

Ecosystem functional diversity and the representativeness of environmental networks across the conterminous United States

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ARTICLE INFO

Keywords:

Environmental networks
Complex terrain
Temporal representativeness
Spatial representativeness
Ecosystem functionality
Ecosystem functional diversity

ABSTRACT

Environmental observatory networks (EONs) are coordinated efforts to provide knowledge that ultimately delivers transformational ecological science from regional to global scales. We used ecosystem functional types (EFTs), a time-varying land surface classification, as an alternative way to characterize ecosystem functional heterogeneity based on carbon uptake dynamics. We assessed the representativeness of the eddy-covariance sites of AmeriFlux and NEON, and their combined core sites (i.e., sites with long-term support) across the conterminous United States (CONUS) based on: a) the number of different EFT categories (EFT_{mode}) represented by each network, b) representativeness of the EFT inter-annual variability (EFT_{int} ; number of unique EFTs within each pixel during years 2001–2014), and c) the spatial representation of EFT_{mode} and EFT_{int} based on a maximum entropy approach (i.e., spatial functional heterogeneity). AmeriFlux represents 50% of all possible EFT categories, includes most of EFT_{int} values (9 out of 14), and represents 55% of the spatial functional heterogeneity across CONUS. NEON represents 23% of all possible EFT categories, 7 out of 14 possible EFT_{int} values, and 23% of the spatial functional heterogeneity across CONUS. The combined effort of AmeriFlux and NEON core sites represents 33% of all possible EFT categories, 7 out of 14 possible EFT_{int} values, and 46% of the spatial functional heterogeneity across CONUS. We used the NEON ecoclimatic domains to summarize our results within a geographical context. The least represented NEON ecoclimatic domains were Desert Southwest, Southern Rockies and Colorado Plateau, Great Basin, Northern Plains, and Central Plains. Our results provide insights about the potential of AmeriFlux to address questions regarding decadal and inter-annual variability of ecosystem functional heterogeneity across CONUS.

1. Introduction

Environmental observatory networks (EONs) are organizations that are affiliated in a flexible way that agree to join efforts towards a common purpose while retaining their individual objectives, resources, and management. It has been discussed that EONs are the proper structure to address complex, global and socially imperative issues

(Scholes et al., 2017). EONs promote collection and dissemination of environmental data along with efforts towards standardization of protocols, data sharing and synthesis activities. Furthermore, EONs have provided value added products that include databases, maps, conceptual models, software/analytical tools for ecological modeling, and virtual communities of practice. These products have been useful for the scientific community and policy makers to assess knowledge gaps

Abbreviations: CONUS, conterminous United States; EFTs, ecosystem functional types; EFT_{int} , ecosystem functional type inter-annual variability; EONs, environmental observatory networks; NEON, National Ecological Observatory Network

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<https://doi.org/10.1016/j.agrformet.2018.07.016>

Received 8 March 2017; Received in revised form 20 April 2018; Accepted 16 July 2018

Available online 20 August 2018

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and expand the frontiers of ecological understanding (Ciais et al., 2014; Running et al., 1999). Examples of EONs include: AmeriFlux, National Ecological Observatory Network (NEON), FLUXNET, Integrated Carbon Observation System (ICOS), the Spectral Network (SpecNET), Long Term Ecological Research Network, among others (Peters et al., 2014).

Among different research efforts, the aforementioned EONs have monitored the exchange of matter (e.g., H_2O , CO_2 , CH_4) and energy (e.g., heat and solar radiation) between terrestrial ecosystems and the atmosphere to better understand biosphere-atmosphere interactions (Baldocchi et al., 2001, 2012; Law, 2005). Consequently, representativeness studies are of prime importance to discern when, where, and at what frequency EONs have been measuring or should measure ecological processes (Baldocchi et al., 2012; Jongman et al., 2017; Vaughan et al., 2001; Vos et al., 2000). These assessments inform EONs on how to increase their utility, so the generated information could be applicable at regional and/or global scales (Ciais et al., 2014; Jongman et al., 2017; Schimel and Keller, 2015). Thus, there is a pressing need to design different scientific approaches to assess the representativeness of EONs for current and near-future applications (Lovett et al., 2007; Jongman et al., 2017).

A spatial and temporal representativeness analyses would inform where to establish new study sites and the basis to determine whether to maintain/remove current sites across networks. Thus, these analyses provide insights to improve management decisions and optimize network operability and interoperability (Vargas et al., 2017; Jongman et al., 2017). Previous studies have analyzed the spatial representativeness of national eddy-covariance networks (i.e., Canadian Carbon Program, ChinaFlux) and have concluded that the degree of fine-scale ecosystem processes across landscapes determine the number of study sites needed within a network to properly monitor those processes (Chen et al., 2012, 2011; He et al., 2015). Other studies have used cluster-based approaches to delineate spatial sampling domains and assess the spatial representativeness of EONs, and suggested arrangements of study sites of EONs such as CarboEurope-IP (Sulkava et al., 2011) and FLUXNET (Kumar et al., 2016). Representativeness studies across the conterminous United States (CONUS) have concluded that arid and semiarid ecosystems, as well as elevational changes, were under-represented by AmeriFlux during the first decade of the 2000's (Hargrove et al., 2003; Yang et al., 2008).

In general, studies on EONs representativeness have used information regarding the spatial heterogeneity of mean climate conditions and plant functional types (PFTs) composition to represent the dynamics of ecosystem processes (i.e., carbon uptake; Hargrove et al., 2003; Kumar et al., 2016), along with ecosystem productivity and seasonality (Cramer et al., 2001; Falge et al., 2002). However, recent studies have discussed that the variability of ecological processes at the ecosystem level is insufficiently explained by using the PFTs approach (Bond-Lamberty et al., 2016; Petchey and Gaston, 2006; Petrakis et al., 2017; Reichstein et al., 2014; Wright et al., 2006).

Arguably, ecosystem functionality could complement the evaluation of the representativeness of EONs by incorporating several aspects: First, information on ecosystem functionality complements descriptions based solely on climate or vegetation structure; for example, by complementing information of climate drivers with information on canopy productivity, and the temporal patterns of seasonality or phenology (Valentini et al., 1999; Alcaraz et al., 2006; Alcaraz-Segura et al., 2017). Second, the inertia of ecosystem structural attributes may delay the quantification of ecosystem responses to environmental changes, while ecosystem processes (i.e., exchange of energy and matter of an ecosystem) have a faster quantifiable response (Milchunas and Lauenroth, 1995; Mouillot et al., 2013). Third, ecosystem function offers an integrative response to environmental drivers and changes (Nagendra et al., 2013; Vaz et al., 2015). Last, functional attributes allow the qualitative and quantitative assessment of ecosystem services (Costanza et al., 1997).

We explored the applicability of Ecosystem Functional Types (EFT)

(Alcaraz et al., 2006) as an alternative way to characterize ecosystem functional heterogeneity (Alcaraz-Segura et al., 2013) and assess the representativeness of eddy covariance sites across AmeriFlux and NEON. EFTs have been conceptually defined as groups of ecosystems or patches of the land surface that share similar dynamics of matter and energy exchanges between the biota and the physical environment (Alcaraz et al., 2006; Paruelo et al., 2001). The EFT concept is analogous to the Plant Functional Type (PFT) concept but defined at a higher level of biological organization. As species can be grouped into plant functional types based on common species traits, ecosystems can be grouped into ecosystem functional types based on their similar ecosystem functioning. In practice, EFT is a time-varying land surface classification based on remote sensing vegetation indexes (i.e., MODIS-EVI) that are used to represent the spatial patterns and temporal variability of key ecosystem functional traits (i.e., productivity, seasonality and phenology) without prior knowledge of vegetation type or canopy architecture (Alcaraz-Segura et al., 2017, 2013; Cabello et al., 2013). Therefore, the ecosystem functional characterization obtained with EFTs can infer information on vegetation structure and composition (e.g., canopy architecture, vegetation type, PFT), because they constitute complementary dimensions of biodiversity complexity (Noss, 1990; Pettorelli et al., 2016).

The overarching goal of this study was to assess the representativeness of AmeriFlux and NEON based on ecosystem functional diversity characterized by EFTs across CONUS. These networks monitor a wide range of ecosystem types (Novick et al., 2017; Schimel et al., 2007), and recently have joined forces to have a long-term monitoring plan to support specific core sites. Data from both AmeriFlux and NEON support governmental and intergovernmental programs and reports, such as the North American Carbon Program (NACP), State of the Carbon Cycle Report (SoCCR), the UN Intergovernmental Panel on Climate Change (IPCC), and multiple regional to global syntheses activities. We assess the representativeness of these networks by analyzing the categorical, temporal, and spatial representation of EFTs across CONUS. Specifically, we quantify the representativeness of (a) the historical AmeriFlux archive (i.e., all sites active and inactive within the AmeriFlux network), (b) core and relocatable NEON sites, and (c) the joint effort of AmeriFlux and NEON active core sites. In light of the 20th anniversary of the AmeriFlux network, we asked three interrelated research questions: What are the spatial and temporal patterns of EFTs across CONUS? How do the historical AmeriFlux archive and planned NEON sites represent spatial and temporal patterns of EFTs across CONUS? and What is the representativeness of the joint effort of AmeriFlux and NEON core sites? We used the 17 NEON ecoclimatic domains across CONUS as geographical categories to organize and summarize the results of this study. Our EFT-based approach provides an alternative framework to previous assessments of the representativeness of EONs (Hargrove et al., 2003; Yang et al., 2008; Chen et al., 2012), it is explicitly based on ecosystem functional attributes derived from publicly available data, provides insights for the design, improvement, and growth of EONs, and it is applicable to other EONs around the world.

2. Materials and methods

2.1. Environmental observatory networks

AmeriFlux is an integrated “bottom-up” effort from principal investigators (PIs) to coordinate eddy covariance measurements across the most common ecosystems in the United States and the Americas (Keller et al., 2011; Law, 2005; Novick et al., 2017). The historical AmeriFlux archive represents the total wealth of information collected by all active and inactive study sites registered since the establishment of AmeriFlux. The historical AmeriFlux archive has a total of 207 registered study sites across the CONUS and 46 of those sites are currently considered to be core sites (revised on 7/2017). Those core sites have

received direct support and funding from the AmeriFlux Management Program (AMP) and are more likely to remain active (i.e., long-term, > 10 years) than independently funded sites (AMP, 2017). The number of active sites within the AmeriFlux archive has varied through time due to multiple factors (e.g., available funding, human resources, project timelines).

The National Ecological Observatory Network (NEON) is an ecological observatory platform that is organized under a “top-down” approach, which is designed for discovering, understanding and forecasting of ecosystem processes at a continental scale (Kampe et al., 2010; Schimel et al., 2011). NEON observations are distributed across 20 ecoclimatic domains (i.e., NEON domains), which act as spatial sampling domains and represent regions of distinct landforms, vegetation, climate and ecosystem dynamics (Keller et al., 2011; Schimel et al., 2007). NEON domains are derived from ecoclimatic variables that are clustered based on a multivariate statistical approach, the clusters are formed in a way that each of them grouped the same fraction of the total ecoclimatic variance (Hargrove and Hoffman, 1999; Keller et al., 2011). Each NEON domain is represented by one core wild land site (total 20 observatory sites, 17 within CONUS) and additional relocatable sites (39 within CONUS) to represent the ecoclimatic properties and gradients within and among NEON domains (Keller et al., 2011; Schimel et al., 2011), or address grand challenge areas as described by the National Academy of Sciences (NRC, 2001, 2005, 2007). Throughout this study, we used the 17 NEON domains across CONUS to organize and summarize our results.

Finally, AmeriFlux and NEON have a unique opportunity for long-term monitoring by joining efforts from core sites. AmeriFlux has selected 46 core sites while NEON has designed 17 core observatory sites across CONUS ($n = 68$ of AmeriFlux plus NEON core sites). Thus, there is a need to provide information of potential representativeness as these networks join long-term monitoring efforts.

2.2. Terrain complexity

We used terrain complexity as a static topographic metric derived from a digital elevation model. Complex topography is an important limitation for the eddy-covariance technique as it influences the assumption of horizontal homogeneity required for a proper estimation of biosphere-atmosphere fluxes (Göckede et al., 2004). Terrain complexity was derived from a publicly available digital elevation model consisting of a 30-arc second resolution global topographic/bathymetric grid (Becker et al., 2009). Terrain complexity was defined by calculating ± 1 standard deviation of the terrain altitude within areas of approximately $0.05^\circ \times 0.05^\circ$. We used this resolution to represent the major topographic characteristics of CONUS as this resolution is widely used in country-scale or regional studies (Löw et al., 2011; Piao et al., 2015; Chrysoulakis et al., 2003). We used this metric to describe the mean terrain complexity for each one of the NEON domains across CONUS.

2.3. Ecosystem functional types

The basis of the concept of EFTs assumes that by using time-series of satellite images it is possible to identify and map areas with similar ecosystem functional characteristics (Alcaraz-Segura et al., 2017; Alcaraz et al., 2006; Paruelo et al., 2001). Spectral indices derived from satellite images can provide information about key ecosystem functional aspects such as primary production, evapotranspiration, surface temperature and albedo (Fernández et al., 2010; Lee et al., 2013; Paruelo et al., 1997).

In this work, we used a holistic approach to assess ecosystem functioning (Jax, 2010). The regional ecosystem functional heterogeneity was characterized by means of EFTs derived from the seasonal dynamics of the Enhanced Vegetation Index (EVI), as a surrogate of carbon gain dynamics (Alcaraz-Segura et al., 2013). We used the

2001–2014 time-series of satellite images of the EVI from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) product MOD13C2 with a spatial resolution of $0.05^\circ \times 0.05^\circ$ across CONUS. We used this resolution to characterize the patterns at the country scale as done in other studies (Löw et al., 2011; Piao et al., 2015; Chrysoulakis et al., 2003). EFTs were derived from three meaningful metrics of the EVI seasonal curve related to the dynamics of terrestrial carbon gains: a) annual mean (EVI_{Mean}) as an estimator of primary production; b) EVI seasonal coefficient of variation (EVI_{sCV}) as a descriptor of seasonality; and c) the month of the annual maximum EVI value (DMAX) as an indicator of phenology. Those three metrics represent more than 80% of variance in the annual EVI time series (Alcaraz et al., 2006; Paruelo et al., 2001). The range of values of each EVI metric was divided into four intervals, giving a potential number of 64 EFTs as previously done (i.e., $4 \times 4 \times 4 = 64$; Alcaraz-Segura et al., 2013). To obtain the intervals for EVI_{mean} and EVI_{sCV}, we extracted the first, second, and third quartiles for each year, and then calculated the inter-annual mean of each quartile. For EVI_{DMAX}, the four intervals agreed with the four seasons of the year (Alcaraz-Segura et al., 2013).

We labeled all 64 EFT categories using a previously published nomenclature, where two letters and one number describe each category (Alcaraz-Segura et al., 2017; Paruelo et al., 2001). Therefore, each EFT category is a summary of the information contained in the three EVI metrics for each $0.05^\circ \times 0.05^\circ$ grid pixel. The first letter (capitalized) represents the EVI_{Mean}, which ranged from A (low primary productivity) to D (high primary productivity). The second letter represents EVI_{sCV}, which ranged from a (high seasonality) to d (low seasonality; Alcaraz-Segura et al., 2013). The third position is a number that represents DMAX, which indicates the phenology stage during the year (1–4: spring, summer, autumn, and winter, respectively, Alcaraz-Segura et al., 2013). For example, Aa1 represents an EFT category of low productivity, high seasonality and with a growing season with a spring maximum. In contrast, Dd2 represents an EFT with a high productivity, low seasonality and a growing season with summer maximum.

2.4. Network representativeness analyses

2.4.1. Categorical representativeness

To summarize the spatial heterogeneity of ecosystem functioning for the 2001–2014 period, we calculated the mode of the annual EFT maps. We refer to this as the EFT_{mode} and consequently it corresponds to the most dominant EFT for each pixel during the 14-year period. The categorical representativeness analysis evaluated whether each one of the EFT_{mode} categories found across CONUS was represented by: (a) the historical AmeriFlux archive; (b) NEON sites; or (c) AmeriFlux and NEON core sites. In addition, we analyzed how the AmeriFlux network has represented the EFT categories as sites have been added or became inactive in the network throughout the 2001–2014 period.

2.4.2. Temporal representativeness

EFT categories can change through time in a particular pixel as they represent annual dynamics of terrestrial carbon gains within each pixel across CONUS. Thus, we used the number of unique EFTs occurring within each pixel throughout the 2001–2014 period as an indicator of the inter-annual variability in ecosystem functioning (EFT_{int}). For example, if a pixel displayed three unique EFT categories from 2001 to 2014, then EFT_{int} was 3; despite if one EFT was more abundant than the other two. An EFT_{int} of 14 meant that every year there was a unique EFT within that pixel. The temporal representativeness analysis evaluated whether different values of inter-annual variability (EFT_{int}) were covered by: (a) the historical AmeriFlux archive; (b) NEON sites; or (c) AmeriFlux and NEON core sites.

2.4.3. Spatial representativeness

We assessed the spatial functional heterogeneity of the network

using a probability distribution technique based on maximum entropy distribution (Phillips et al., 2004, 2006). We used this approach to express the suitability of the study sites to monitor the range of ecosystem functional heterogeneity across CONUS. The maximum entropy approach (Maxent) is largely used in estimating the relationship between spatial observations (i.e., site locations) and environmental or spatial properties (i.e., EFT_{mode} and EFT_{int}) associated with those locations across a well-defined geographic region (i.e., CONUS). Entropy can be seen as a measure of dispersedness, while the maximum entropy approach maximizes the entropy distribution of a set of environmental properties within a geographic space (Elith et al., 2011). Here, we performed a Maxent analysis for: (a) the historical AmeriFlux archive; (b) NEON sites; and (c) AmeriFlux and NEON core sites, to represent the spatial functional heterogeneity of EFT_{mode} and EFT_{int} (i.e., environmental properties) across CONUS. The randomness of the Maxent model was tested using the area under the curve (AUC) of the training data (i.e., EFT_{mode} and EFT_{int}) and that of a random prediction as recommended (Fielding and Bell, 2016; Hijmans, 2012; Liu et al., 2011; Phillips et al., 2004). A random classification has a typical value for the area under the curve equal to 0.5, while a non-random classification (i.e., distinction between potential presence and absence) has values closer to 1. The final result derived from our Maxent model are expressed using a Kappa index derived from cross-validation, where Kappa index of 1 indicates areas with characteristics that are more likely to be monitored by the study sites (i.e., sampling locations). We reported our results on spatial representativeness as the percentage ratio of those pixels with a Kappa index equal to 1 divided by the total number of pixels for each NEON ecoclimatic domain. See Supplementary Methods for more detail.

Table 1

Dominant Ecosystem Functional Types (EFT_{mode}), mean EFT inter-annual variability (EFT_{int}) and mean terrain complexity for each NEON ecoclimatic domain across the conterminous United States.

NEON ecoclimatic domain	Two most dominant EFT_{mode}	Mean EFT inter-annual variability (EFT_{int})	Mean terrain complexity
Northeast	Db2, Da2	3.3	63.1
Mid Atlantic	Db2,Dc2	3.8	30.1
South East	Dc2,Dd2	3.9	8.1
Atlantic Neotropical	Dd2,Cd2	4.9	1.7
Great Lakes	Ca2,Cb2	3.5	13.9
Appalachian and Cumberland Plateau	Db2,Da2	3.7	54.4
Prairie Peninsula	Ca2,Cb2	3.5	15.1
Ozark Complex	Db2,Dc2	4.2	22.7
Northern Plains	Ba2,Bb2	4.7	35.1
Central Plains	Bc2,Bb2	6.6	25.1
Southern Plains	Cc1,Cc2	6.7	20.1
Northern Rockies	Cd2,Bd2	5.1	207.6
Great Basin	Ad1,Ac1	5.6	142.6
Southern Rockies and Colorado Plateau	Ad2,Bd2	5.2	147.0
Desert Southwest	Ad1, Ad2	6.0	120.1
Pacific Northwest	Dd2,Cd2	3.5	194.2
Pacific Southwest	Bd1,Cd1	4.7	168.0

Note: The EFT_{mode} represents the summary of the spatial heterogeneity of ecosystem functioning of the 2001–2014 period. EFT_{int} represents the average number of unique EFT that occurred within an ecoclimatic domain during the 2001–2014 period. Terrain complexity was defined by calculating the ± 1 standard deviation of the terrain altitude within areas of approximately $0.05^\circ \times 0.05^\circ$.

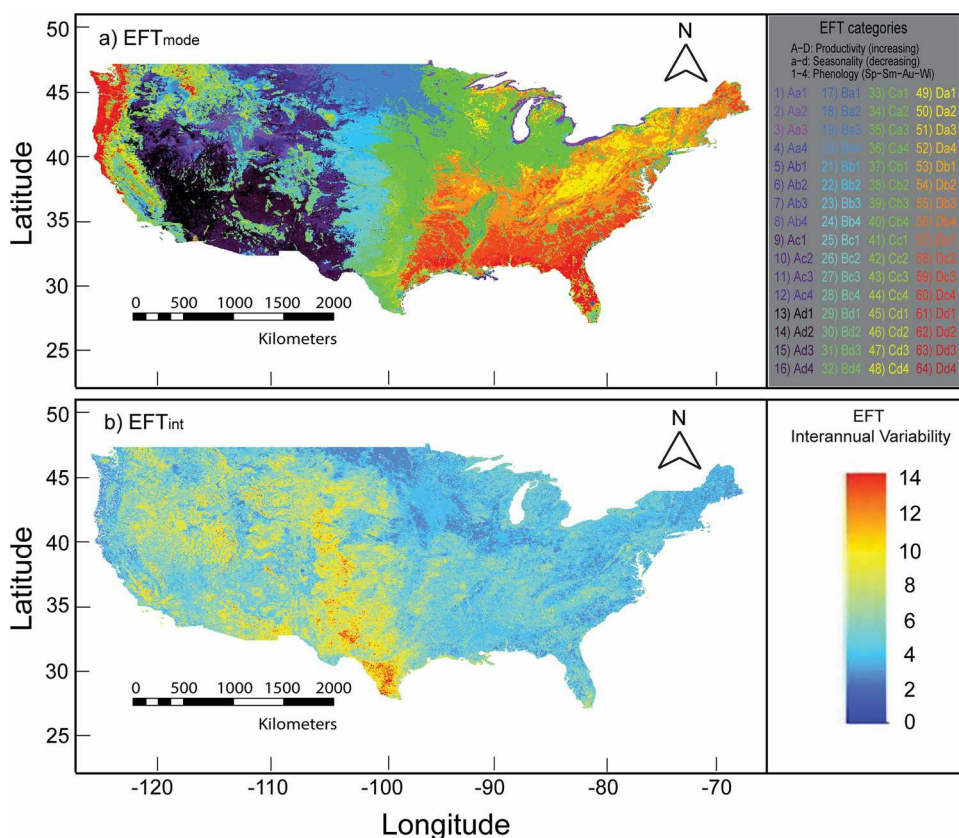


Fig. 1. Spatial distribution and inter-annual variability of Ecosystem Functional Types (EFTs) across the conterminous United States (CONUS) during the 2001–2014 period: a) spatial patterns of the mode of EFTs for the 2001–2014 period (EFT_{mode}); and b) inter-annual variability of EFTs (EFT_{int} ; i.e., number of unique EFTs that occurred in the 14-year period), where red areas represent high inter-annual variability and blue areas low inter-annual variability. EFTs were calculated from Moderate Resolution Imaging Spectroradiometer Enhanced Vegetation Index (MODIS-EVI). Capital letters correspond to the EVI annual mean (EVI_Mean) level, ranging from A to D for low to high productivity. Small letters show the seasonal coefficient of variation (EVI_sCV), ranging from a to d for high to low seasonality for carbon uptake. The numbers indicate the season of maximum EVI (DMAX): (1) spring, (2) summer, (3) autumn, (4) winter. The map uses the $0.05^\circ \times 0.05^\circ$ Global Climate Modeling Grid in geographic projection with Datum WGS84.

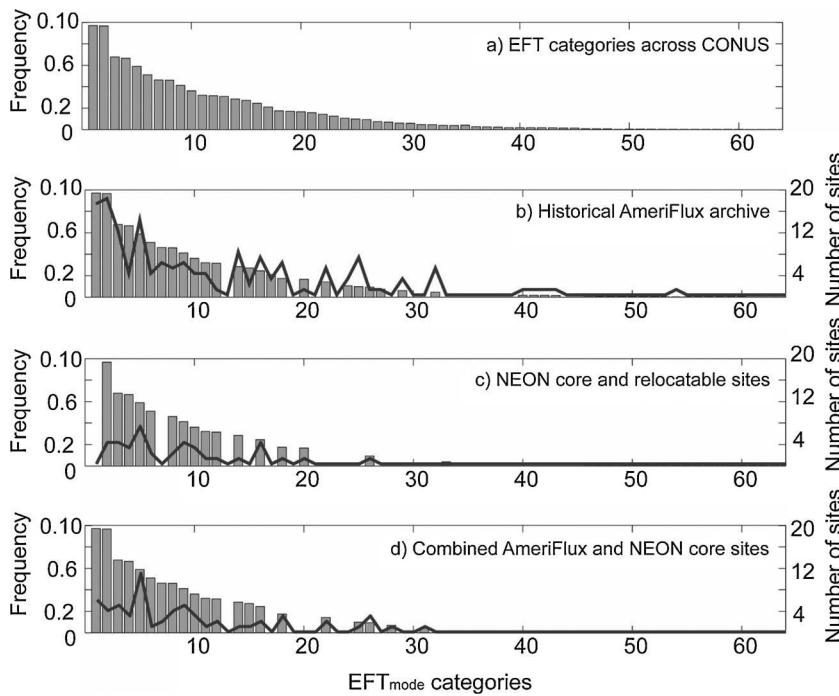


Fig. 2. Categorical representativeness of the Ecosystem Functional Type mode (EFT_{mode}) of the 2001–2014 period across CONUS. EFT_{mode} corresponds to the most dominant EFT for the 14-year period at each pixel. a) Frequency of EFT_{mode} across CONUS; b) EFT_{mode} categories represented by the historical AmeriFlux archive; c) EFT_{mode} categories represented by current AmeriFlux and NEON core sites. Grey bars indicate represented frequency of EFT_{mode} categories, and lines represent the number of study sites in each EFT_{mode} category. Note that missing bars in b, c and d illustrate that those EFT_{mode} categories are not represented by the networks.

3. Results

3.1. Categorical representativeness

The EFT_{mode} for the 2001–2014 period across CONUS (Fig. 1 and Table 1) showed that ecosystems with high productivity were located in the NEON ecoclimatic domains of Northeast, Mid-Atlantic, Southeast, Appalachians and Cumberland Plateau, and the Ozark Complex. In contrast, ecosystems with low productivity were found at the Great Basin, Desert Southwest and Southern Rockies, and Colorado Plateau. The ecosystems with the highest seasonality were common in the Great Lakes, Prairie Peninsula, Northern Plains, Northeast, and Appalachians and Cumberland Plateau; while ecosystems with the lowest seasonality occurred in the South East, Central Plains, and Southern Plains. Most ecoclimatic domains were dominated by ecosystems with growing season with summer maxima, except for the Great Basin, Pacific Southwest and Desert Southwest where the growing season maxima was reached during spring.

The historical AmeriFlux archive covered 31 out of the 64 possible EFT_{mode} categories (Fig. 2). In contrast, NEON sites only represented 16 EFT_{mode} categories (Fig. 2c), and the combined efforts of the AmeriFlux and NEON core sites represented 21 EFT_{mode} categories (Fig. 2d). The frequency distribution of the number of sites (across AmeriFlux and NEON networks) did not follow the frequency distribution of EFT_{mode} categories (Fig. 2). In other words, the most abundant EFT_{mode} categories across CONUS did not have the largest number of monitoring sites.

Year-specific categorical representativeness of AmeriFlux changed through time as eddy covariance sites have been added or became inactive from the network (Table 2). Despite the sustained increase in the number of eddy covariance sites across the years, the number and EFT_{mode} categories represented by AmeriFlux have remained relatively constant since 2007. The most common EFT_{mode} categories represented by AmeriFlux are *Ca2* (i.e., ecosystems with medium high productivity, very high seasonality, and summer maximum) and *Db2* (i.e., ecosystems with very high productivity, low seasonality, and summer maximum).

Table 2

Changes in categorical representativeness of the AmeriFlux network in terms of number of EFT_{mode} categories represented by active sites for each year between 2001 and 2014.

Year	Number of sites	Number of EFT_{mode} categories	Most represented EFT_{mode} categories
2001	37	16	Dd2 (6), Ca2 (5)
2002	46	17	Dd2 (7), Ca2 (7)
2003	50	19	Db2 (8), Dd2 (7)
2004	77	24	Db2 (13), Ca2 (10)
2005	78	24	Ca2 (11), Db2 (10)
2006	81	26	Ca2 (13), Db2 (10)
2007	99	28	Ca2 (14), Db2 (11)
2008	98	29	Ca2 (14), Db2 (9)
2009	108	29	Ca2 (20), Db2 (9)
2010	107	30	Ca2 (20), Db2 (9)
2011	111	30	Ca2 (22), Db2 (9)
2012	117	31	Ca2 (21), Db2 (10)
2013	124	31	Ca2 (21), Db2 (11)
2014	131	31	Ca2 (20), Db2 (11)

Note: numbers in parenthesis under "Most represented EFT_{mode} categories" represent number of active sites for each EFT_{mode} category. For example, during year 2014 there were 20 active sites in the AmeriFlux network for EFT_{mode} category *Ca2*.

3.2. Temporal representativeness

We mapped the patterns of EFT_{int} (i.e., number of unique EFT that occurred in a pixel during the 2001–2014 period) across CONUS (Fig. 1b). The highest EFT_{int} was found in the Southern and Central Plains, while the lowest variability was found in the Great Lakes, Prairie Peninsula, Pacific Northwest, and Northeast (Table 1). Across CONUS, the most common values of EFT_{int} were between 3 and 5, EFT_{int} values < 3 or > 9 were less common, and the maximum value of EFT_{int} was 14 (Fig. 3a).

The historical AmeriFlux archive included information of sites with EFT_{int} values between 1 and 9, and where values between 3 and 5 were

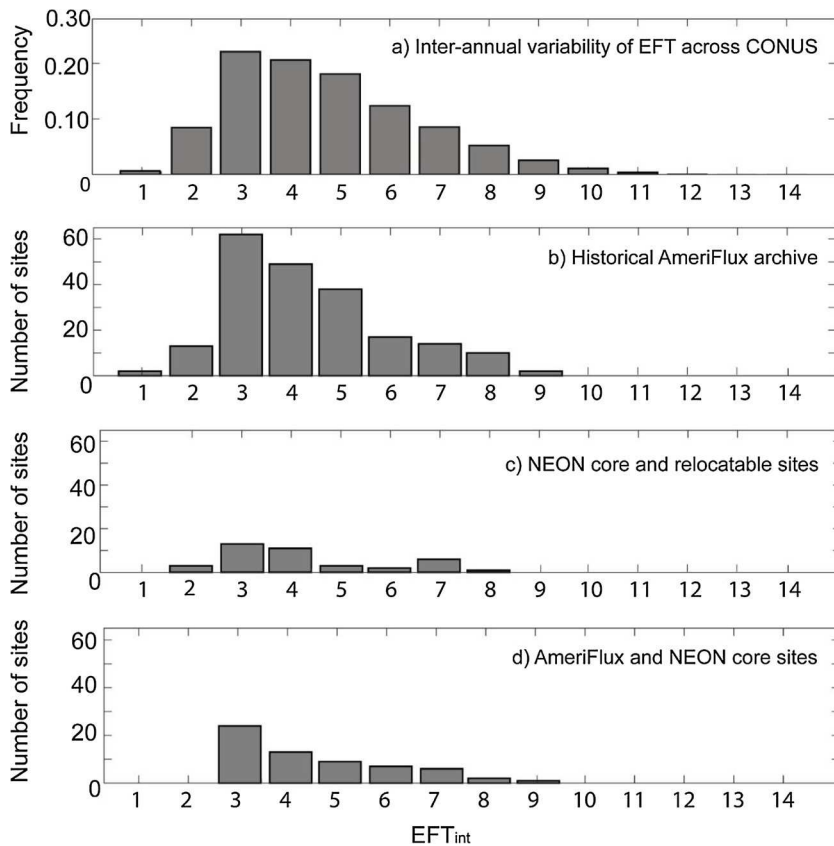


Fig. 3. Representativeness of the inter-annual variability of EFTs during the 2001–2014 period across CONUS. Inter-annual variability of EFTs is expressed as the number of unique EFTs occurring in each 0.05° pixel during the 14-year period (EFT_{int}). (a) Histogram distribution of EFT_{int} values across CONUS. Number of sites representing each value of EFT_{int} for (b) historical AmeriFlux archive; (c) NEON sites; and (d) current AmeriFlux and NEON core sites. X-axes represent EFT_{int} values for each panel.

also the most common (Fig. 3b). Nearly 80% of study sites within the AmeriFlux network were located at EFT_{int} values between 3 and 6; 7% at EFT_{int} values ≤ 2 ; and 12% at EFT_{int} values ≥ 7 . Across NEON sites, EFT_{int} values 3, 4 and 7 were the most common (Fig. 3c). The combined effort of AmeriFlux and NEON core sites did not include EFT_{int} values < 3 or > 9 , despite the fact that EFT_{int} value 2 is relatively abundant across CONUS (Fig. 3a).

Individual monitoring sites within the historical AmeriFlux archive had between 1 and 28 years of available eddy-covariance information (Fig. 4). Most study sites (62) were located at an EFT_{int} value of 3 (Fig. 3b and Fig. 4), and 42 of these sites had > 3 years of available information (Fig. 4). Sites at EFT_{int} values of 4 (49 sites) and 5 (38 sites) were also common, with 29 and 24 sites having more than 4 and 5 years of available information, respectively. Only one site with > 9 years of information was located at an EFT_{int} value of 9 (Fig. 4).

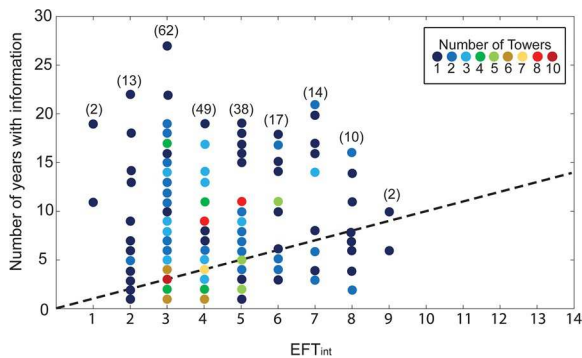


Fig. 4. Representativeness of the inter-annual variability of EFTs (i.e., EFT_{int}) and number of years with information in the historical AmeriFlux archive. The X-axis represents values of EFT_{int} , and the Y-axis represents the number of years with eddy covariance information per site available in the historical AmeriFlux archive. Colors represent the number of sites that report a specific number of years with eddy covariance information for each value of EFT_{int} . Numbers in parenthesis indicate the number of total study sites available for each EFT_{int} value within the historical AmeriFlux archive. For example, there is a total of 2 sites in the historical AmeriFlux archive (number in parenthesis) with an EFT_{int} value of 9 (see X-axis), where one single site (color of the circle [dark blue]) has 6 years of information (see Y-axis) and a second single site (color of the circle [dark blue]) has 10 years of information (see Y-axis). The dashed line represents the threshold where the number of years of available information is equal to EFT_{int} .

3.3. Spatial representativeness

The maximum entropy analysis provides information on the representativeness of AmeriFlux, NEON and the combined core sites to monitor the spatial functional heterogeneity. The overall spatial representativeness is expressed as the ratio of all pixels with a Kappa index equal to 1 divided by the total number of pixels across each NEON ecoclimatic domain. This resulted in a spatial representativeness of 55% by the historical AmeriFlux archive, 23% by NEON sites, and 46% by the combined AmeriFlux and NEON core sites of the CONUS surface (Table 3 and Supplementary Fig. 1). The most represented ecoclimatic domains by the historical AmeriFlux archive were Great Lakes, Prairie Peninsula, Northeast, and Appalachians and Cumberland Plateau whereas the least represented were Desert Southwest, Northern Plains and Great Basin (Table 3 and Supplementary Fig. 1). NEON sites had high spatial representation across the Northeast, Appalachians and Cumberland Plateau and Mid Atlantic domains, whereas the least represented domains were Desert Southwest, Northern Plains, and Southern Rockies and Colorado Plateau (Table 3). The most represented ecoclimatic domains by the combined effort of AmeriFlux and NEON core sites were Pacific Northwest, Northeast and Mid-Atlantic, whereas the least represented were Desert Southwest, Northern Plains, and Southern Rockies and Colorado Plateau (Table 3 and Supplementary Fig. 1).

Maxent model was tested using the area under the curve (AUC; see

Table 3

Spatial representativeness for each network and the combined core sites across NEON ecoclimatic domains. Each percentage corresponds to the ratio of pixels with a kappa index equal to 1 divided by the total number of pixels for each NEON domain.

NEON ecoclimatic domain	Historical AmeriFlux archive (%)	Core and relocatable NEON sites (%)	AmeriFlux and NEON core sites (%)
Northeast	89	85	84
Mid Atlantic	58	68	64
South East	55	54	58
Atlantic Neotropical	79	25	36
Great Lakes	92	30	46
Appalachians and Cumberland Plateau	89	70	58
Prairie Peninsula	91	10	24
Ozark Complex	63	52	44
Northern Plains	12	1	5
Central Plains	39	1	31
Southern Plains	55	8	40
Northern Rockies	48	12	40
Great Basin	20	4	17
Southern Rockies and Colorado Plateau	26	1	16
Desert Southwest	6	1	6
Pacific Northwest	83	39	87
Pacific Southwest	73	23	63

Supplementary methods). The AUC for the historical AmeriFlux archive (0.65), NEON sites (0.59), or AmeriFlux and NEON core sites (0.63) were always higher than the AUC of a random prediction (0.5); thus, supporting the applicability of the maximum entropy analysis. The relative contribution of each variable to the maximum entropy analyses was 88% for EFT_{mode} and 12% for EFT_{int} ; consequently, our results for spatial functional heterogeneity have a larger weight on the information contained in the spatial distribution of EFT_{mode} .

4. Discussion

4.1. Categorical representativeness

Our results demonstrate how the characterization of ecosystem functional heterogeneity made by EFTs at the regional scale can be applied to assess the representativeness of EONs. EFT_{mode} showed a contrasting pattern of carbon gain dynamics across CONUS. The ecoclimatic domains located in temperate humid conditions (Bailey, 1983) such as Northeast, Appalachian and Cumberland Plateau, Mid Atlantic, South East, Atlantic Neotropical and the Pacific Northwest showed high productivity, low seasonality, and had a growing season with summer maxima (Fig. 1a and Table 1). In contrast, ecoclimatic domains located in grasslands and open-shrublands under dry conditions such as Great Basin, Desert Southwest and the Southern Rockies and Colorado Plateau showed the lowest productivity, low seasonality, and the growing season was tightly coupled with water availability (e.g., spring in Mediterranean regions, summer across the North American Monsoon region).

Our results demonstrate that ecosystem functional heterogeneity is well represented by the historical AmeriFlux archive, which included nearly 50% of all possible EFT_{mode} categories across CONUS. The AmeriFlux network, as a bottom-up community effort, has experienced the removal and addition of eddy covariance sites over the last two decades. Thus, at any given year, some EFT_{mode} categories could have been added or removed based on the location of active eddy covariance sites. The network has constantly increased the number of active sites across years, but the number of represented EFT_{mode} categories has remained relatively constant (~ 30 categories) since 2007. Furthermore, ecosystems with very high or medium high productivity,

very high or low seasonality, and with growing seasons with summer maximum (Ca2, Db2) have been the most commonly monitored since 2005, likely due to the interest on large terrestrial carbon sinks (Running et al., 1999). It is likely that AmeriFlux will continue providing information from these and other EFT_{mode} categories as researchers address unexplored ecological questions across ecosystems.

The long-term perspective of AmeriFlux and NEON core sites will provide information of the 12 most dominant EFT_{mode} categories across CONUS (33% of all possible EFT_{mode} categories). That said, the probability distribution of these core sites did not follow the probability distribution of EFT_{mode} categories across CONUS (Fig. 2). This means that the most abundant EFT_{mode} categories do not necessarily have the largest number of study sites. Looking forward, these results open questions about network design, such as: a) Should new monitoring sites emphasize research on ecosystems within EFTs with the most frequency of occurrence (i.e., Ca2 and Db2)? or b) Should new monitoring sites aim to represent the probability density distribution of ecosystem functional heterogeneity across CONUS? Long-term monitoring core sites are and will continue to be limited due to the financial and pragmatic requirements for their operation, but the joint effort by AmeriFlux and NEON provides an exciting and unique opportunity for decadal-scale information that otherwise would not be available.

4.2. Temporal representativeness

The inter-annual variability of EFTs showed contrasting patterns across CONUS. We postulate that NEON ecoclimatic domains with lower EFT_{int} values are typified by forested ecosystems in temperate humid regions, which are mainly constrained by temperature, light and nutrient cycling (Allen and Chapman, 2001; Nemani et al., 2000; Vargas et al., 2010). In contrast, ecoclimatic domains with high EFT_{int} values are represented by grasslands and shrublands across water-limited regions, and are sensitive to changes in timing and magnitude of precipitation that substantially influence carbon gain dynamics (Arredondo et al., 2016; Schwinning et al., 2004; Vargas et al., 2010). Quantifying EFT_{int} values is important as recent studies have highlighted the need of long-term flux data records to describe the inter-annual variability of carbon uptake (Novick et al., 2017; Zscheischler et al., 2016).

We highlight that EFT_{int} represents the number of changes in EFT categories within a single pixel. This does not necessarily mean that changes in EFTs are changes in vegetation structure or composition (e.g., changes from a forest to a grassland). Changes in EFT categories could be the result of ecosystem structural changes such as those imposed by land-use change (e.g., deforestation), but also the result of more subtle changes. For example, a pixel could represent a grassland throughout our study period (i.e., 2001–2014), but displayed a EFT_{int} value of 5. This means that the plant functional type and vegetation structure was the same (i.e., grasslands) throughout the study period, but there were changes in terms of productivity, seasonality and phenology that resulted in different EFT categories. This could happen for instance, as a result of droughts, floods or fires. In addition, the same EFT_{int} value of 5 could be present in grasslands, shrublands, or evergreen forests, but it only indicates unique changes in EFT categories throughout the study period. Thus, site-specific interpretation of our results should take into consideration the underlying plant functional type and history (land use or weather) at a location of interest. Overall, our results highlight the importance of network representativeness to understand how changes in biophysical forcing factors could influence ecosystem functional heterogeneity across regions and the whole CONUS. We recognize that this approach requires further development and research, but also acknowledge that the addition of EFT information has already improved the performance of regional climate (Lee et al., 2013) and biodiversity models (Alcaraz-Segura et al., 2017, 2013).

The historical AmeriFlux archive has a good representation of the

inter-annual variability of EFTs across CONUS. Most eddy covariance sites within AmeriFlux have EFT_{int} values between 3 and 6, which are also the most common values across CONUS. In contrast, NEON lacks representation of EFT_{int} values < 3 and has a higher representation of sites with an EFT_{int} value of 7. The long-term perspective of AmeriFlux and NEON core sites will provide information of EFT_{int} values between 3 and 9. Both the historical AmeriFlux archive and NEON do not have sites at EFT_{int} values > 9, regardless there are pixels with EFT_{int} values up to 14 across CONUS. We recognize that areas with high EFT_{int} values are rare, and properly monitoring their long-term carbon dynamics will require decades due to their high inter-annual variability. Long-term monitoring of ecosystems with low EFT_{int} values could provide information about ecosystem resiliency from weather variability and disturbances; while monitoring ecosystems with high EFT_{int} values could provide information from the most sensitive ecosystems in terms of carbon uptake dynamics.

Many AmeriFlux study sites have more years with site-specific measurements than the annual temporal variability of EFT (EFT_{int}) associated to the location of those sites (Fig. 4). For example, the network has information of 62 sites located at an EFT_{int} value of 3, but > 40 sites have over 3 years of site-specific measurements. On one end of the spectrum, there are 2 sites with over 10 years of site-specific measurements at the EFT_{int} value of 1, where questions about ecosystem stability and resiliency could be asked. On the other end of the spectrum, there are 4 sites (out of 10) at the EFT_{int} value of 8 with over 10 years of site-specific measurements, where we can ask questions about sensitivity and variability of ecosystem processes. Overall, our results support that the AmeriFlux network has unique information to address questions regarding inter-annual variability of carbon gain dynamics, ecosystem stability and resiliency across the CONUS.

4.3. Spatial representativeness

Our results show that the historical AmeriFlux archive includes information of ecosystem functional heterogeneity for 55% of the CONUS. This contrast with the 23% of the CONUS represented by NEON sites, but the sites in this network are fewer and with a long-term perspective than the wide bottom-up effort of AmeriFlux. It is important to mention that the combined effort of AmeriFlux and NEON core sites represents 46% of CONUS surface, demonstrating that few but strategically located sites could represent a large proportion of the continental ecosystem functional heterogeneity.

In general, AmeriFlux and NEON (individually) do not properly represent ecosystems dominated by grasslands and shrublands across water-limited ecosystems. These results are in accordance with previous studies that identified an overall high representativeness of temperate forested ecosystems by the AmeriFlux network (Hargrove et al., 2003; Yang et al., 2007), but to our knowledge no assessment has been done for the NEON eddy covariance sites. Historically, there has been a (bias) better representation of ecosystems with larger potential to uptake and store carbon, likely due to the large interest on quantifying and characterizing the processes that control large terrestrial carbon sinks (Cramer et al., 2001; Luo et al., 2007; Running et al., 1999). We highlight that these forested lands are of critical importance for the regional carbon budget of North America (Hayes et al., 2012) and the world (Pan et al., 2011). That said, there is an increasing interest to improve the representation of water-limited ecosystems in ecosystem processes-based models (Biederman et al., 2016; Vargas et al., 2013) as is important to understand how their inter-annual variability contributes to the regional-to-global carbon balance (Ahlström et al., 2016; Biederman et al., 2016; Poulter et al., 2014).

Our results provide evidence that there is a lack of representation by the historical AmeriFlux archive and NEON sites across the Desert Southwest, Southern Rockies and Colorado Plateau, Great Basin, Northern Plains, and Central Plains ecoclimatic domains. These regions have been recognized to have wide range of bioclimatic drivers

(Gilmanov et al., 2005; Zhang et al., 2010) and anthropogenic activities such as land-use-change (Chuluun and Ojima, 2002). Thus, research in these regions represent an opportunity to better understand socio-ecological processes and the nexus of food, energy, and water systems (Bazilian et al., 2011).

The combined effort of the AmeriFlux and NEON core sites lacks representation of the Prairie Peninsula ecoclimatic domain. These core sites have good representation of the CONUS surface (46%) and almost represent the same ecoclimatic domains as the historical AmeriFlux archive and NEON sites (Table 3 and Supplementary Fig. 1). The Midwest corn belt of the United States produces over 35% of the global corn production and is part of the Prairie Peninsula (Graham et al., 2007; Ort and Long, 2014). Hence, the ecosystem functional heterogeneity of this region represents a network limitation when long-term carbon dynamics for agro-ecosystems are considered for the spatial representativeness of the CONUS. The lower representation at this and other ecoclimatic domains brings attention to the limitations to cover a heterogeneous landscape with few core sites.

Finally, complex topography creates ecological niches that could influence carbon dynamics across topographic gradients and landscapes (Katul et al., 2006; Swanson et al., 1988). For example, it has been estimated that nearly 70% of the carbon uptake across the western CONUS occurs at high elevation, with about 50–85% taking place on complex terrain (Schimel et al., 2002). Unfortunately, complex topography is a large limitation for implementation of the eddy covariance technique as it is often violates assumptions for the technique for annual carbon budgets and promotes advection processes (Göckede et al., 2004). Congruently, three of the least represented NEON ecoclimatic domains are also characterized by complex topography (Southern Rockies and Colorado Plateau, Great Basin, Desert Southwest; Table 1). These results support previous reports that suggest AmeriFlux lacks representation of the western mountain ranges of the CONUS (Hargrove et al., 2003). We argue that monitoring ecosystem functional heterogeneity across complex terrain represents a final frontier for AmeriFlux and NEON networks that could limit an accurate spatial inference of carbon dynamics across CONUS.

4.4. Considerations and network inferences

We provide an alternative approach to assess representativeness of EON's based on metrics of ecosystem functional heterogeneity that complements previous assessments based on vegetation climatic or structural features. We interpret EVI dynamics as a surrogate for ecosystem carbon gain dynamics. There are known limitations when using EVI, especially in evergreen and water-limited ecosystems, that could influence the assumption that EVI is closely related to carbon gain dynamics (Ha et al., 2015; Sims et al., 2014). Hence, our EFT classification may inherit the intrinsic limitations of EVI and consequently there could be area-specific biases; for example: a) areas with apparent low inter-annual variability (i.e., EFT_{int}) could actually have larger inter-annual variability (e.g., evergreen forests); and b) areas with apparent low seasonality could in fact have larger seasonality (e.g., grasslands and shrublands). That said, there is strong evidence that EVI is still the best predictor for describing carbon gain dynamics at the continental scale (Rahman et al., 2005; Sims et al., 2006). Arguably, there is no definitive and universal definition for PFTs where there could be different criteria to develop classifications (Ustin et al., 2004). Similarly, there could be different criteria to develop classifications of EFTs (e.g., carbon gains, water balance, energy balance). We propose that the current limitations for calculation of EFTs based on EVI as a surrogate of carbon gain could be addressed with long-term remote sensing information on solar induce chlorophyll fluorescence (Joiner et al., 2011), or new pigment indexes sensitive to seasonality of evergreen conifers (Gamon et al., 2016).

The historical AmeriFlux archive is unique for representing regional biosphere-atmosphere interactions (focused in CONUS) and is only rivaled by information from European networks. The number of active

sites has consistently grown every year, but the number of sites sharing data has decreased since 2005 (Novick et al., 2017). This means that our representative analysis of the historical AmeriFlux archive is only applicable if all sites share the available data (Fig. 4). Our analyses of the combined effort of AmeriFlux and NEON core sites likely represent the long-term representativeness of carbon uptake dynamics across CONUS, as data from these sites is available and funding for operation is less uncertain. New representativeness analyses could be based on other ecosystem functional processes such as ecosystem CO₂ losses to the atmosphere (i.e., ecosystem respiration), energy balance, water fluxes, or dynamics of non-CO₂ gases. Finally, an aspirational goal of AmeriFlux is to provide a collaborative and networking platform for all eddy-covariance sites across the Americas. This effort has fundamental benefits because understanding of global environmental challenges is only reached through international programmatic and scientific collaborations (Vargas et al., 2012); therefore, there are open research questions for the potential representativeness of the joint efforts of all regional networks across the Americas.

5. Conclusions

We used EFTs as an alternative approach to assess the representativeness of AmeriFlux and NEON to monitor ecosystem functional heterogeneity across CONUS. This analysis complements previous studies based on climatic or vegetation structural characteristics (Hargrove et al., 2003; Yang et al., 2008), and addresses the interests for considering alternative information on ecosystem functionality (Bond-Lamberty et al., 2016; Petrakis et al., 2017; Petchey and Gaston, 2006; Reichstein et al., 2014; Valentini et al., 1999; Wright et al., 2006). Throughout its 20-year history of biosphere-atmosphere flux observations, the AmeriFlux network provides representation of spatial functional heterogeneity for 55% of CONUS. The joint effort of AmeriFlux and NEON core sites provides a long-term opportunity for representation of spatial functional heterogeneity for 46% of CONUS. The historical AmeriFlux archive also provides unique information about temporal variability of ecosystem functional heterogeneity due to decadal monitoring efforts at multiple study sites. Overall, representation could be enhanced across the Desert Southwest, Southern Rockies and Colorado Plateau, Great Basin, Northern Plains, and Central Plains of the NEON ecoclimatic domains. Most of these regions are characterized by complex terrain and therefore represent a scientific and methodological challenge to measure biosphere-atmosphere fluxes. This study provides insights for EONs design and improvement, is based on publicly available data, and is applicable to other networks around the world.

Acknowledgments

This work is part of the North American Carbon Program, and the authors thank all the contributors toward developing the AmeriFlux and NEON observational design to make this study possible. SV and MG acknowledges Consejo Nacional de Ciencia y Tecnología (CONACyT) for a PhD scholarship. RV, NAB, DJH acknowledge support from US Department of Agriculture (2014-67003-22070). RV and HWL acknowledge support from the National Science Foundation (EF-102980 and 1652594). DAS acknowledges support from ERDF and the Spanish MINECO (grant JC2015-00316 and project CGL2014-61610-EXP). NEON is a project sponsored by the National Science Foundation and managed under cooperative support agreement (EF-1029808) to Battelle Inc. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of our sponsoring agencies or the environmental networks. This study would not have taken shape if it were not for meaningful engagement with community members and our mentors. We thank three anonymous reviewers and Margaret Torn for insightful comments to improve this manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2018.07.016>.

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