-term stable ecosystem functional states that can be derived from biosphere-atmosphere flux observations or by remote sensing (see also Reichstein *et al.*, 2014). The dissertation also advances the understanding how EFPs as emergent properties of the ecosystem that embed the response of ecosystem functioning to climate variability can be directly linked to plant traits. Paper one proposes methods for up-scaling plant traits to ecosystem level and introduces opportunities that a large integrated plant trait database like TRY (Kattge *et al.*, 2011) offers in this regard. Paper 2 interrogates for the first time to what extend plant traits from databases can be used in ecosystem functioning-plant trait studies. I show the opportunities and limitations that trait data from an integrated database offer and argue that although such studies can reveal patterns it is preferable to have time and space synchronized for EFP and trait measurements. Using temporally and spatially synchronized data Paper 2 shows that site differences of maximum photosynthetic capacity (GPPsat) can best be explained by a combination of leaf C/N ratio and leaf phosphorus concentration as predictors. The finding can be used for model parameterization and validation.

Ecosystems are not inherently static (Hastings, 2004). As a result of internal dynamics even in the absence of environmental variability ecosystems vary over time and space with respect to their fluxes (Scheffer *et al.*, 2009). This is one reason why it is important to have EFP and trait data synchronized over time. However, the FLUXNET sites we used to derive EFPs, showed differences in the magnitude of inter-annual variation of GPPsat. Paper 3 indicates for the first time the significance of stand age and species richness as factors controlling these differences. Please find more detailed discussion on specific aspects of the three studies in the following section.

4.1 Paper 1 - Plant traits in the context of EFPs

In Paper 1 (Musavi *et al.*, 2015) I suggested and investigated empirical paths to analyze the imprint of plants on ecosystem functioning based on observations. I advance the understanding of EFPs as ecosystem attributes that have the response of plants to environmental changes embedded in them and can be used to understand the mediating control of plants on ecosystem functioning (Reichstein et al., 2014, Musavi *et al.*, 2015). EFPs can be estimated in a comparable and standardized manner at eddy covariance (EC) sites and thereby facilitate cross-site comparisons. I present different EFP types such as light use efficiency, photosynthetic capacity, etc. estimated from biosphere-atmosphere fluxes or retrieved by remote sensing (using a literature search) and suggest their potential links to plant traits and vegetation structure in an intelligible structure (Musavi *et al.*, 2015). These EFPs can be estimated at all FLUXNET sites distributed throughout the globe (e.g. Pastorello *et al.*, 2017) or can be retrieved at grid cells globally using remote sensing products (Houborg *et al.*, 2015, Houborg *et al.*, 2016).

Most of the FLUXNET sites are located in the northern hemisphere and the number of sites is very low in South America and Africa. Only a few sites exist in central and south west Asia. Therefore the global network of FLUXNET sites does not cover all types of ecosystems and extreme events (Mahecha *et al.*, 2017), nor the different ecosystem sensitivities to climate variability (Seddon *et al.*, 2016). An additional issue using FLUXNET data is that only less than half of the sites have more than 5 years of data and the years with data are not always overlapping in the different sites. With the increasing availability of satellite remote sensing data measuring a variety of relevant ecological variables (Kerr & Ostrovsky, 2003) EFPs can also be studied using these data. Most of the satellite remote sensing data will become available at global scale, with high spatial and temporal resolution, still they need to be validated by ground data (e.g. *in-situ* observations of biosphere-atmosphere fluxes). A promising strategy to fully understand EFP-vegetation relationships can be using satellite information in tandem with ground data, such as retrieving light use efficiency (LUE) from fluxes to link to *in-situ* N% in comparison to LUE from remote sensing (Garbulsky *et al.*, 2014, Hilker *et al.*, 2008) in relation to N% - also retrieved from remote sensing (e.g. Martin *et al.*, 2008).

Plant traits measured at the leaf level have to be scaled up to the canopy level to be compared to EFPs. Besides trait upscaling based on species mean trait values and species cover data, calculating for example, community weighted means (CWM), an alternative approach to derive trait values at the ecosystem level would account for ecosystem LAI (as the total number of leaves present) and for each species light absorption along a vertical canopy trajectory using the Lambert–Beer law of extinction and plant height (Musavi *et al.*, 2015). Especially in dense canopies accounting for the vertical distribution of leaves within the canopy will improve the photosynthesis predictions, since leaf traits such as nitrogen content of the leaves will have a higher contribution to photosynthesis in sunlit leaves than shaded leaves in the lower canopy (Wu *et al.*, 2017). While this approach might be useful in forests where plants are located in different strata, it is not more efficient than abundance weighting in e.g. grasslands.

A challenging aspect using *in-situ* measurements of plant traits is the low total number of sites with this data and the limited types of traits measured. One way of circumventing this scarcity is using plant traits from an integrated database like TRY (Kattge *et al.*, 2011). As a case study in Fig.5 in Musavi *et al.* (2015) I showed the comparison of upscaled leaf nitrogen concentration based on the FLUXNET ancillary database and using species mean trait values from TRY database and species abundance from the FLUXNET ancillary database. Though this is only a case study, I argue that it is indicative of a unique opportunity that plant traits of the global database of TRY can provide in this context – they can represent the spatial variability of *in-situ* traits (see Fig. 5 in Musavi *et al.*, 2015). A first look into the databases showed that for more than 100 FLUXNET sites, I could estimate EFPs and have the information of dominant plant species of the sites that can be used to link plant traits from TRY (e.g. specific leaf area) to EFPs (Musavi *et al.*, 2015). As an additional test I also reran the correlation done by Kergoat *et al.* 2008 using their estimates, light use efficiency for sites and plant traits extracted from TRY

(Musavi et al., 2015). The results were very similar and thus strengthened the assumption that it is possible to use species averaged traits from TRY to study the relations between plant traits and EFPs, since the intraspecific variability of plant traits might be ignored at large scale studies (Kazakou *et al.*, 2014), where trait differences between sites are determined by species turnover (Albert *et al.*, 2011). Nevertheless, it has been shown that it is possible to ignore intra-specific traits variability to analyse changes in the ecosystems (Al Haj Khaled *et al.*, 2005, Garnier *et al.*, 2001). While it is known that traits exhibit seasonal variation (Karavin & Kilinc, 2011, Palacio *et al.*, 2008), using traits from TRY in relation to EFPs is based on the fact that most of the traits are measured from matured leaves in peak of growing season. Therefore it can be related to EFPs such as photosynthetic capacity, which is also associated to mid growing season. In the next paper I evaluate the suitability of using traits from a database in relation to EFPs derived from fluxes.

4.2 Paper 2 - Spatial and temporal synchronization of plant traits and EFPs

In Paper 2, I analyzed for the first time the relevance of spatial and temporal synchronization of traits and EC flux measurements for the characterization of the imprint of plant traits on EFPs. Various plant traits (e.g. N_{mass}, SLA, LDMC) have been shown to influence ecosystem function (Garnier *et al.*, 2004, Ma *et al.*, 2010, Ollinger *et al.*, 2008, Reich, 2012). For some of these traits species signals are strong enough to allow us using global trait databases to characterize local plant species (Garnier *et al.*, 2001, Kazakou *et al.*, 2014). Further it is suggested that at global scales the differences between species are more relevant than intraspecific trait variability (Albert *et al.*, 2011). However, the relevance of intraspecific variation for ecosystem function has not been addressed yet across globally distributed EC sites. Equally important we assume that EFPs should be stable in the absence of disturbance and stand replacements, although they might show some degree of inter-annual variation (IAV) due to growth e.g. in forest (Musavi *et al.*, 2015).

Appreciating the increase of data availability of EC fluxes and plant traits, it was timely to test how we can benefit from these databases complementing our knowledge on EFP-plant relationships. It was never tested before whether it is possible to use trait information from databases in the context of studies on the link between plant traits and ecosystem functioning derived from EC fluxes.

As a first step, I compared different types of estimates for ecosystem photosynthetic capacity for their IAV. IAV was among the lowest and most robust for an estimation based on light response curves that accounts for the variation in radiation and that uses a moving window approach accounts for variation in meteorological variables (GPPsat, Musavi *et al.*, 2016). To extract the annual values of the time series of GPPsat I used a 90th percentile approach as this was more robust to outliers (Muavi *et al.*, 2016). However, GPPsat estimates calculated using GPP in response to PAR were more robust than those using APAR (GPPsat.structure). I thus consider both of them in relation to plant traits (Musavi *et al.*, 2016). This is because the use of APAR will account for the differences between ecosystem structures and their seasonal variability (Wang & Jarvis, 1990).

To upscale the plant traits I used community weighted means of plant traits based on the dominant species at the sites. This is because only the most dominant species were reported from the sites of my study. In addition, this approach is in accordance to the most used and tested “mass-ratio hypothesis” (Grime, 1998a). This hypothesis states that only the traits of the most abundant species matter for the ecosystem functioning because they are the most adapted ones to their environment and that is why they became dominant (Vile *et al.*, 2006). Using functional diversity indices (e.g. Mason *et al.*, 2005) such as Rao’s Q (Botta-Dukat, 2005, Rao, 1982) was not possible in my study, because the sampling and recording of plant species at the sites was not done systematically and throughout the season (because it was not possible for all PIs to make all the requested samplings). Nevertheless, it has been discussed that using functional diversity indices in relation to ecosystem processes and functions would result in different and contrasting results (Garnier *et al.*, 2015). I also could not use the upscaling method suggested in Paper I, because I did not have the consistent *in-situ* plant height measures of the individual species.

Both estimates of photosynthetic capacity (GPPsat, GPPsat.structure) showed a strong link to plant traits such as leaf nitrogen, carbon or phosphorus concentration and C/N ratio. The relationships were consistent, whether PAR or APAR was used. However, using APAR for the estimates adds uncertainties that were introduced while smoothing and reconstructing the time series of daily FAPAR from 16-days data to daily (Kandasamy *et al.*, 2013). Also, the mismatch of eddy covariance footprint vs satellite footprint (Cescatti *et al.*, 2012) is an important issue: the FAPAR product has a spatial resolution of 1×1 km and is therefore much bigger than the eddy covariance footprint of the sites. Nevertheless, including information on ecosystem structure (i.e. LAI) adds complementary information to the relationship between GPPsat and leaf nitrogen content, which confirms the importance of canopy structure in studies of ecosystem functioning (Baldocchi & Meyers, 1998, Reich, 2012). I showed that the interaction between LAI and N% contributes to explain between site variability of GPPsat. Thus one can use LAI as a structural input – influenced by traits such as leaf angle and leaf size (Falster & Westoby, 2003)- when comparing GPPsat to plant traits instead of using the structural information for the estimation of GPPsat.structure. While N% can give us information on the quality of the leaves, to make a fair comparison to GPPsat we need to also consider the quantity of leaves at the site, which can be gained by considering LAI. But it is also important to have in mind that remote sensing LAI estimates or derived from hemispheric photography saturates at high values (e.g. Deng *et al.*, 2006), while GPPsat does not. This is when additional leaves have no effect on the reflectance due the overlapping of leaves, especially when LAI is derived from RS or hemispheric photography (Reichenau *et al.*, 2016).

I used sites with different plant functional types and environments so that the differences between the locations and vegetation types would be large enough to be able to use species mean trait values based on the TRY database and minimize impact of intraspecific trait variability. I compared results where trait estimates were based on TRY or were directly measured at FLUXNET sites, while ecosystem photosynthetic capacity was either represented by site averaged estimates across years or the exact year of trait measurements. While the general patterns of the relationships between plant traits and estimates of ecosystem photosynthetic capacity was kept using traits from TRY, the strength of the relationship (coefficient of determination) was weaker in comparison to using *in-situ* plant traits. Next to high intraspecific variability in some of the used traits, other reasons for this result could be; 1. Not all species and traits have a good sampling cover in the database. Some species have more than hundreds of values for a given trait, while others might have only few. It is, therefore, difficult to have real species mean trait value when using database information. 2. Site specific manipulations such as fertilization can strongly deviate trait values from averaged values from the database (e.g. leaf nitrogen and phosphorous content). Unfortunately these manipulations are not always reported in the FLUXNET auxiliary database. 3. Leaf sampling is usually done at the peak of the growing season, which corresponds to the estimated annual values of photosynthetic capacity. Yet plant traits in non-forest sites like grasslands can have considerable variability during the year (Ma *et al.*, 2011). However, we expected the loss of local information on adaptation of plants to their environments when using traits from TRY. I show that the averaged plant trait values could be used to find some general patterns and first guesses of which trait-EFPs to investigate. Of course, site history and aging of the ecosystems adds to the variability of the plant traits (Becknell & Powers, 2014). Besides considering that plant traits have temporal variability due to development stages, vegetative phenology or changes in the environment (Mickelbart, 2010, Römermann *et al.*, 2016) it makes it necessary to use *in-situ* measurements.

The best fit was reached when photosynthetic capacity estimates were corresponding to the exact year of trait sampling (of *in-situ* traits) instead of the average estimates (averaged over the available years of data at the sites). Indeed, it is evident in my study that the photosynthetic capacity estimates have considerably high IAV even after removing data of disturbed years and choosing the estimates with least IAV. Therefore I conclude that not only plant traits must be measured *in-situ* but also that the two – plant traits and ecosystem photosynthetic capacity – should coincide timewise for best results (‘synchronization of plant traits and EFPs’). This is consistent with studies, which show that the IAV of ecosystem photosynthesis is effected by the plastic response of the ecosystems to environment intervened by plant traits (Grassi *et al.*, 2005, Ma *et al.*, 2010). Although some traits like SLA do not vary with phenology, others can change during the course of the year and with phenology (Römermann *et al.*, 2016). Therefore the synchronization of the trait-EFP timing can play an important role in the strength of the relationship. At last using site measurements of traits and photosynthetic capacity responding to the same year, I show that leaf carbon, nitrogen and phosphorous stoichiometry is the most important factor explaining between sites variability of photosynthetic capacity. Still this is done using only 20 sites and has to be confirmed by using many more sites.

In summary I show strong restriction on the use of mean trait values from large trait databases in the analysis on the ecosystem functioning. The variation of traits with phenology makes it necessary to measure them several times during the season (Römermann *et al.*, 2016). This might not be always feasible because it requires extensive sampling over the growing season. In this direction, more studies on the seasonal variability of traits are needed for understanding which traits to collect (lower variability during season) and what times of the year. Although, FLUXNET towers distributed globally cover a variety of different ecosystem types, they are mostly equipped to measure fluxes only. Little is invested on collecting information on plant species composition and characterizing their traits. Regular data collection of this kind parallel to fluxes could unravel the impact of plants on ecosystem function and thus contribute to improve biosphere-atmosphere models. Only recently networks like NEON (http://www.neoninc.org/) and ICOS (https://www.icos-ri.eu/) have started to standardize protocols for ancillary measurements of plant traits at flux tower sites.

I generalized the photosynthetic capacity property of the sites by using the mean of annual 90th percentile of GPPsat time series (occurring at the peak of the growing season when the leaves are sampled), assuming that this value will be stable annually. Although, my assumption hold true for some sites, a few of the sites indicated a high range of annual GPPsat values. While this contributed to the weak correlations realized when mean traits from TRY were used, it remains to be understood why different sites showed remarkable differences with respect to their IAV of photosynthetic capacity: was this determined by differences in abiotic or biotic drivers, like climate variation or pest outbreaks, or by site specific conditions, like vegetation properties. This is what I address in my next paper. This study would be relevant, because low IAV of EFPs might be an indication for ecosystem resilience under climate change.

“The identification of properties that contribute to the persistence and resilience of ecosystems despite climate change constitutes a research priority of global relevance.” (Seddon *et al.*, 2016, page 229)

4.3 Paper 3 - Impact of stand age and species richness on IAV of EFPs

From Musavi *et al.* 2016 (Paper 2) it became clear that GPPsat estimates have substantial IAV, even after removing site-years with confounding factors like disturbance such as fire events. Moreover, the magnitude of the IAV was varying between sites and it was apparently not dependent on the PFT of the sites. Hence, I delved into underlying differences between sites to identify determinants for the magnitude of the GPPsat IAV (Musavi *et al.*, 2017). According to previous studies on longer time scales variation of ecosystem fluxes could be better explained by vegetation responses to climate than by the climate variables themselves (Ma *et al.*, 2010, Richardson *et al.*, 2007, Urbanski *et al.*, 2007). Following previous studies on forest resilience

(Thompson *et al.*, 2009) I hypothesized that stand age and species richness must have a role in how some sites were quite stable in GPPsat (low cvGPPsat) and some looked unstable (high cvGPPsat) and had high IAV. The hypothesis is based on the idea that with forest aging next to species diversity, their structure also becomes more diverse and both of these properties can help buffering climate change in forests (Wirth *et al.*, 2009). Thereby, it is assumed that ecosystems persisted for long time have higher adaptive capacity, at least regarding the climate variability that they have been exposed to (Scholes *et al.*, 2014). I tested the hypothesis while also considering a wide range of potentially confounding factors, like mean climate and its variability, soil properties and structural properties of the forests, like LAI.

I show that although the IAV of GPPsat is closely linked to environmental variables, the differences of the coefficient of variation of GPPsat (cvGPPsat) between sites is best explained by stand age and species richness of the sites, while stand age has a much higher contribution. Soil conditions in forests can improve over time by various effects, such as an increasing depth of humus layer that also brings increased water storage capacity or expansion of favorable microbial communities (von Oheimb *et al.*, 2014). I evaluated the effect of soil by using soil nutrient availability classes at the sites, but other data such as soil organic content, porosity or PH of the soil might be more informative. In addition, older stands might also have deeper tap root systems that provide access to deeper water (von Oheimb *et al.*, 2014, Wirth, 2009), a property that substantially contributes to the stability of dry and seasonally dry ecosystems or during drought events. Continuous formation and regrowth of gaps in old forest creates a rough canopy surface and complex structure in the canopy (Ogunjemiyo *et al.*, 2005) and species composition that allows for more complementary use of light, water and nutrients (Wirth *et al.*, 2009). In addition, it has been shown that compared to forests with monospecific stands, forest with mixed stands are less affected by climate variability due to species competition in good years and facilitation in bad years (del Rio *et al.*, 2014). This indicates the importance of species richness as an additional factor in regulating climate effects on ecosystem functioning. This is conforming to previous studies in grasslands stating communities with higher plant species richness are more resistant to, and recover more fully from, a major drought in respect to their primary productivity (Tilman *et al.*, 2006) or species composition (Frank & McNaughton, 1991). The positive effect of species interaction might be more prominent when the ecosystem is already for a long time prone to stress, such as drought (Grossiord *et al.*, 2014). This could be why stand age has a stronger relationship with cvGPPsat than species richness itself. Older forests might already have experienced many stressful conditions, which - in the long term - they have adapted to by appropriate changes in species composition. Thereby, old forests could evolve a high functional richness compared to the younger ones as it is confirmed by a study in the tropics (Becknell & Powers, 2014). Facilitation and complementarity effects are rather linked to the functional richness of the species than to taxonomic richness (i.e. species richness) (Butterfield & Callaway, 2013). Functional richness might develop in time more adaptive compared to species richness, which may already be high in young stands, but not necessarily well adapted to the local growth conditions of the individual plants (Fargione *et al.*, 2007). This could explain the poor link between cvGPPsat and species richness when species richness was the only covariate. We therefore conclude that it is more fruitful to study the functional diversity of plants (using plant traits), especially functions related to resource acquisition efficiency or tolerance to environmental stresses (capacity of species facing challenges) instead of just the number of taxonomic units (Bengtsson *et al.*, 2000). However, in long-term perspective species richness can be beneficial as a backup source in times of species loss, e.g. due to disturbances or climate change, to have other species capable to carry on ecosystem processes (Folke *et al.*, 1996).

Part of the unexplained variance of cvGPPsat by stand age and species richness could be also associated to disturbance or management, which were not documented for the sites and thereby we were not able to account for them. In summary, considering the poor link between cvGPPsat and the magnitude of changes in climate and environmental variables, one can assume that forests with older stands and higher species richness have a more stable photosynthetic capacity. Younger forests are not only more unstable but also cannot compensate for the initial carbon loss for some years after reestablishments, while old forest stands retain their capacity to sequester CO_2 for long periods (Coursolle *et al.*, 2012, Luyssaert *et al.*, 2008). Considering the global relevance of properties that contribute to the ecosystem persistence and resilience (Seddon *et al.*, 2016) especially in the context of climate change, we conclude that society will benefit from preserving our current old growth forests and their species diversity. Thereby, we might think of changing management of forest accordingly, since managed forest might not be different regarding species richness but are usually cut below 100 years (Schulze *et al.*, 2009). However, the question remains whether older and more species rich forests are also stable regarding other

EFPs than GPPsat, such as WUE or RUE. Furthermore, it remains to be seen whether stand age and species richness have the same effect in non-forest areas.

5. CONCLUSION

The diversity of plants and their vital role in biosphere-atmosphere exchanges is one of the largest sources of uncertainty in terrestrial biosphere models. Improving the predictability of these models will help to have better predictions on ecosystem functioning and consequently ecosystem services under climate change.

I expanded the newly established concept of EFPs, with reviewing different types of EFPs and their possible links to specific vegetation structure and plant traits. I state that they are ecophysiological properties of ecosystems that are relatively stable in the absence of disturbance, extreme events or stand replacement and have the response of ecosystems to climate embedded. Thereby, they are suitable means for empirically analyzing plants controls on ecosystem functioning. To the previous literature, I have added the assessment of the potential and limitation that trait information from databases can offer in understanding EFP-plant relationships considering scarce *in-situ* measurements at eddy covariance sites (FLUXNET). I show that a generalization of the both plant traits and GPPsat by using mean values fails for different reasons; high trait plasticity due to variability during the growing season in some traits and also along different environmental gradient and high IAV in GPPsat. I show when traits from global datasets are linked with site specific EFPs (i.e. photosynthetic capacity) the correlations are weak, because these approaches are missing the synchronization of plant traits and EFPs in space and time. The synchronization of photosynthetic capacity and plant traits substantially improved the correlations, because of IAV of photosynthetic capacity and the intraspecific variability of the plant traits in time and space. Although, for an optimal analysis one might need plant trait measured several time during the growing season, but still the minimalistic approach of using annual mean trait values can unfold important trait-EFP relationships. Using the *in-situ* trait information from the limited number of sites I show that the close link between photosynthetic capacity and leaf stoichiometry of C, N, and P, which is in alignment with previous studies. Further, my study has shown that photosynthetic capacity as a characteristic attribute of the ecosystems is far from constant over years in some ecosystems. In Paper 3 I show that the IAV of photosynthetic capacity is in line with the IAV of environmental factors. However, I show that it is more resilient to climate variability (lower magnitude of IAV) in older forest stands with higher species richness. As Huete 2016 states it is of high importance to consider forest age and biodiversity (e.g. species richness, functional plant traits) when vegetation response (embedded in EFPs) to climate variability is targeted for better prediction in earth system models.

“Only through an understanding of vegetation's responses to current climate variability can we improve predictions of the future consequences of such variability on our planet's ecosystems and biodiversity, as well as on our own food security and welfare.” (Huete, 2016)

6. OUTLOOK

Following the main results of studies comprising this dissertation, I promote continuous measurements of plant traits and estimation of species composition at FLUXNET sites over time, which recently has become part of the agenda of projects like NEON and ICOS. Remote sensing can contribute to acquire canopy level traits and thereby circumventing also the upscaling issue of *in-situ* plant traits and besides it can provide means to study temporal and spatial variability of plant traits in synchrony with EFPs. With the current number of different types of RS data, it could be possible in the future to refine the retrievals of biological properties by integrating information of different RS data such as LiDAR, radar (used for acquiring structural properties), hyperspectral and optical systems (that can have potential for deriving plant traits). However, measures of diversity are difficult to address by remote sensing because of resolution limitation (Jetz *et al.*, 2016). Thus we still have to rely on *in-situ* measurements. In the future, with the increase of trait measurements at the sites, I would like to analyse the relationship between the stability of GPPsat (also other EFPs like light use efficiency) and estimates of vegetation functional diversity of the sites. In addition, it would be highly interesting to understand whether other site EFPs characterizing efficiency in using water, radiation, nitrogen and carbon could explain the stability of GPPsat and whether these EFPs increase with the increase in functional diversity. Also, it would be highly relevant to include the information on biomass, canopy complexity, and different soil properties in the picture.

Nowadays the emerging new global products derived from satellite observations or modeling such as, biomass (Schepaschenko *et al.*, 2017), different soil data (Hengl *et al.*, 2017) and novel machine learning products on global upscaled half hourly GPP, latent heat and latent energy (Bodesheim *et al.*, 2018) can provide the means to test some of the realized relationships at site level at global scale.

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Dissertation
Talie Sadat Musavi
The imprint of plants on ecosystem functioning

Author contribution statement

Title:	The imprint of plants on ecosystem functioning: A data-driven approach
Journal:	International Journal of Applied Earth Observation and Geoinformation
Year of publication:	2015
DOI:	10.1016/j.jag.2015.05.009
Authors:	Talie Musavi, Miguel D. Mahecha, Mirco Migliavacca, Markus Reichstein, Martine Janet van de Weg, Peter M. van Bodegom, Michael Bahn, Christian Wirth, Peter B. Reich, Franziska Schrodt, Jens Kattge

Talie Musavi
Designed research · Wrote paper · Conceptualized paper · Analyzed data · Submitted paper · Discussed paper · Edited paper

Miguel D. Mahecha
Designed research · Conceptualized paper · Edited paper · Discussed paper

Mirco Migliavacca
Wrote paper · Edited paper · Discussed paper

Markus Reichstein
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Martine Janet van de Weg
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Michael Bahn
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Dissertation
Talie Sadat Musavi
The imprint of plants on ecosystem functioning

Author contribution statement

Title:	Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits
Journal:	Ecology and Evolution
Year of publication:	2016
DOI:	10.1002/ece3.2479
Authors:	Talie Musavi, Mirco Migliavacca, Martine Janet van de Weg, Jens Kattge, Georg Wohlfahrt, Peter M. van Bodegom, Markus Reichstein, Michael Bahn, Arnaud Carrara, Tomas F. Domingues, Michael Gavazzi, Damiano Gianelle, Cristina Gimeno, André Granier, Carsten Gruening, Kateřina Havránková, Mathias Herbst, Charmaine Hrynkiw, Aram Kalhori, Thomas Kaminski, Katja Klumpp, Pasi Kolari, Bernard Longdoz, Stefano Minerbi, Leonardo Montagnani, Eddy Moors, Walter C. Oechel, Peter B. Reich, Shani Rohatyn, Alessandra Rossi, Eyal Rotenberg, Andrej Varlagin, Matthew Wilkinson, Christian Wirth, Miguel D. Mahecha

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Designed research· Contributed analytical tools · Conceptualized paper · Edited paper · Discussed paper

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Dissertation
Talie Sadat Musavi
The imprint of plants on ecosystem functioning

Author contribution statement

Title:	Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity
Journal:	Nature Ecology and Evolution
Year of publication:	2017
DOI:	10.1038/s41559-016-0048
Authors:	Talie Musavi, Mirco Migliavacca, Markus Reichstein, Jens Kattge, Christian Wirth, T. Andrew Black, Ivan Janssens, Alexander Knohl, Denis Loustau, Olivier Roupsard, Andrej Varlagin, Serge Rambal, Alessandro Cescatti, Damiano Gianelle, Hiroaki Kondo, Rijan Tamrakar, Miguel D. Mahecha

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Designed research· Collected and processed data · Analyzed data · Contributed analytical tools · Conceptualized paper · Discussed paper · Wrote paper · Submitted paper

Mirco Migliavacca
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6.	Degree:	*Doctor rerum naturalium (Dr. rer. nat.)*	
7.	External reviewer:	Prof. Dr. Christiane Werner	Institut für Forstwissenschaften, Fakultät für Umwelt und natürliche Ressourcen, Albert-Ludwigs-Universität Freiburg, Georges-Köhler-Allee 053 / 054, 79110 Freiburg, DE christiane.werner@cep.uni-freiburg.de +49 761 203 8303
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Topic related publications and activities

Talie Musavi, Mirco Migliavacca, Markus Reichstein, Jens Kattge, Christian Wirth, T. Andrew Black, Ivan Janssens, Alexander Knohl, Denis Loustau, Olivier Roupsard, Andrej Varlagin, Serge Rambal, Alessandro Cescatti, Damiano Gianelle, Hiroaki Kondo, Rijan Tamrakar & Miguel D. Mahecha, (2017): Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity. Nature Ecology & Evolution, 1: 0048. doi:10.1038/s41559-016-0048.

Mirco Migliavacca, Oscar Perez-Priego, Micol Rossini, Tarek S. El-Madany, Gerardo Moreno, Christiaan van der Tol, Uwe Rascher, Anna Berninger, Verena Bessenbacher, Andreas Burkart, Arnaud Carrara, Francesco Fava, Jin-Hong Guan, Tiana W. Hammer, Kathrin Henkel, Enrique Juarez-Alcalde, Tommaso Julitta, Olaf Kolle, M. Pilar Martín, **Talie Musavi**, Javier Pacheco-Labrador, Andrea Pérez-Burgueño, Thomas Wutzler, Sönke Zaehle, Markus Reichstein, (2017). Plant functional traits and canopy structure control the relationship between photosynthetic CO_2 uptake and far-red sun-induced fluorescence in a Mediterranean grassland under different nutrient availability, New Phytologist, 214, 3, 1078-1091.

Talie Musavi, Musavi, T., Migliavacca, M., van de Weg, M. J., Kattge, J., Wohlfahrt, G., van Bodegom, P. M., Reichstein, M., Bahn, M., Carrara, A., Domingues, T. F., Gavazzi, M., Gianelle, D., Gimeno, C., Granier, A., Gruening, C., Havránková, K., Herbst, M., Hrynkiw, C., Kalhori, A., Kaminski, T., Klumpp, K., Kolari, P., Longdoz, B., Minerbi, S., Montagnani, L., Moors, E., Oechel, W. C., Reich, P. B., Rohatyn, S., Rossi, A., Rotenberg, E., Varlagin, A., Wilkinson, M., Wirth, C. and Mahecha, M. D. (2016): Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits. Ecology and Evolution, 6: 7352–7366. doi:10.1002/ece3.2479.

Talie Musavi, Miguel D. Mahecha, Mirco Migliavacca, Markus Reichstein, Martine Janet van de Weg, Peter M. van Bodegom, Michael Bahn, Christian Wirth, Peter B. Reich, Franziska Schrodt, Jens Kattge, (2015): The imprint of plants on ecosystem functioning: A data-driven approach. International Journal of Applied Earth Observation and Geoinformation. 43, 119–131. doi: 10.1016/j.jag.2015.05.009.

Talks

Talie Musavi, et al. (Sep/2015) Considerations on a data-driven approach to identify plant's imprint on ecosystem functioning. Ecology at the interface-13th European ecological federation conference, Rome, Italy.

Talie Musavi, et al. (Apr/2015) Considerations on a data-driven approach to identify plant's imprint on ecosystem functioning. European geoscience union (EGU) General Assembly, Vienna, Astria.

Talie Musavi et al. (Sep/2013) Linking plant traits at ecosystem scale to ecosystem functions as observed by eddy covariance measurements. TRY workshop, Leipzig, Germany.

Talie Musavi, et al. (Mar/2013) On the imprint of plants on ecosystem function, iDiv annual meeting - Linking vegetation and plant trait databases, Leipzig, Germany.

Posters

Talie Musavi, et al. (Apr/2017) The magnitude of interannual variability of ecosystem photosynthetic capacity is controlled by stand age and biodiversity. European geoscience union (EGU) General Assembly, Vienna, Astria.

Talie Musavi, et al. (Dec/2015) Can community weighted mean plant traits explain ecosystem functional properties?, First annual iDiv conference, Leipzig, Germany.

Talie Musavi, et al. (Apr/2013) Linking plant traits at ecosystem scale to ecosystem functions as observed by eddy covariance measurements, European geoscience union (EGU) General Assembly, Vienna, Astria.

Interviews

Presented paper 3 in a national press 3sat-nano (Mar/2017) Alte Wälder atmen besser, http://www.3sat.de/mediathek/?mode=play&obj=65571

Presented paper 3 in regional press in MDR Thüringen (Feb/2017)

Curriculum vitae

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Selbstständigkeitserklärung (Declaration of independent work)

Ich versichere, dass ich die Anforderungen nach §8 (2) der Promotionsordnung der Fakultät für Biowissenschaften, Pharmazie und Psychologie der Universität Leipzig eingehalten habe. Insbesondere versichere ich, dass die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind. Ich versichere, dass, außer den in der Liste der Co-Autoren genannten Personen, keine weiteren Personen bei der geistigen Herstellung der vorliegenden Arbeit beteiligt waren. Ich versichere, dass die vorgelegte Arbeit in gleicher oder in ähnlicher Form keiner anderen wissenschaftlichen Einrichtung zum Zwecke einer Promotion oder eines anderen Prüfungsverfahrens vorgelegt und auch veröffentlicht wurde.

August 17th of 2018 Talie Sadat Musavi

IMPRS GBGC
International Max Planck Research School
for Global Biogeochemical Cycles

Certificate Supplement

Ms. Talie Musavi

born on September 19, 1983

in Vienna, Austria

At the International Max Planck Research School high potential students have the opportunity to work on their Ph.D. theses in the framework of a structured programme providing excellent research conditions.
She carried out (amongst others) the following curricular activities in the respective categories and earned in total 30.2 credit points (1 CP = 25-30 hours of work ≈ 5-day block course).

	CP
Courses related to global biogeochemical cycles - Biogeochemical cycles in the earth system - an overview - Soil, soil biology & soil hydrology - Terrestrial biosphere	**∑ 3.0**
Transferable skill courses - Rules on good scientific practice - Leadership skills - Scientists need more - Presentation skills - Career planning - Grant proposal writing - Data visualization - Scientific writing	**∑ 3.3**
Skill & elective courses - Earth observation techniques - Applied statistics & data analysis - Greenclycles II: Nitrogen in the Earth System - Eddy covariance flux measurement fundamentals 2012, KIT's Institute of Meterology and Climate Research, Garmisch-Partenkirchen, Germany - Intensive R course, Leipzig, Germany - International functional traits course, Colombia	**∑ 7.9**
Outreach activities - Research stay at Vrije Universiteit Amsterdam 2012, The Netherlands and at the University Leipzig - Poster presentation at European Geosciences Union General Assembly 2013, Vienna, Austria - Oral presentation at iDiv conference 'Linking vegetation & plant trait database' 2013, Leipzig, Germany - Oral presentation at European Geosciences Union General Assembly 2015, Vienna, Austria - Oral presentation during the site visit of the reviewers of the IMPRS-gBGC, Jena, Germany - Poster presentation at iDiv conference 2015, Leipzig, Germany - Oral presentation at 13th European Ecological Federation Conference 2015, Rome, Italy - Oral presentation at GEO BON 2016, Leipzig, Germany - Oral presentation for high-school students at MPI-BGC, Jena, Germany - Organization of the PhD conference on Earth System Science 2014, Jena, Germany - TV interviews with the regional press (MDR Thüringen) and national press (ZDF)	**∑10.0**

Max Planck Institute
for Biogeochemistry

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