Functional convergence of biosphere–atmosphere interactions in response to meteorology

Christopher Krich1,2, Mirco Migliavacca1, Diego G. Miralles2, Guido Kraemer1,3, Tarek S. El-Madany1, Markus Reichstein1, Jakob Runge4, and Miguel D. Mahecha3

1Max Planck Institute for Biogeochemistry, 07745 Jena, Germany
2Hydro-Climate Extremes Lab (H-CEL), Faculty of Bioscience Engineering, Ghent University, Ghent, Belgium
3Remote Sensing Centre for Earth System Research, Leipzig University, 04103, Leipzig, Germany
4German Aerospace Center, Institute of Data Science, 07745, Jena, Germany

Correspondence: Christopher Krich (ckrich@bgc-jena.mpg.de)

Abstract. Understanding the dependencies of the terrestrial carbon and water cycle is a prerequisite to anticipate their behaviour under climate change conditions. However, terrestrial ecosystems and the atmosphere interact via a multitude of variables, time- and space scales. Additionally, the interactions might differ among vegetation types or climatic regions. Today, novel algorithms aim to disentangle the causal structure behind such interaction from empirical data. Visualising the estimated structure in networks, the nodes represent relevant meteorological determinants and land-surface fluxes, and the links dependencies among them possibly including their lag and strength. Here we show that biosphere–atmosphere interactions are strongly shaped by meteorological conditions. For example, we find that temperate and high latitude ecosystems during peak productivity exhibit very similar biosphere–atmosphere interaction networks as tropical forests. In times of anomalous conditions like drought though, both ecosystems behave more like Mediterranean ecosystems during their dry season. Our results demonstrate that ecosystems from different climate or vegetation types have similar biosphere–atmosphere interactions if their meteorological conditions are similar. We anticipate our analysis to foster the use of network approaches as they allow a more comprehensive understanding of the state of ecosystem functioning. Long term or even irreversible changes in network structure are rare and thus can be indicators of fundamental functional ecosystem shifts.

1 Introduction

Ecosystems and the atmosphere constantly exchange energy, matter, and momentum (Bonan, 2015). These interactions result in biosphere–atmosphere fluxes (in particular carbon, water and sensible heat fluxes) that are shaped by a variety of climatic conditions and states of the terrestrial biosphere (McPherson, 2007). Understanding how biosphere–atmosphere fluxes interact and how they causally depend on the short-term meteorological and long-term climate conditions is crucial for building predictive terrestrial biosphere models (Detto et al., 2012; Green et al., 2017). However, the exact causal structure of dependencies between surface and atmosphere variables is still subject to unknowns (Baldocchi et al., 2016; Miralles et al., 2019). For example, we still do not understand well under which conditions certain climate extremes turn ecosystems into carbon sources or sinks (Sippel et al., 2017; Flach et al., 2018; von Buttlar et al., 2018). One reason for our incomplete understanding is that the
causal dependencies underlying biosphere–atmosphere interactions might vary among ecosystems due to their structure and long-term adaptation to climatic conditions. An other is that causal techniques are still rarely used. The collection of global long-term observation of biosphere–atmosphere fluxes measured via the eddy covariance method in FLUXNET (Baldocchi, 2014) should, however, allow us to disentangle such questions.

A variety of causal discovery methods have been developed over the past few years (see Runge et al., 2019a, for a recent overview). They allow to infer causal networks from empirical data enabled by certain general assumptions about the underlying processes. Some methods only consider two variables, such as (bivariate classical) Granger causality (Granger, 1969), convergent cross mapping (Sugihara et al., 2012), or transfer entropy (Schreiber, 2000). Other methods allow us to understand how multiple variables interact, accounting for common drivers and mediators by using conditioning approaches as suggested by multiple studies (Detto et al., 2012; Goodwell and Kumar, 2017; Papagiannopoulou et al., 2017; Claessen et al., 2019; Runge et al., 2019b). One example for the latter is PCMCI, a combination of the PC algorithm (named after its inventors Peter and Clark (Spirtes and Glymour, 1991)) and the Momentary Conditional Independence (MCI) test (Runge et al., 2019b). Krich et al. (2020) showed that the PCMCI approach is useful to assess causal dependencies of ecosystem fluxes and atmospheric variables.

In this study, we use multivariate time series from global ecological observation networks such as FLUXNET to investigate how biosphere–atmosphere interactions vary across vegetation types and climate zones. If biosphere–atmosphere interactions substantially vary across climate gradients or among vegetation types, then this may indicate that responses to climatic extremes may differ substantially and require terrestial biosphere models to account for them differently. If, however, the opposite applies and ecosystems of the Earth exhibit similar biosphere–atmosphere interaction types, then common principles can be identified that can serve as empirical reference for global vegetation models. The assessment of these questions includes investigating the effect of extreme meteorological events on the network structure of biosphere–atmosphere interactions.

To do so, we characterise biosphere–atmosphere interactions as weighted networks estimated via PCMCI (see Sect. 2.3). The nodes in these networks represent biosphere–atmosphere fluxes and meteorological variables (see Sect. 2.1). Any significant dependence among the variables is depicted as a link between the respective nodes and the link strength is measured by the MCI partial correlation value (see Sect. 2.2). We estimated overall 10.038 networks from 119 ecosystems using sliding windows of three months over the available time-series length. This captures also an ecosystem’s temporal development. Each of the estimated networks constitutes one high-dimensional observation with a network’s links spanning the high dimensional space. Projecting this high dimensional space onto two dimensions using methods of non-linear dimensionality reduction (here t-SNE, see Sect. 2.4) reveals the dominant features of transitions between different states of biosphere–atmosphere interactions, i.e., which links are strong descriptors of differences between networks. We then start with analysing the structure of the low dimensional embedding (Sect. 3.1). Subsequently we focus on ecosystem level behaviour, i.e. the seasonal median (Sect. 3.3) and individual years during extreme conditions (Sect. 3.4). Section 3.5 puts the results into broader perspective.
2 Data and Methods

2.1 Eddy-covariance observations

We used eddy covariance data from the FLUXNET database (Baldocchi et al., 2001) aggregated to daily time resolution. To maximise the available ecosystems and time series length, we took the union of the LaThuile Fair use (Baldocchi, 2008) and FLUXNET2015 Tier 1 (Pastorello et al., 2020) datasets (Nelson et al.) with at least 5 years of measurement. If a site year was available in both datasets we selected the one from FLUXNET2015. A detailed list of used sites and years is given in table A1. The final dataset contains sites from the major plant functional types and covers the major Koeppen-Geiger climate classes, i.e. tropical to polar climate zones. The majority of sites belong to evergreen needleleaf forests, grasslands and deciduous broadleaf forests. The dominant climate classes are continental, temperate and dry climates. The dataset’s variables, including meteorological and eddy covariance measurements, were quality checked, filtered, gap-filled, and partitioned with standard tools (Papale et al., 2006; Pastorello et al., 2020) and provided with per-variable quality flags. We extracted following variables, comparable between the two dataset, and their corresponding quality controls (if available): shortwave downward radiation (or global radiation, \( R_g \)), air temperature (T), net ecosystem exchange (NEE) (positive values signify carbon uptake into the biosphere), vapour pressure deficit (VPD), sensible heat (H), latent heat flux (LE), gross primary productivity (GPP), precipitation (P) and soil water content (SWC, measured at the shallowest sensor). Within the FLUXNET2015 dataset these variables are named as: "SW_IN_F_MDS", "TA_F_MDS", "NEE_VUT_USTAR50", "VPD_F_MDS", "H_F_MDS", "LE_F_MDS", "GPP_NT_VUT_USTAR50", "P", "SWC_F_MDS_1", respectively. Correspondingly for the LaThuile dataset: "Rg_f", "Tair_f", "NEE_f", "VPD_f", "LE_f", "H_f", "GPP_f", "precip", "SWC1_f", respectively. GPP is calculated via the commonly used night time flux partitioning (Reichstein et al., 2005). Here GPP is the difference between NEE and ecosystem respiration. The latter is estimated via a model which is parameterized using night time values of NEE.

2.2 PCMCI

To analyse biosphere–atmosphere interactions, we estimated network structures using the causal network discovery algorithm PCMCI. PCMCI is tailored to estimate time-lagged dependencies from potentially high-dimensional and autocorrelated multivariate time series. Dependencies can be interpreted causally under certain assumptions. The algorithm is explained from a biogeoscience viewpoint in Krich et al. (2020). A comprehensive description from theoretical assumptions to numerical experiments is given in Runge et al. (2019b).

As a brief summary, PCMCI efficiently conducts conditional independence tests among the contemporaneous (i.e. the dependence between two non-lagged variables) and time-lagged (up to some maximum time lag) variables to reconstruct a dependency network. While PCMCI can also be combined with nonlinear tests, here we estimate conditional independence using partial correlation (ParCorr), implying that we only consider linear dependencies. Partial correlation between X and Y given Z is defined as the correlation between the residuals of X and Y after regressing out the (potentially multivariate) condition Z.
PCMCI has two phases. In the first phase, the ’condition selection’, a superset of lagged parents of each variable is estimated based on a fast variant of the PC algorithm (Spirtes and Glymour, 1991). In the second phase 'momentary conditional independence' (MCI) among all pairs of contemporaneous and lagged variables \((X_i^{t-\tau}, X_j^{t})\) for \(\tau \geq 0\) is estimated. The MCI test removes the influence of the lagged drivers (obtained in the first phase) and yields p-values (based on a two-sided t-test) for causal links among each time-lagged and contemporaneous variable pair. The strength of links is here given by the MCI partial correlation. Lagged links are directed forward in time and contemporaneous dependencies are left undirected. A causal interpretation of links rests on the standard assumptions of causal discovery (Runge et al., 2019b). In particular, a statistical independence (here at a 0.1 two-sided significance level) between a pair of variables conditional on the other lagged variables is interpreted as the absence of a causal link (Faithfulness condition). On the other hand, a causal interpretation of the estimated links is here to be understood only with respect to the variables included in the analysis. Unobserved common drivers can still render links as spurious. In the present context we aim to classify networks and a causal interpretation of each link is not the focus. The dependence structure among variables can finally be visualised by weighted networks with link weights given by the MCI partial correlation. MCI partial correlation removes the influence of other lagged drivers and autocorrelation, yielding a better interpretation of the strength of a causal mechanism than the common Pearson correlation. At the same time, MCI partial correlation values are normalised in \([-1, 1]\) and can, hence, well be compared between variable pairs with different units of measurement.

2.3 Network Estimation

Networks are estimated using PCMCI between the variables \(R_g, T, NEE, VPD, H\) and \(LE\) using time lags between zero to five days (see Supplementary Material Table B1 for settings). Based on findings in Krich et al. (2020), we subtracted a smoothed seasonal mean from each variable to remove the common driver influence of the seasonal cycle that would yield spurious dependencies. The seasonal mean was smoothed by setting the high frequency components (> 20 days\(^{-1}\)) of its Fourier transform to zero. We estimated networks in sliding windows of three months, taking the centre month as the time index of each network. To avoid effects on the network structure from gap-filling we used the following quality flag thresholds. A daily datapoint is not used if its quality flag is below 0.6 (i.e. more than 60% of measured and good quality gap filled data). In case more than 25% of datapoints of the three month window are flagged as bad quality, the time window is removed from the analysis. To analyse the factors influencing network structure, we consider the mean values over the respective time period of the variables included in the network calculation, and additionally those of GPP, P and SWC. GPP, P and SWC were not included in the network calculation because certain characteristics can impinge on network estimation. GPP is derived using NEE and T. Any of the links GPP–T and GPP–NEE thus could be due to its processing rather than an actual dependence. P, on the other hand, typically yields non intuitive results due to its binary character (precipitation - no precipitation).

2.4 Dimensionality Reduction

Applying above described procedure we obtained 10.038 networks for the different months and sites. Each network, with 6 variables and 6 time lags, contains 216 links and can, hence, be embedded into a 216 dimensional space. However, here we only
focus on the 15 contemporaneous links since we found them to be strongest and most robust. Therefore, the dimensionality reduction step was performed on those links only. For the dimensionality reduction, we tested principal component analysis (PCA; Pearson, 1901), t-distributed stochastic neighbour embedding (t-SNE; Maaten and Hinton, 2008), and uniform manifold approximation and projection (UMAP; McInnes et al., 2018). PCA is the standard method for dimensionality reduction, it is commonly used, linear, fast, and easily interpretable regarding the meaning of its axes (the principal components). A PCA embedding typically fails to reveal complex clusterings, because it maintains large scale gradients but often produces embeddings in which far away points appear very close in the embedding. In contrast t-SNE preserves local neighbourhoods which makes it very good at visualising clusters in the data and non-linear relationships. Drawbacks are the difficult interpretability of the embedding axes due to the non-linear nature and its fairly long computation time for large datasets. UMAP was developed as an improvement of t-SNE regarding computation time while having an embedding with similar properties as t-SNE.

As we are dealing with an unsupervised method there is no obvious measure to assess the quality of an embedding, as each method optimises a different error function. A measure commonly used for the comparison and characterisation of dimensionality methods is the agreement between \( K \)-ary neighborhoods (the \( K \) nearest points to an observation) in the high dimensional and low dimensional space. The measure \( R_{NX}(K) \) (Lee et al., 2015) gives a measure of the improvement of the embedding of \( K \)-ary neighborhoods over random embeddings. For an embedding with random coordinates we obtain \( R_{NX}(K) \approx 0 \) and if the \( K \)-ary neighborhoods are perfectly preserved we obtain \( R_{NX}(K) = 1 \). As this measure depends on the neighborhood size, \( K \), we can draw a curve over \( K \) that characterizes if the method is better at maintaining global or local neighborhoods. The area under the \( R_{NX}(K) \) curve gives an idea of the overall quality of the embedding. An intercomparison of the three dimensionality reduction methods using this measure shows t-SNE to perform best (see Fig. A1, B1, C1).

### 2.5 Clustering and median network trajectories

On the reduced space we applied a clustering method named Ordering Points To Identify the Clustering Structure (OPTICS; Ankerst et al., 1999). Clusters are found by identifying regions of high density that contain a certain number of datapoints. The cluster borders are defined by a certain drop in reachability of further datapoints. This allows points that lie outside the reachability of neighbouring clusters to remain unclustered. Following settings were used for clustering: \( \text{min}_\text{samples}=80 \), \( \text{max}_\text{eps}=8 \) and \( \xi=0.5 \). We calculated mean networks for each cluster by calculating the mean MCI value for each contemporaneous link of each network contained in the cluster and only took those links that had an absolute value above 0.2. Further, for each ecosystem, we calculated an annual median trajectory within the t-SNE space which is composed of its monthly median networks. To this end, we calculated non-intersecting convex hulls which consisted of at least three datapoints (networks within the t-SNE space belonging to the same ecosystem, representing the same month, in at least three years). The monthly median network is the average of the networks lying on (\( \geq 3 \) networks) or in the inner hull (\(< 3 \) networks).
3 Results and Discussions

3.1 Two-dimensional embedding of biosphere–atmosphere networks

The dimensionality reduction method t-SNE performed best at projecting the high dimensional space created by the networks contemporaneous links onto two dimensions (cf. Sect. 2.4, Fig. A1, B1). The two-dimensional embedding of biosphere–atmosphere interactions is ordered primarily by dependencies including carbon flux (NEE) and energy distributions (LE, H). This can be seen in Fig. 1 which shows the embedding colour coded by the strength of individual links, i.e. MCI partial correlation values. The colouring reveals that the link strengths are ordered along gradients. The strongest gradients measured via distance correlations (Székely et al., 2007) are given by the links NEE–LE ($\rho = 0.75$), Rg–LE ($\rho = 0.73$) and T–H ($\rho = 0.69$). The connection between carbon and water fluxes as well as the role of energy input to sustain water fluxes are well known and investigated dependencies (Beer et al., 2010; Luyssaert et al., 2007). Further, gradients of mean climatic conditions emerge. This is depicted in Fig. 2 showing again the low dimensional embedding, this time colour coded by the networks’ underlying mean conditions, i.e. the average over the respective time window, of the exchange rates (GPP, NEE, LE and H) as well as meteorological conditions (Rg, T, VPD, P). Clearly, the mean exchange rates and meteorological conditions - although not considered in the estimation of the networks - are related to the observed biosphere–atmosphere interactions. On the contrary, corresponding vegetation types and Köppen-Geiger classes are not much related as displayed in the Supplementary Material section Fig. D2. The results show that a high dimensional space encompassing more than 10000 ecosystem networks representing the states of biosphere–atmosphere interactions from ecosystems of various geographic origins can be reduced to a compact two dimensional manifold characterised by four edges and gradients of biosphere and atmosphere conditions. While gradients in MCI partial correlation strength are expected as they were used as features in the dimensionality reduction, gradients in climatic and biospheric conditions were not. This information thus must be entailed in the networks’ structure. To better grasp the distribution of network structures, we further analyse the emerging clusters.

3.2 Clusters of characteristic ecosystem–atmosphere networks

As we apply a significance threshold to each link of the estimated network structures (see Sect. 2.3), the networks typically lack weak links. This leads to a certain degree of clustering among the networks, which we identified using the OPTICS approach (see Sect. 2.5; Ankerst et al., 1999)) (Fig. 3a). Cluster boundaries are shown by the convex hulls in Fig. 3b, where we also visualise the mean interaction networks of each cluster. Based on this analysis we can identify four archetypes of network structures:

- Type 1 is a sparsely connected network. Links, if present, are very weak and predominantly exist among atmospheric variables. Mean atmospheric conditions are characterised by low energy input (low $R_g$ and $T$). Carbon and water fluxes are consequently close to zero, and daily averages of sensible heat can even reach negative values. Such conditions reflect high latitude ecosystem winter states experienced by ecosystems like the evergreen needle leave forests (ENF) of Finnland.
Figure 1. Two-dimensional embedding of three-monthly biosphere–atmosphere networks realised via t-SNE. Shown is the distribution of link strengths among the networks. The strength is estimated via MCI partial correlation values. Subfigures are sorted by the distance correlation of the link’s MCI value with the axes (value in upper right corner). As $R_g$ can only be a cause, connections including $R_g$ are directed $\rightarrow$.

i.e. Hyytiälä (FI-Hyy) and Sodankyla (FI-Sod) as well as Canada, i.e., the UCI-1850 burn site (CA-NS1) and Quebec - Eastern Boreal (CA-Qcu) during December and January.

Type 2 consists of strong links among atmospheric variables but LE and NEE are weakly, not, or even negatively connected. This network structure coincides with high energy input (high $R_g$ and T) but low water availability (low P and SWC, high VPD). A high Bowen ratio, i.e. the ratio between sensible heat and latent heat, representing aridity, and low carbon fluxes are the consequence. These conditions are typically present at semi-arid ecosystems like the woody savanna (WSA) Santa Rita Mesquite (US-SRM) as well as the grasslands Santa Rita (US-SRG), Audubon Research Ranch (US-Aud) and Sturt Plains (AU-Stp) during dry season.
Type 3 exhibits the same strong links among $R_g$, VPD and H as Type 2 but T is weakly or not connected and the opposite for LE and NEE. $R_g$ and T are considerably lower than in Type 2 but because of sufficient water availability the Bowen ratio is between 0 and 1. Typical ecosystems in this state are mid to high latitude forests during spring or autumn, e.g. Harvard Forest EMS Tower (US-Ha1, deciduous broadleaf forest (DBF)), Roccarespampoli 1 (IT-Ro1, DBF), Vielsalm (BE-Vie, mixed forest (MF)) and Hyytiälä (FI-Hyy, ENF).

Type 4 is fully and strongly connected. Both energy input and water availability are high leading to Bowen ratios around 1. This network state is typically present in tropical forests like the Guyaflux site in French Guiana (GF-Guy) (evergreen broadleaf forest (EBF)) but can temporarily be also reached by a variety of other ecosystems, e.g. mid and high latitude forests like Hainich (DE-Hai, DBF), Tharandt (DE-Tha, ENF), BE-Vie (MF), FI-Hyy (ENF) as well as woody savannas (WSA) as Howard Springs (AU-How) and grasslands as Daly River Savanna (AU-Dap).

The archetypes of networks are located at the edges of the two-dimensional space and thus could define two imaginary axes. From a physical point of view, energy is required for each process and interaction to occur, e.g. photosynthesis or evaporation (Bonan, 2015). Therefore, transitions along the axis connecting the network types 1 and 4 might be interpreted as energy
controlled as dependencies among all variables fade or increase consistently. Transitions along the axis connecting network types 2 and 3 are explainable by a combination of water availability and a temperature gradient. Low water availability but high temperatures lead to low carbon and water fluxes and thus low connectivity. On the other hand, sufficient water and medium temperatures allow for fluxes but likely reduce the influence of varying temperatures leading to connected NEE and LE but disconnected T. And indeed these patterns and gradients exist. Mean $R_g$ is lowest at network type 1 and almost linearly increases towards network type 4. P is lowest at network type 1 and 2. In combination with high energy input network type 2 has lowest SWC values and the highest Bowen ratios (see Supplementary Material section Fig. D2). SWC is higher but quite dispersed elsewhere suggesting that at a certain point water limitations are fading out. T values of course also show an increase from network type 1 to 4 (as radiation) but also from network type 3 to 2 and are actually rather low (8°C to 15°C) at network type 3 (see Fig 2). As meteorological conditions affect biosphere productivity, network type 1 and 2 exhibit low, type 3 medium and type 4 high productivity i.e. estimated as GPP. In short, the clustering revealed that changes in energy and water availability can explain major transitions between different states of biosphere–atmosphere interactions. Having an understanding of the low dimensional embedding’s structure now allows us to analyse specific ecosystem behaviour.

**Figure 3.** Structure of the two-dimensional embedding. left: t-SNE space clustered by the OPTICS approach (Ankerst et al., 1999). Colours represent different clusters, black dots are not attributed to a cluster. Indicated are the four archetypes of network connectivity and the networks underlying meteorological conditions. right: Convex hulls of clusters and their average network, i.e. average over all networks belonging to one cluster. Average networks are thresholded at a minimum link strength of 0.2. A finer clustering can be found in the Supplementary Material section Fig. D1.
3.3 Ecosystems’ median trajectories

Each point in the reduced t-SNE space represents a biosphere–atmosphere interaction network for a given month and ecosystem. Hence, we can trace an ecosystem’s trajectory through time. An ecosystem’s median annual trajectory (see Sect. 2.5) within the low dimensional space reflects seasonal patterns of meteorological conditions (Fig. 4). For example, mid-latitude sites like FR-Pue (EBF), DE-Hai (DBF) and FI-Hyy (ENF) exhibit a strong seasonal variation of $R_g$ and span a long distance in the t-SNE space. In contrast, tropical ecosystems like GF-Guy (EBF) constantly have high $R_g$ and exhibit predominantly network type 4 indicative of high productive conditions - while DE-Hai or FI-Hyy reach this connectivity pattern only during peak growing season. US-SRM (WSA), however, has similar or even higher $R_g$ values throughout the year but barely manages to deviate from type 2 which is in accordance with its low water availability. The amount of precipitation further aligns with differences and characteristics of the trajectories of FR-Pue, DE-Hai and FI-Hyy. For example, FI-Hyy shows some deviation towards edge 2 in February and March, FR-Pue in June, July and August. For both, mean precipitation is lowest during these month. The strong control by energy and water availability is in line with a recent analysis showing that variability in land-surface processes is largely explained by productivity measures as well as water and energy availability. Both, water and energy availability, need to be high for high productive states, yet the lack of either of them leads to low productivity (Kraemer et al., 2020). This biosphere state triangle is found in our analysis by the network type 1 (cold), 2 (dry) and 4 (high productivity). Yet, a fourth network type (type 3) is naturally occurring in the t-SNE space as we here include interactions with the atmosphere.

3.4 Deviations from ecosystem median trajectories

Climatic extremes are visible in an ecosystem’s trajectory as strong deviations from the median trajectory. Figure 5 shows the trajectories of ecosystems during anomalous dry or wet conditions. During the European heatwave of 2003, in July and August the trajectories of two temperate central European forests, DE-Hai and DE-Tha, no longer manage to establish a network structure resembling network type 4, typical for these ecosystems during their high productive phase. Instead they are shifted towards network type 2, associated with drier conditions (Fig. 5a, b). Similarly, the ecosystem BR-Sa3 (EBF) in the Brazilian tropical rainforest shows substantial deviations towards network type 2 during the exceptional dry season of 2001 (Aug, Sep, Oct) (Marengo et al., 2018) (Fig. 5c). In contrast, US-Wkg is a grassland accustomed to dry conditions and thus predominantly exhibits low water and carbon fluxes resulting in network structures as of network type 2, i.e. water and carbon fluxes are barely or even disconnected. Carbon and water fluxes of semi-arid ecosystems, however, are known to respond quickly and strongly to sufficient precipitation (Potts et al., 2019; Leon et al., 2014; Reynolds et al., 2004). This sensitivity is found to carry over to the network structure as well. The network structure of US-Wkg becomes fully connected (network type 4) in September 2014 with above average precipitation (NOAA) (Fig. 5d). The relevance of climatic conditions in controlling biosphere–atmosphere interactions on three monthly time windows thus shows also on ecosystem level as they are strong enough to explain deviations from an ecosystem’s median trajectory and lead to the detection of climatic extremes.
3.5 Functional convergence of biosphere–atmosphere interactions

We have seen that networks representing biosphere–atmosphere interactions are strongly shaped by prevailing mean meteorological conditions. Moreover, the visualisation of ecosystem trajectories within the t-SNE space (Fig. 4, 5) and the distributions of vegetation types and climatic regions (Supplementary Material Fig. D2) reveal that ecosystems across vegetation types and climatic regions can exhibit similar biosphere–atmosphere interactions if their meteorological conditions are similar. For example, at high radiation and water availability, i.e. optimal growing conditions, ecosystems exhibit fully connected networks (type 4) as well as high carbon and water fluxes. Diverging from optimal growing conditions, links in the networks weaken and disappear. This behaviour can be understood as functional convergence of ecosystems which corroborates the hypothesis that ecosystems have a low number of key processes that determine ecosystem behaviour (Lambert, 2006; Meinzer, 2003; Shaver et al., 2007) rendering their behaviour transparent and predictable. Criticism might rise as the larger part of the biosphere–atmosphere interaction network indeed is a pure atmospheric network, i.e. Rg, T, VPD and H. Thus strong associations of networks and their trajectories with atmospheric conditions could be dominated by changes in this atmospheric network. Fig.
Figure 5. Abnormal conditions in meteorological conditions (here precipitation) become visible in an ecosystem’s trajectory. left: Trajectories within the low dimensional space of the ecosystems Hainich (DE-Hai, DBF), Tharand (DE-Tha, ENF), Santarem-Km83-Logged Forest (BR-Sa3, EBF) and Walnut Gulch Kendall Grasslands (US-Wkg, GRA). right: Three monthly average of daily precipitation data.
1, however, suggests the opposite. The strongest gradients are given by the links NEE–LE and Rg–LE and transitions along the axis connecting type 2 and 3 (cf. Fig. 3) are dominated by changes in biosphere connectivity, i.e. LE and NEE.

In fact, the dominance of climatic drivers in controlling the temporal evolution of ecosystem functioning emerges also in other studies (Musavi et al., 2017; Schwalm et al., 2017) as they showed that carbon fluxes are primarily controlled by climatic factors. Yet, these and others also show the role of biotic factors in shaping the responses of ecosystem processes to climatic variability. For example, Musavi et al. (2017) revealed in a global ecosystem study that species diversity and ecosystem age decrease inter annual variability of GPP. Similarly, Wagg et al. (2017) discovered biodiversity to increase long-term stability of ecosystem productivity. In regional studies Wales et al. (2020) found the stability of net primary production to be affected by the kind and severity of disturbances. Tamrakar et al. (2018) showed that seasonal carbon fluxes were more sensitive to environmental conditions in a homogeneous forest compared to a heterogeneous one. It would be of interest to investigate, to which degree the effects of biotic factors also translates to the sensitivity of the network structure.

Furthermore, extreme heat and drought events (Sippel et al., 2018) or compound events in general (Zscheischler et al., 2020) can severely disrupt ecosystem functions. The time of recovery from such disturbances is a crucial parameter in assessing ecosystem resilience. Schwalm et al. (2017) showed that the recovery time measured as the recovery in GPP is primarily influenced by climate but secondarily by biodiversity and CO$_2$ fertilisation. Assessing the recovery time via GPP already puts the ecosystem functioning into focus. The here presented framework, i.e. the sensitivity of an ecosystem’s network structure to meteorological conditions, might be a valuable asset to study reaction time and strength to and recovery from extreme events as it not only utilises one variable but the interactions of a set of variables, thereby capturing more comprehensively an ecosystem state. A drawback is the reduced temporal resolution (a certain time period of daily or even half hourly measurements is aggregated to one network) which can be offset by the here used moving window approach to a certain degree. Especially with regard to climatic extreme conditions in recent years with observed vegetation dieback in, for example, DE-Hai (Schuldt et al., 2020), further studies could also shed light on the role of adaptation in shaping biosphere–atmosphere interactions. Our study suggest that adaptation to a lesser degree limits the range of possible interactions but enables to sustain and persist certain conditions for longer periods. The focus of further studies thus could be to elucidate the role of biotic factors in influencing ecosystem trajectories as well as the role of adaptation and the response to extreme events.

4 Conclusions

We analysed the functional behaviour of a variety of ecosystems using the FLUXNET database of eddy covariance measurements. In particular, we examined the interaction structure between biosphere–atmosphere fluxes as well as atmospheric state variables using PCMCI, an algorithm to estimate causal relationships from empirical time series. In total we included 119 measurement sites with cumulative 1067 measurement years leading to 10038 monthly networks. Using non-linear dimensionality reduction, we found four archetypes of network states defining the edges of the low dimensional embedding. They are characterised on the one hand by a fully connected and almost unconnected network structure and on the other hand by an antagonistic coupling of carbon and water flux with temperature - when one is strongly coupled, the other is decoupled. The
transitions between these states correlate well with gradients of meteorological drivers, i.e. radiation and water availability. The movement of an ecosystem within that space therefore strongly aligns with changes in meteorological conditions. This, however, also leads to similar behaviour under similar conditions for strongly contrasting ecosystems. For example, forests of mid or even high latitudes exhibit similar interaction structure as tropical forests given high radiation and water availability during summer. Yet, this state can also be reached by predominantly dry ecosystems like steppe grasslands given sufficient precipitation. In contrast if productive ecosystems are struck by a severe drought, like central European ecosystems in 2003, the behaviour can adapt more to that of a Mediterranean ecosystem. Overall this analysis shows that the biosphere-atmosphere interaction structure can adapt flexibly to prevailing conditions and is widely independent of vegetation type and climatic region. Such behaviour is strong evidence for functional convergence of ecosystems, i.e. their behaviour is determined by a low number of key processes. For further studies, we suggest, to focus on the role of biotic factors as, for example, plant functional types, ecosystem age and adaptation. These factors could play crucial roles in coping strategies of climatic extremes.

Code availability. Code scripts can be found at https://github.com/ckrich/Functional-convergence-of-biosphere-atmosphere-interactions-in-response-to-meteorology

Data availability. The eddy covariance data of the FLUXNET sites can be downloaded from the official webpage (https://fluxnet.fluxdata.org/).
| FLUXNET-ID | start year | end year | data reference |
|------------|------------|----------|----------------|
| BE-Lon     | 2004       | 2014     | Moureaux et al. (2006) |
| BE-Vie     | 1996       | 2014     | Aubinet et al. (2001) |
| BR-Sa3     | 2000       | 2004     | Saleska et al. (2003) |
| CA-Mer     | 1998       | 2005     | Laffleur et al. (2003) |
| CA-NS1     | 2001       | 2005     | Goulden et al. (2006) |
| CA-NS2     | 2001       | 2005     | Bond-Lamberty et al. (2004) |
| CA-NS3     | 2001       | 2005     | Wang et al. (2002a) |
| CA-NS5     | 2001       | 2005     | Wang et al. (2002b) |
| CA-NS6     | 2001       | 2005     | Wang et al. (2002c) |
| CA-Qcu     | 2001       | 2006     | Gissans et al. (2006) |
| CA-Qfo     | 2003       | 2010     | Chen et al. (2006) |
| CA-SF2     | 2001       | 2005     | Raymond and Jarvis (1999a) |
| CA-SF3     | 2001       | 2006     | Raymond and Jarvis (1999b) |
| CH-Cha     | 2005       | 2014     | Merbold et al. (2014) |
| CH-Dav     | 1997       | 2014     | Zielis et al. (2014) |
| CH-Fru     | 2005       | 2014     | Imer et al. (2013) |
| CH-Lae     | 2004       | 2014     | Etzold et al. (2011) |
| CH-Oe1     | 2002       | 2008     | Ammann et al. (2009) |
| CH-Oe2     | 2004       | 2014     | Dietiker et al. (2010) |
| CZ-BK1     | 2004       | 2014     | Acosta et al. (2013) |
| CZ-BK2     | 2004       | 2012     | - |
| CZ-wet     | 2006       | 2014     | Dušek et al. (2012) |
| DE-Akm     | 2009       | 2014     | - |
| DE-Geb     | 2001       | 2014     | Anthoni et al. (2004b) |
| DE-Gri     | 2004       | 2014     | Prescher et al. (2010a) |
| DE-Hai     | 2000       | 2012     | Knohl et al. (2003) |
| DE-Kli     | 2004       | 2014     | Prescher et al. (2010b) |
| DE-Lkb     | 2009       | 2013     | Lindauer et al. (2014) |
| DE-Obe     | 2008       | 2014     | - |
| DE-Spw     | 2010       | 2014     | - |
| DE-Tha     | 1996       | 2014     | Grünewald and Bernhofer (2007) |
| DE-Wet     | 2002       | 2006     | Anthoni et al. (2004a) |

Continued on next page
Table A1 – Continued from previous page

| FLUXNET-ID | start year | end year | data reference               | FLUXNET-ID | start year | end year | data reference               |
|------------|------------|----------|------------------------------|------------|------------|----------|------------------------------|
| DK-NuF     | 2008       | 2014     | Westergaard-Nielsen et al. (2013) | US-Prr     | 2010       | 2014     | Ruehr et al. (2012d)         |
| DK-Sor     | 1996       | 2014     | Pilegaard et al. (2011)      | US-SP1     | 2000       | 2005     | Thomas et al. (1999a)        |
| DK-ZaH     | 2000       | 2014     | Lund et al. (2012)           | US-SP2     | 1998       | 2004     | Thomas et al. (1999b)        |
| ES-ES1     | 1999       | 2006     | Sanz et al. (2004)           | US-SP3     | 1999       | 2004     | Thomas et al. (1999c)        |
| FI-Hyy     | 1996       | 2014     | Suni et al. (2003)           | US-SRG     | 2008       | 2014     | Ruehr et al. (2012e)         |
| FI-Kaa     | 2000       | 2006     | Aurela et al. (2007)         | US-SRM     | 2004       | 2014     | Scott et al. (2008)          |
| FI-Sod     | 2001       | 2014     | Thum et al. (2007)           | US-Syv     | 2001       | 2014     | Desai et al. (2005)          |
| FR-Fon     | 2005       | 2014     | Delpierre et al. (2016)      | US-Ton     | 2001       | 2014     | Tang et al. (2003)           |
| FR-Gri     | 2004       | 2014     | Loubet et al. (2011)         | US-Twt     | 2009       | 2014     | Hatala et al. (2012)         |
| FR-Hes     | 1997       | 2006     | Granier et al. (2000)        | US-UMB     | 2000       | 2014     | Rothstein et al. (2000)      |
| FR-LBr     | 1996       | 2008     | Berbigier et al. (2001)      | US-UMd     | 2007       | 2014     | Nave et al. (2011)           |
| FR-Pue     | 2000       | 2014     | Rambal et al. (2004)         | US-Var     | 2000       | 2014     | Xu et al. (2004)             |
| GF-Guy     | 2004       | 2014     | Bonal et al. (2008)          | US-WCr     | 1999       | 2014     | Potter et al. (2001)         |
| HU-Bug     | 2002       | 2006     | Nagy et al. (2005)           | US-Whs     | 2007       | 2014     | Scott et al. (2006)          |
| IL-Yat     | 2001       | 2006     | Grünzweig et al. (2003)      | US-Wkg     | 2004       | 2014     | Emmerich (2003)              |
| IT-Amp     | 2002       | 2006     | Gilmanov et al. (2007)       | ZA-Kru     | 2000       | 2013     | Archibald et al. (2009)      |
| IT-BCi     | 2004       | 2014     | Vitale et al. (2016)         | ZM-Mon     | 2000       | 2009     | Merbold et al. (2009)        |
Table B1. PCMCI parameters that were used differently from default settings.

| PCMCI parameter       | Setting          |
|-----------------------|------------------|
| significance α        | 0.1              |
| α_{pc}                | None             |
| tau_min               | 0                |
| tau_max               | 5                |
| selected_variables    | T, NEE, VPD, H, LE |
| mask_type             | 'y'              |
| fdr_method            | 'fdr_bh'         |
Figure A1. Quality assessment of dimensionality reduction techniques. To visualize and subsequently analyse the network space we reduce its dimensionality. We compared PCA, t-SNE and UMAP including various parameter settings (here: PCA’s leading two principal components, t-SNE with perplexity 30, and UMAP with n_neighbors equal 5 for 2 dimensions). The test statistic $R_{NX}(k)$ (y-axis) gives the improvement of the embedding of $k$-neighborhoods (x-axis) over a random embedding. The area under the curves (preserving the log-scaled x-axis) is given in the legend and gives an idea of the overall quality of the embedding Lee et al. (2015). We chose t-SNE with perplexity 30, as it preserves best local neighbourhoods and performs well on larger distances.

Appendix C: Results and Discussion
Figure B1. Same metric as Fig. A1. Optimisation of the dimensionality reduction via t-SNE by using different perplexity values.
Figure C1. Same metric as Fig. A1. Optimisation of the dimensionality reduction to two dimensions via UMAP by using different values for the parameter $n_{\text{neighbors}}$. 

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Figure D1. As Fig. 3 but with smaller clusters exhibiting the finer structure of the t-SNE space.
Figure D2. t-SNE space coloured by underlying mean Bowen ratio and precipitation, as well as the ecosystems respective Koeppen Geiger class and IGBP type.
**Author contributions.** CK and MDM designed the study with contributions from all other authors. CK conducted the analysis and wrote the manuscript. All authors helped to improve the manuscript.

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