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.

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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.
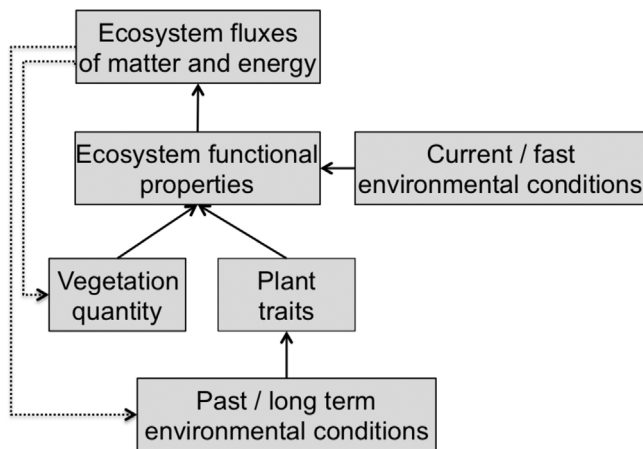
First, the identification of robust empirically derived biodiversity effects on ecosystem functioning can become valuable for model benchmarking, and allow for testing whether the assumed relationships between plant traits and ecosystem functions in models are comparable to those observed (e.g., Luo 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 influ-
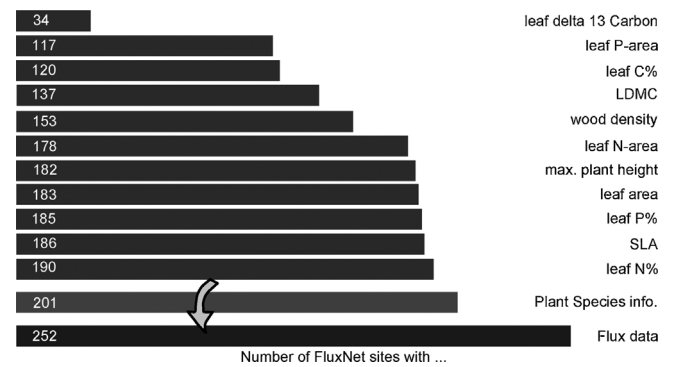
Fig. 2. The number of FLUXNET sites with traits in TRY. Bottom: Number of sites with available flux data in the FLUXNET La Thuile database. The second bar provides the number of sites with information of dominant plant species available in the FLUXNET ancillary database. The arrow indicates that we could 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).

ence of biotic and abiotic controls on the various components of the processes (Fig. 1).

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
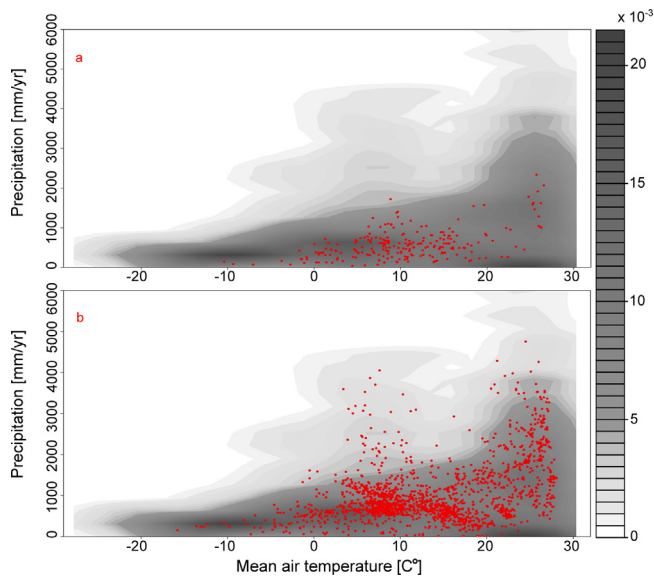
Fig. 3. The distribution of (a) FLUXNET sites, (b) measurement locations from TRY (of various plant traits) in climate space spanned by mean annual temperature and mean annual precipitation. Kernel density estimation was used to show the density of land surface pixels at $0.5° \times 0.5°$ resolution 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/m² 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:
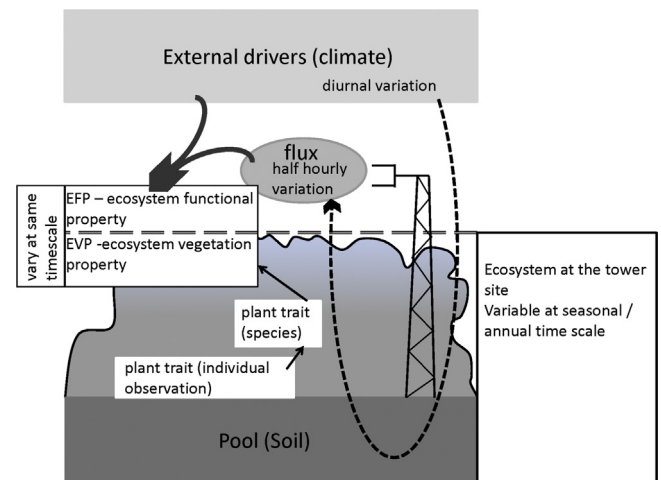
Fig. 4. Top-down and bottom up approaches to determine flux-based ecosystem functional properties (EFP) and trait-based ecosystem vegetation properties (EVPs). To link plant traits measured at the level of individual plants to EFPs, one first needs to upscale plant traits to ecosystem level.

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

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
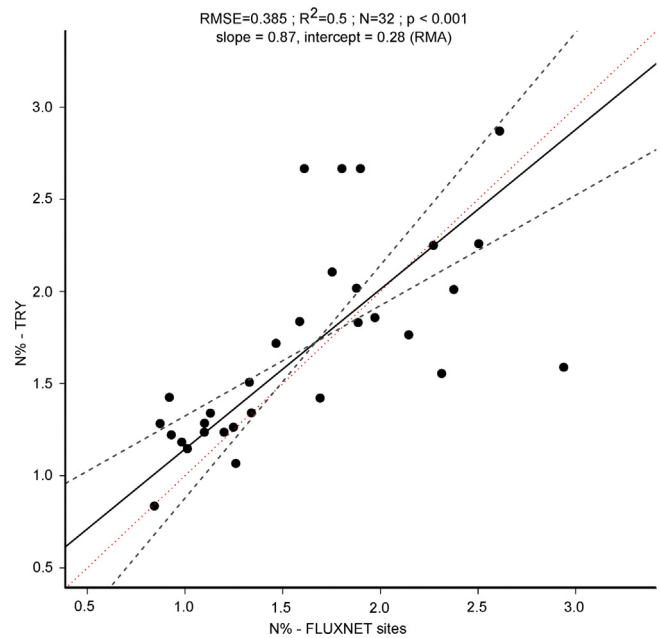

Fig. 5. Comparison of leaf nitrogen content per leaf dry mass (N%) reported in the FLUXNET ancillary database (N% – FLUXNET sites) and up-scaled using species mean trait values from the TRY database and species abundance from the FLUXNET ancillary database (N% – TRY). In case of more than one value reported 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 ($R = 0.72$).

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.

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
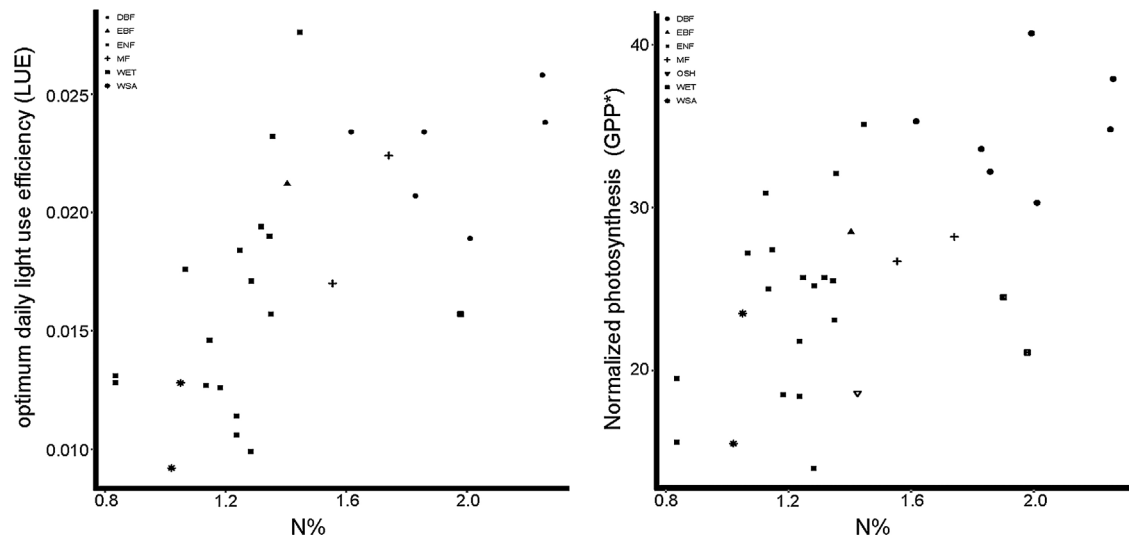
Fig. 6. Optimum daily light-use-efficiency (LUE, mol/mol) and canopy normalized photosynthesis (GPP*, μmols^{-1} m^{-2}) versus leaf nitrogen content per dry mass (N, %). LUE and GPP* are reported by Kergoat et al. (2008) for a range of eddy covariance sites with different dominant plant functional types (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; Inversion RTM; Empirical regressions	(Zhang et al., 2014) (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 Empirical models	(Houborg and Boegh, 2008) (Gitelson, 2011)	Inversion radiative transfer model Empirical models	(Hobourg and Boegh, 2008) (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 SIF	(Hilker et al., 2008; Garbulsky et al., 2014) (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.

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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