https://doi.org/10.5194/bg-2022-191
Preprint. Discussion started: 13 September 2022

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Revisiting and attributing the global controls on terrestrial ecosystem functions of climate and plant traits at FLUXNET sites with causal networks

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Submitted to: *Biogeosciences*

https://doi.org/10.5194/bg-2022-191
Preprint. Discussion started: 13 September 2022

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Abstract

Using statistical methods that do not emphasize the systematic causality to attribute climate and plant traits to control ecosystem function may produce biased perceptions. We revisit this issue using a Bayesian network (BN) capable of quantifying causality. Based on expert knowledge and climate, vegetation, and ecosystem function data from the FLUXNET flux stations, we constructed a BN containing the causal relationship of 'climate-plant trait-ecosystem function'. Based on the sensitivity analysis function of the BN, we attributed the control of climate and plant traits to ecosystem function and compared the results with those based on Random forests and correlation analysis. The main conclusions of this study include: BN can be used for the quantification of causal relationships between complex ecosystems and climatic and environmental systems, and enables the analysis of indirect effects among variables. The control of ecosystem function by climate variables (especially mean temperature and mean vapor pressure deficit) may have been underestimated previously, and the mechanism of indirect effects of climate variables on ecosystem function through plant traits should be emphasized in future studies. Further inclusion of temporal information in BN holds promise for improving the analysis of lagged effects and interactions and feedback effects between variables.

1 Introduction

Terrestrial ecosystems provide a variety of important ecosystem functions for our society (Manning et al., 2018). It is essential to understand the potential changes in ecosystem functions in the context of global climate change (Grimm et al., 2013). The response of terrestrial ecosystem function to changes in climate change, plant traits, and environmental conditions, and the corresponding mechanisms, are complex due to enormous spatial and temporal variations across ecosystems, climate zones, and also space-time scales (Diaz and Cabido, 1997; Madani et al., 2018; Myers-Smith et al., 2019). Given the enormous variations, on the global scale, these issues have not been clarified well.

In the past decades, measurements of ecosystem functions are increasingly available to support studies of the relations between ecosystem functions and climate and environmental systems. For example, eddy-covariance flux tower observations (Baldocchi, 2014) for carbon flux (i.e., net ecosystem exchange (NEE)) and water flux (i.e., evapotranspiration (ET)) have been widely used to investigate changes in ecosystem functions and their responses to climate change, vegetation condition changes, etc (Jung et al., 2020, 2010; Migliavacca et al., 2021; Peaucelle et al., 2019). With the increase in such observations, various statistical analysis methods such as emerging machine learning (Barnes et al., 2021; Migliavacca et al., 2021; Reichstein et al., 2019; Shi et al., 2022b, a, 2020b; Tramontana et al., 2016) have been used to mine the hidden information on the effects of climate change and its induced changes in vegetation, etc. on ecosystem function variables such as carbon and water flux, which has not been understood in depth by process-based models (e.g., biogeochemistry models (Sakschewski et al., 2016)). For example, using Random forests (RF) and principal component analysis (PCA), a recent study (Migliavacca et al., 2021) quantified the three main axes of terrestrial ecosystem function and their drivers based on observations of carbon and water fluxes of FLUXNET (Pastorello et al., 2020) and various climate and plant trait variables. Generally, data-driven approaches have become increasingly important recently in this area (Reichstein et al., 2019).

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Preprint. Discussion started: 13 September 2022


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However, compared to the process-based models, most of these data-driven approaches lack representation of the systematic causality and detailed processes in the relations between ecosystem function and climate and environments, despite the widely recognized complex causal interactions of ecosystems with climate and environmental systems (Reichstein et al., 2014). Conventional methods such as multiple linear regression have been questioned in attribution studies of the relationship between climate and the carbon cycle (Wang et al., 2022). For example, the use of multiple linear regression may underestimate the direct effect of soil moisture possibly due to the covariance between variables (Wang et al., 2022). For machine learning techniques, although current common algorithms such as RF (Migliavacca et al., 2021) can report the importance of features (IMP) to measure their contributions to the prediction model, IMP-based attribution to the target variable can also be unreliable when we aim to explain systematic causality (Gregorutti et al., 2017). Therefore, it is commonly important to recognize the difference between correlation and causality in these approaches and emphasize the systematic causality in the systems and also detailed causal relations between features in a data-driven approach.

Bayesian network (BN) is a causal model based on conditional probability representation (Friedman et al., 1997; Pearl, 1985) that characterizes the transmission of cause and effect through conditional probabilities between variables. Currently, BN has been used in modeling causal relationships in many fields and has demonstrated advantages in causal interpretation, including in the fields such as hydrology and ecology (Chan et al., 2010; Keshtkar et al., 2013; Milns et al., 2010; Pollino et al., 2007; Shi et al., 2021a, b; Trifonova et al., 2015). However, BN has rarely been used in the study of attribution of changes in ecosystem function. Therefore, this study used BN to attribute the controls of climate and plant traits on ecosystem function by quantifying the causal relationships involved. The data used are from a previous study (Migliavacca et al., 2021) which extracted ecosystem function, climate, and plant trait variables for FLUXNET flux stations. The construction of the causal structure of BN referred to the previous expert knowledge of this system (Reichstein et al., 2014). Further, by comparing BN-based attribution analysis, linear correlation analysis, and RF-based IMP reported by the previous study (Migliavacca et al., 2021), we investigated the adding-values of using BN for causal analysis and discussed its prospects in this paper.

2 Methodology

2.1 Data

The used variables (Table 1) include the carbon and water fluxes of the FLUXNET flux tower sites and the ecosystem function variables derived from them, and information on the corresponding climatic variables as well as plant traits:

a) Ecosystem function variables: underlying Water Use Efficiency (uWUE), maximum evapotranspiration (ETmax), maximum surface conductance (GSmax), maximum net CO2 uptake of the ecosystem (NEPmax), Gross Primary Productivity at light saturation (GPPsat), Mean basal ecosystem respiration at a reference temperature of 15 °C (Rb).
b) Plant trait variables: ecosystem scale foliar nitrogen concentration (Nmass), Maximum Leaf Area Index (LAImax), Maximum vegetation height (Hc), Aboveground Biomass (AGB).

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c) Mean incoming shortwave radiation (SWin), Mean temperature (Tair), Mean Vapor Pressure Deficit (VPD), Mean annual precipitation (P), and cumulative soil water index (CSWI).

These data have different producing processes, including those calculated from flux data, site records, extracted from remote sensing data, etc. The specific calculation methods can be found in the previous study (Migliavacca et al., 2021).

Table 1. The variables used and the discretization of their values in BN.

Variable node	Definition and units	Type	Approach (Migliavacca et al., 2021)	Discretization in BN (thresholds for classifications)
uWUE	underlying Water Use Efficiency [gC kPa^0.5 kgH_2O^{-1}]	Ecosystem function	calculated from GPP, VPD, ET	0.0, 2.5, 3.5, 5.5
ETmax	maximum evapotranspiration in the growing season [mm]	Ecosystem function	computed as the 95th percentile of ET in the growing season	0.05, 0.15, 0.30, 0.45
GSmax	maximum surface conductance [m s^{-1}]	Ecosystem function	computed by inverting the Penman-Monteith equation after calculating the aerodynamic conductance	0, 0.01, 0.02, 0.06
NEPmax	maximum net CO2 uptake of the ecosystem [umol CO_2 m^{-2} s^{-1}]	Ecosystem function	computed as the 90th percentile of the half-hourly net ecosystem production in the growing season	0, 15, 30, 45
GPPsat	Gross Primary Productivity at light saturation [umol CO_2 m^{-2} s^{-1}]	Ecosystem function	computed as the 90th percentile estimated from half-hourly data by fitting the hyperbolic light response curves	0, 15, 30, 50
Rb	Mean basal ecosystem respiration at a reference temperature of 15 °C [umol CO_2 m^{-2} s^{-1}]	Ecosystem function	derived from night-time NEE measurements	0, 2, 4, 12
Nmass	ecosystem scale foliar nitrogen concentration [gN 100 g^{-1}]	Plant trait	computed as the community weighted average of foliar N% of the major species at the site sampled at the peak of the growing season or gathered	0.5, 1.25, 2.0, 4.5

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			from the literature (Musavi et al., 2016, 2015; Fleischer et al., 2015; Flechard et al., 2020)	
LAImax	Maximum Leaf Area Index [m^2 m^{-2}]	Plant trait	collected from the literature (Migliavacca et al., 2011; Flechard et al., 2020), the FLUXNET Biological Ancillary Data Management (BADM) product, and/or site principal investigators	0, 3, 6, 13
Hc	Maximum vegetation height [m]	Plant trait	collected from the literature (Migliavacca et al., 2011; Flechard et al., 2020), the BADM product, and/or site principal investigators	0, 5, 20, 80
AGB	Aboveground Biomass derived from the Globbiomass project [t DM ha^{-1}]	Plant trait	extracted from the satellite-based GlobBiomass dataset (Santoro et al., 2021)	0, 50, 150, 350
SWin	Mean incoming shortwave radiation [W m^{-2}]	Climate	from FLUXNET data	50, 125, 200, 275
Tair	Mean temperature [degree C]	Climate	from FLUXNET data	-12, 5, 15, 30
VPD	Mean Vapor Pressure Deficit [hPa]	Climate	from FLUXNET data	0, 4, 8, 27
P	Mean annual precipitation [cm/year]	Climate	from FLUXNET data	0, 40, 80, 260
CSWI	cumulative soil water index	Climate-related soil water availability	computed as a measure of water availability (Nelson et al., 2018)	-100, -20, 0, 5

2.2 BN for analyzing causal relations

2.2.1 BN structures

Based on expert knowledge (Reichstein et al., 2014), we constructed the structure of BN containing the causal relationships between plant traits and ecosystem function variables: 'BN_plant_trait'. The causal links between the variables were referred to the relationship diagram in the upper part of Figure 1. Further, we added the

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109 climate variables and the corresponding causal relationships, expanding 'BN_plant_trait' to
110 'BN_plant_trait+climate', which further incorporates the climate variables and their impacts on the system.
111
112 Each node is discretized for the BN compiling by the software Netica, while the selection of the thresholds for
113 classifications (Table 1) is based on the distribution of the values of each node (Figure 2) and also the meanings
114 of the thresholds. In this step, the three-level discretization (the distribution of a node is divided into three
115 levels) for each node is applied given the limitation of the amount of training data.
116

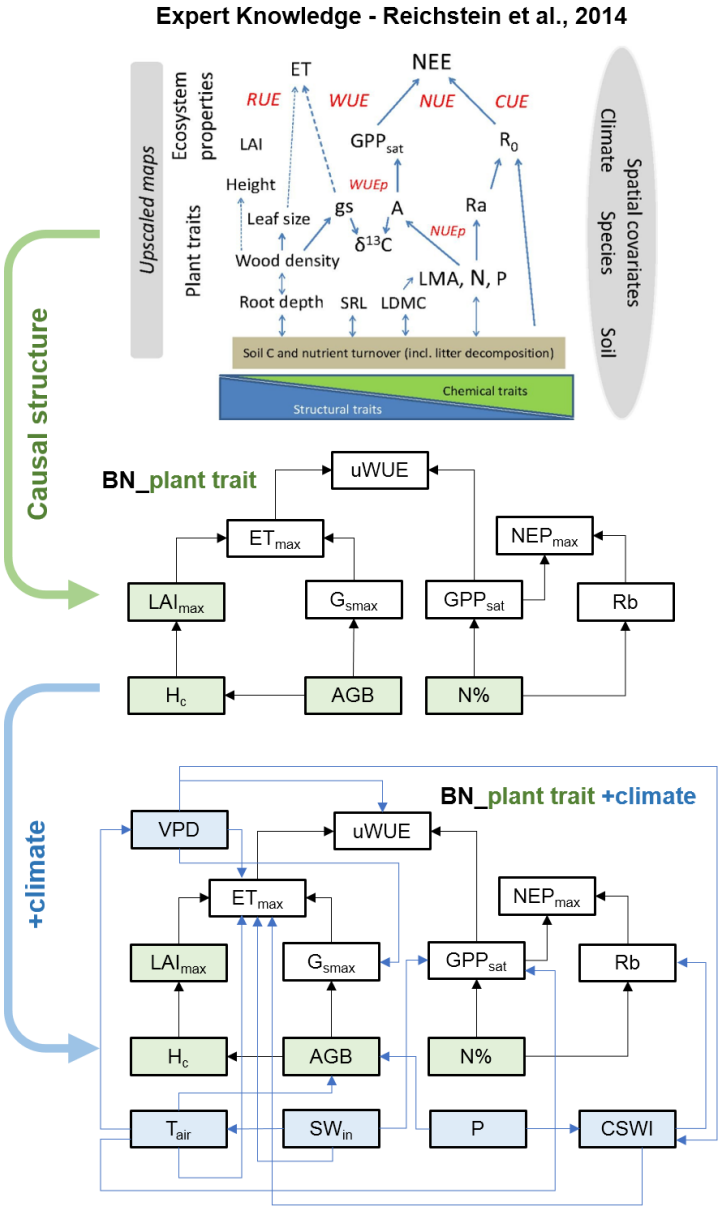

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Figure 1. The structure of two Bayesian networks (BNs) for attribution of variations in ecosystem functions. BN_pure in the lower left part assumes that all variables of plant traits (box in slight green) and climate (box in slight blue) directly affect the ecosystem function variables (box in white). 'BN_plant_trait' in the median part incorporated the causal effects of plant traits (box in slight green) on ecosystem functions (box in white) from expert knowledge as the relation diagram on the upper part (Reichstein et al., 2014). 'BN_plant_trait+climate' in the lower part further incorporated the causal impacts of climate variables (box in light blue).

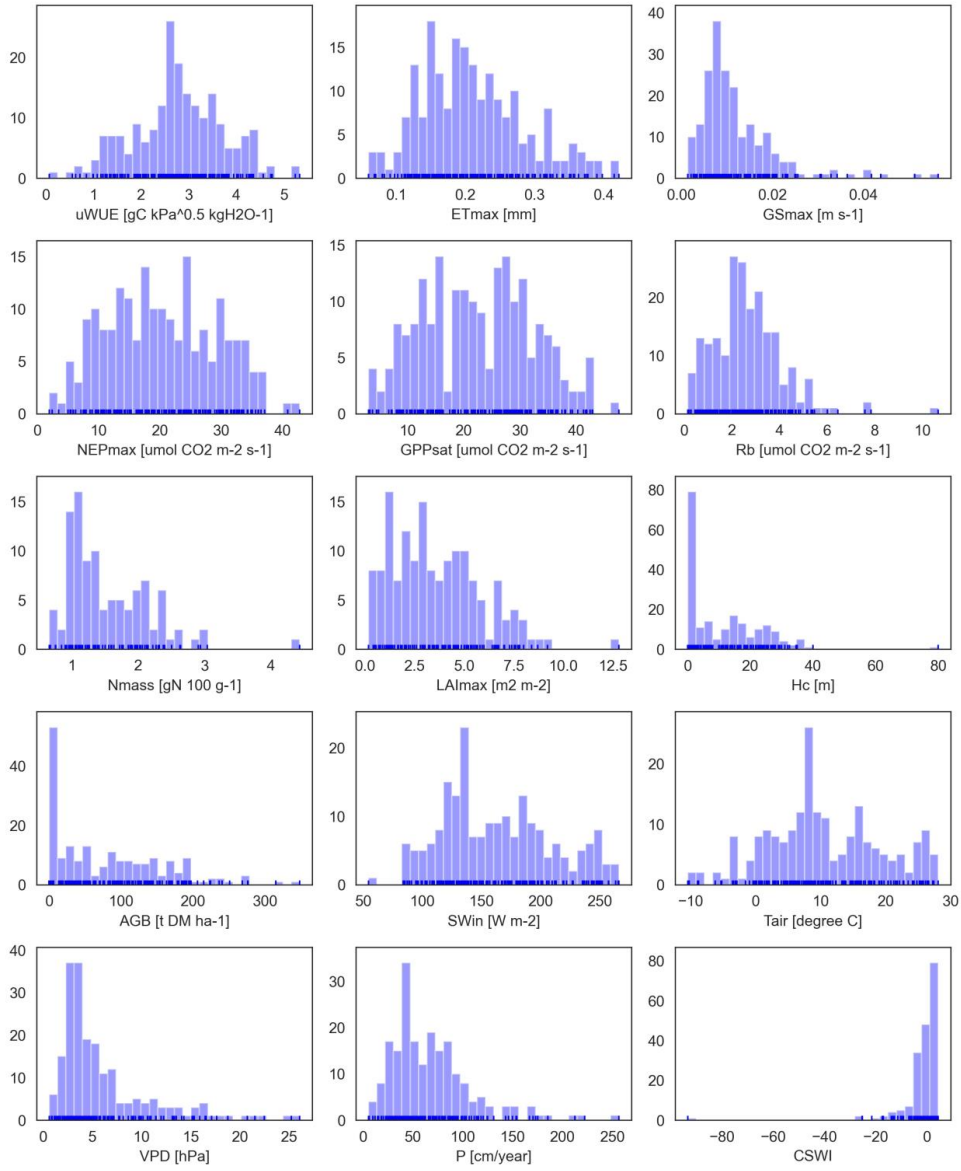

Figure 2. Distributions of values of ecosystem functions and climate and plant trait variables. The vertical axis indicates the number of flux stations.

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2.2.2 Sensitivity analysis based on BN

Based on the Bayesian network (BN), the joint impacts of multiple variables and their causal relations are analyzed. A BN can be represented by nodes X_1, X_2, X_3 to X_n and the joint distribution (Pearl, 1985):

$$\mathrm{Pa}(X) = \mathrm{Pa}(X_1, X_2, \ldots, X_n) = \prod_{i=1}^{n} \mathrm{Pa}\left(X_i \middle| \mathrm{pa}(X_i)\right) \quad (1)$$

where $\mathrm{pa}(X_i)$ is the probability of the parent node X_i. Expectation-maximization (Moon, 1996) is used to address the data with missing values and then compile the BN.

Sensitivity analysis is used for the evaluation of the strength of the causal relations between nodes based on mutual information (MI). MI is calculated as the entropy reduction of the child node resulting from changes found at the parent node (Shi et al., 2020a):

$$\mathrm{MI} = \mathrm{H(Q)\text{-}H(Q|F)} = \sum_q \sum_f P(q, f) \log_2 \left(\frac{P(q,f)}{P(q)P(f)}\right) \quad (2)$$

where H represents the entropy, Q represents the target node, F represents the set of other nodes and q and f represent the status of Q and F.

In this study, we assessed the sensitivity of ecosystem function variables to climate and plant trait variables. Further, to clarify the adding-values of considering causality in the attribution analysis of controls on ecosystem functions, the results of the BN-based sensitivity analysis were compared with the results of additional linear correlation analysis and the previous study using RF (Migliavacca et al., 2021) without considering the causality by comparing the ranking of MI, IMP (the feature importance metric of RF), and Pearson correlation coefficients (the metric of linear correlation analysis) of climate and plant trait variables and their differences in the results of the three methods. Although six ecosystem function variables were directly used in this study, the target variables of the RF-based approach were the first three principal components (PC): PC1, PC2, and PC3 (Migliavacca et al., 2021) of the 12 ecosystem variables (including the six variables selected in this study), the connotations of the target variables were relatively consistent between them.

3 Results

3.1 Correlation analysis

Linear correlation analysis of the variables (Figure 3) showed significant ($P < 0.05$) linear correlations between the ecosystem function variables and some of the climate and plant trait variables. SWin, VPD, and showed negative correlations with these ecosystem function variables. In addition, the majority of the ecosystem function variables showed significant ($P < 0.05$) positive correlations with each other.

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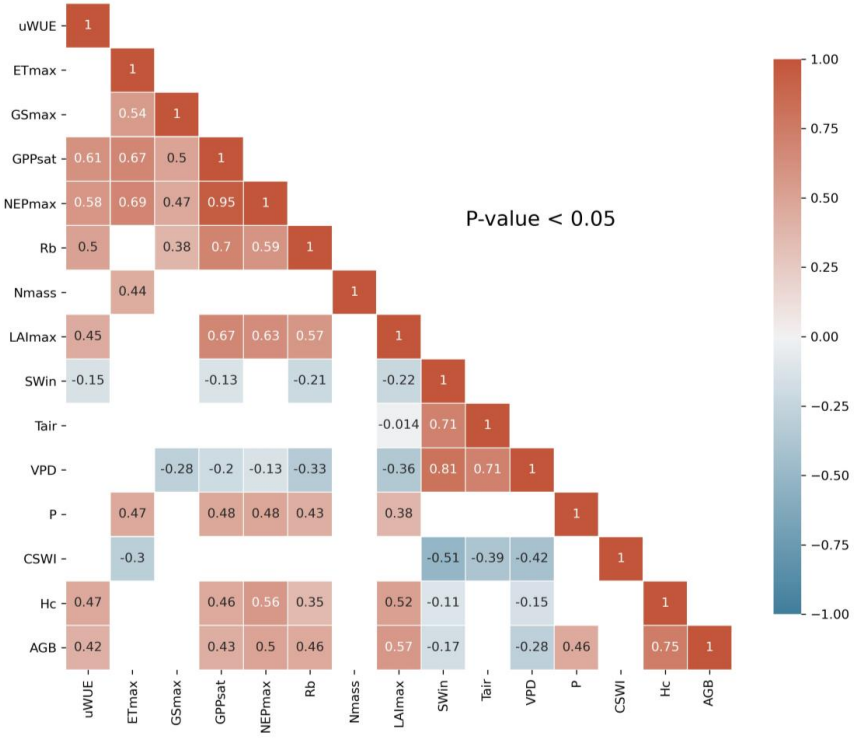

Figure 3. Correlation coefficient matrix of ecosystem service functions and climate and plant trait variables for FLUXNET sites. Only correlation coefficients with p-values less than 0.05 level of significance are shown.

3.2 BN-based analysis

We compiled two different BNs (i.e., BN_plant_trait and BN_plant_trait_climate) (Figure 4) and found that the probability distributions of the values of the common nodes (ecosystem function and plant trait variable nodes) differed little between the two BNs. This indicates that the compilation was successful and that the inclusion of climate variables in BN_plant_trait_climate did not alter the fit of the local networks of ecosystem function and plant trait variables of BN_plant_trait.

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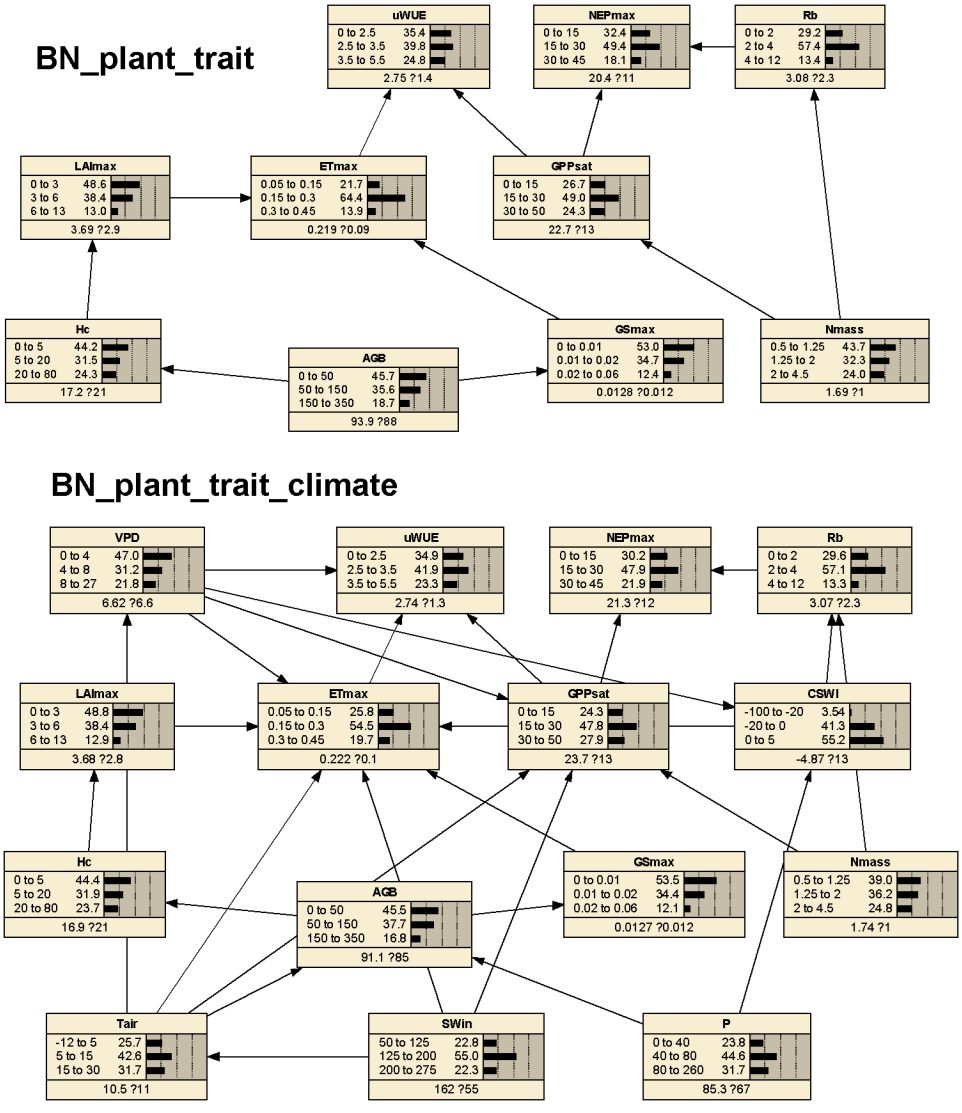

Figure 4.The compiled two BNs ('BN_plant_trait' and 'BN_plant_trait_climate'). The bars of each node represent its probability distribution. At the bottom part of each node, the left and right side values of the '?' are the mean and standard deviation of the distribution, respectively.

We performed sensitivity analyses (Figure 5) on the ecosystem function variables in both BNs to assess their sensitivity to various climate and plant trait variables. We also calculated the difference in sensitivity MI between the two BNs (Figure 5) to compare the change in sensitivity of ecosystem function to each variable after adding further climate variables to the plant trait variables only.

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The sensitivity of different ecosystem function variables to plant traits and climate variables was highly variable in both BNs (except for the similar pattern between GPPsat and NEPmax). The magnitude of sensitivity of ecosystem functional nodes to plant traits and climate variables was related to whether these plant traits and climate variables were set as their parent nodes. In BN_plant_trait, for the carbon fluxes GPPsat and NEPmax, Nmass had a higher sensitivity due to Nmass being set as their parent node. For the water flux ETmax, it does not have high sensitivity to plant trait variables such as LAImax, Hc, and AGB, although these plant trait variables are set as the parent nodes of ETmax. This indicates the difference in the strength of the control effects of plant traits on carbon and water fluxes.

In the sensitivity analysis of BN_plant_trait_climate, the sensitivity patterns of the ecosystem function variables changed as a result of the inclusion of climate variables and the change in causality they introduced. The sensitivity of the ecosystem function variables (except GSmax and Rb) to climate variables was significantly increased (especially for Tair and VPD). Their sensitivity to plant trait variables (e.g., Nmass and LAImax) decreased. Among the controls for ETmax and uWUE, climate variables showed a role beyond plant traits, while among the controls for GPPsat and NEPmax, the climate variable Tair also showed a significant role at a similar level to Nmass. The control of plant traits on ecosystem function in BN_plant_trait is also partially transformed into an indirect effect of climate variables by first controlling plant trait variables and then controlling ecosystem function. For example, in BN_plant_trait_climate, for ETmax, a decrease in the sensitivity of ETmax to LAImax and an increase in the sensitivity to Tair was observed after the loop of Tair controlling LAImax and then ETmax was set. This can be explained by the fact that higher temperatures promote vegetation growth and thus may increase LAImax, which then indirectly contributes to the increase in ETmax. In previous studies based on statistical methods that did not consider the systematic causality, this indirect control on ETmax from Tair may have been included in the contribution of LAImax to ETmax.

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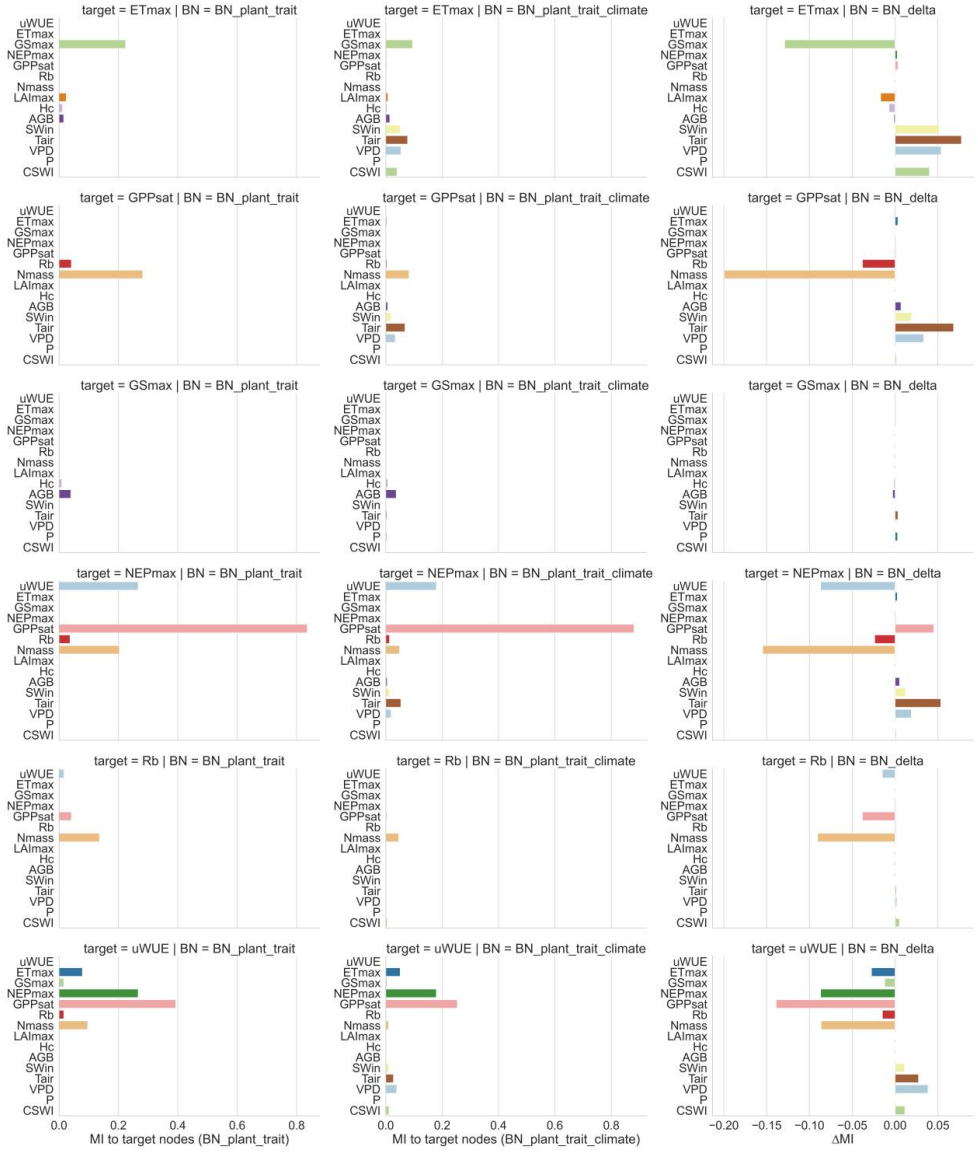

Figure 5. Sensitivity of ecosystem function variables to other variables in different networks based on mutual information (MI). The left column is the sensitivity analysis of BN_plant_trait, the middle column is the sensitivity analysis of BN_plant_trait_climate, and the right column is the difference between the reported sensitivity of BN_plant_trait_climate and the sensitivity of BN_plant_trait. For BN_plant_trait, the MI values of climate variables to ecosystem function variables are all 0 because they do not contain climate variables. For each ecosystem function in these two BNs, its sensitivity to its child node is not shown (set as 0) because child nodes are not considered causal variables and thus are not evaluated in the attribution.

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3.3 Comparing results from RF-based, BN-based analysis, and correlation analysis

To compare the differences between cause-based and non-cause-based attribution or contribution analyses, we compared the importance ranking of variables based on the RF-based IMP in the study of Migliavacca et al., the absolute values of the correlation coefficients from the correlation analysis in this study, and the values of MI from the BN-based sensitivity analysis.

Since plant traits such as LAImax, Hc, and AGB were not set as parent nodes of carbon fluxes such as NEPmax and GPPsat in BN in this study, the effects of LAImax, Hc, and AGB on carbon flux-related variables in ecosystem function were weaker in the BN-based sensitivity analysis than in the RF-based and correlation analyses. However, AGB did not show a significant linear correlation with GSmax in the correlation analysis, suggesting that its control effect on GSmax may be nonlinear but detected by both RF and BN-based attribution analyses. Of the meteorological variables, Tair showed stronger control over ecosystem function variables in the BN-based attribution (compared to other climate and plant trait variables), implying that the RF-based imputation of IMP may have underestimated the role of Tair.

	Methods	Nmass	LAImax	Hc	AGB	SWin	Tair	VPD	P	CSWI
PC1	RF_imp	10.80%	16.60%	14.50%	15.50%	7.60%	9.10%	11.70%	6.70%	4.00%
PC2	RF_imp	5.10%	4.50%	14.90%	5.10%	10.70%	11.20%	7.40%	9.00%	8.30%
PC3	RF_imp	7.00%	2.80%	5.40%	10.70%	9.30%	8.00%	15.40%	6.50%	4.90%
uWUE	BN_sens	0.010	0.000	0.000	0.001	0.011	0.027	0.038	0.000	0.011
ETmax	BN_sens	0.000	0.008	0.005	0.014	0.051	0.077	0.054	0.001	0.040
GSmax	BN_sens	0.000	0.002	0.008	0.037	0.000	0.003	0.000	0.003	0.000
NEPmax	BN_sens	0.049	0.000	0.000	0.005	0.012	0.053	0.019	0.000	0.001
GPPsat	BN_sens	0.082	0.000	0.000	0.007	0.019	0.068	0.033	0.000	0.002
Rb	BN_sens	0.046	0.000	0.000	0.000	0.000	0.001	0.002	0.000	0.005
uWUE	linear_corr		0.45	0.47	0.42	0.15				
ETmax	linear_corr	0.44							0.47	0.30
GSmax	linear_corr							0.28		
NEPmax	linear_corr		0.63	0.56	0.50			0.13	0.48	
GPPsat	linear_corr		0.67	0.46	0.43	0.13		0.20	0.48	
Rb	linear_corr		0.57	0.35	0.46	0.21		0.33	0.43	

Figure 6. Comparisons of relationships of ecosystem functional variables to plant traits and climate variables in different analyses. Method RF_imp is Random forest variable importance (Migliavacca et al., 2021). Method linear_corr is Linear correlation analysis with the absolute values of Pearson correlation coefficients. Method BN_sens is a BN-based sensitivity analysis with sensitivity values MI reported. PC1, PC2, and PC3 are the first three major axes of ecosystem function reported in the study by Migliavacca et al. (Migliavacca et al., 2021) obtained from principal component analysis of 12 ecosystem function variables which including the six variables uWUE, ETmax, GSmax, NEPmax, GPPsat, and Rb used in this study (Method BN_sens and linear_corr in the lower part). The first axis (PC1) explains 39.3% of the variance and is dominated by maximum ecosystem productivity properties, as indicated by the loadings of GPPsat and NEPmax, and maximum evapotranspiration (ETmax). The second axis (PC2) explains 21.4% of the variance and refers to water-use strategies as shown by the loadings of water-use efficiency metrics, evaporative fraction, and GSmax. The third axis (PC3) explains 11.1% of the variance and includes key attributes that reflect the carbon-use efficiency of ecosystems. PC3 is dominated by apparent carbon-use efficiency, basal ecosystem respiration

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(Rb), and the amplitude of evaporative fraction (Migliavacca et al., 2021). The values in each row are in red for high values and in blue for low values, for rows with very few values, the color-based indication is not reliable in ranking the control effects of plant traits and climate variables.

4 Discussions

Previous studies of 'climate-plant trait-ecosystem function' relationships have predominantly used only non-causal statistical methods such as RF (Migliavacca et al., 2021). Based on BN, this study investigates the prospect of using causal networks to revisit and attribute the control of climate and plant trait changes to ecosystem function. Compared to traditional correlation analysis and machine learning methods, BN can uncover the effects of causal relationships between variables. This causality discovery can improve on previous findings for studies of ecosystem-climate interactions.

Because of the inclusion of the constraints provided by expert knowledge (Reichstein et al., 2014), BN-based attribution analysis is relatively reliable and can update our knowledge of the contribution of some teleconnection variables through causal chains. However, since the structure of the expert knowledge graph did not connect LAImax, Hc, and AGB to GPP (Figure 1), LAImax, Hc, and AGB are not set as parent nodes of GPPsat in our BN, and thus the sensitivity of carbon fluxes to LAImax, Hc, AGB, etc. is 0 or close to 0. Therefore, in our BN, the causal controls of LAImax, Hc, and AGB on GPPsat are not shown although they are commonly thought to strongly influence GPPsat and NEPmax. This also demonstrates from another perspective the importance of a reasonable parent node in the attribution analysis using BN, where if a variable cannot be connected to the target variable through a causal loop, the sensitivity of the target variable to it may be low, and this will therefore affect the assessment of the strength of causality. If we want to explicitly measure the response of the target variable to the causality of a variable, it is indeed necessary to set up a causal link between them in BN.

In this study, it was found that the indirect impacts of some meteorological variables such as Tair may be underestimated in the attribution of ecosystem function when using a non-causal approach. This suggests the feasibility of quantifying indirect causal effects among various variables to help us gain a more systematic understanding. The effective implementation of BN-based causal analysis may depend on the reliability of the causal relationships provided by expert knowledge (directional links between variables). We can establish the connection relationships and network structures between variables from expert knowledge and assign the specific quantification of the connection relationships (conditional probability tables) to the observations and data (Shi et al., 2021a). In the future, we can revisit the linkages of ecosystem functions with climate and environmental systems using BN-based causal analysis to understand the strength and mechanisms of the relationships between direct, indirect, and remotely related effects of variables. Such a data-driven causal analysis framework provides more structured information about climate, plant traits, and ecosystem systems, thus making the data-driven approach more transparent and interpretable (compared to previous black-box models (Rudin, 2019)). If further combined with findings from process-based models, it is promising to significantly improve our understanding of the complex 'climate-plant trait-ecosystem function' relationships by comparing detailed relationships and structural influences between variables.

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Besides, the BN in this study was mainly based on data averaged over multiple years, thus possibly partially underestimating the effect of temporal variations in the relationships between variables. Another limitation of the BN proposed above is that the causal relationships between variables are unidirectional, while it is difficult to represent interactions and feedback between variables (Marcot and Penman, 2019). In future studies, to address these two issues, BN based on temporal dynamics can be promising (Figure 7). By refining the interaction of temporal lags between variables, it is possible to incorporate not only temporal variation but also control factors that attribute interactions and feedback between variables. For example, the interaction and feedback mechanisms of VPD, soil moisture, and ET with lag effects (Figure 7) and their impacts on ecosystems have attracted extensive interest from researchers (Anderegg et al., 2019; Humphrey et al., 2021; Lansu et al., 2020; Liu et al., 2020; Xu et al., 2022; Zhou et al., 2019), but conventional statistical methods have been ineffective in analyzing such relationships with both interactive causality and temporal lags. In contrast, the BN proposed here, which incorporates feedback effects and lagged effects that were common in climate-ecosystem relations (Lin et al., 2019), is potentially able to address this issue from a data-driven approach. When further combined with the findings of process-based models, our understanding of climate and ecosystem interactions and feedback and their mechanisms in time is hopefully deepened.

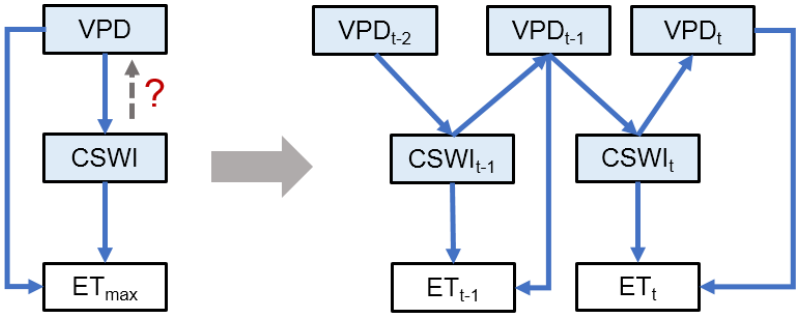

Figure 7. The future BNs with the temporal causality further considered addressing the causality of the interaction between variables. The VPD-CSWI-ET relationship is used here as an example. t, t-1, and t-2 denote the current period, the last period, and the period before the last period, respectively. The network on the left only considers the effect of VPD on CSWI without considering the feedback of CSWI on the VPD. The network on the right characterizes the VPD-CSWI interaction with the feedback from CSWI at period t-1 to VPD at period t.

5 Conclusion

By emphasizing causality, based on BN, we revisited and attributed the contribution of climate and plant traits to global terrestrial ecosystem function. The major conclusions of this study include:

1. BN can be used for the quantification of causal relationships between complex ecosystems and climatic and environmental systems and enables the analysis of indirect effects among variables.

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2. The control of ecosystem function by climate variables (especially Tair and VPD) may have been underestimated in the past, and the mechanism of indirect effects of climate variables on ecosystem function through plant traits should be emphasized in future studies.
3. Further inclusion of temporal information in BN holds promise for improving the analysis of lagged effects and interactions and feedback effects between variables.

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Financial support

This research was supported by the National Natural Science Foundation of China (Grant No. U1803243), the Key projects of the Natural Science Foundation of Xinjiang Autonomous Region (Grant No. 2022D01D01), the Strategic Priority Research Program of the Chinese Academy of Sciences (Grant No. XDA20060302), and High-End Foreign Experts Project.

Author Contributions

HS and GL initiated this research and were responsible for the integrity of the work as a whole. HS performed formal analysis and calculations and drafted the manuscript. HS were responsible for the data collection and analysis. GL, PDM, TVdV, OH, and AK contributed resources and financial support.

Competing interests

The authors declare that they have no conflict of interest.

Code availability

The codes that were used for all analyses are available from the first author (shihaiyang16@mails.ucas.ac.cn) upon request.

Data availability

The data used in this study can be accessed by contacting the first author (shihaiyang16@mails.ucas.ac.cn) upon request.

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