Dynamic process connectivity explains ecohydrologic responses to rainfall pulses and drought

Allison E. Goodwell^{a,b}, Praveen Kumar^{a,1}, Aaron W. Fellows^c, and Gerald N. Flerchinger^c

^aDepartment of Civil and Environmental Engineering, University of Illinois at Urbana–Champaign, Urbana, IL 61801; ^bDepartment of Civil Engineering, University of Colorado Denver, Denver, CO 80217; and ^cNorthwest Watershed Research Center, Agricultural Research Service, US Department of Agriculture, Boise, ID 83712

Edited by Ignacio Rodriguez-Iturbe, Texas A&M University, College Station, TX, and approved July 26, 2018 (received for review January 7, 2018)

Ecohydrologic fluxes within atmosphere, vegetation, and soil systems exhibit a joint variability that arises from forcing and feedback interactions. These interactions cause fluctuations to propagate between variables at many time scales. In an ecosystem, this connectivity dictates responses to climate change, land-cover change, and weather events and must be characterized to understand resilience and sensitivity. We use an information theory-based approach to quantify connectivity in the form of information flow associated with the propagation of fluctuations between variables. We apply this approach to study ecosystems that experience changes in dry-season moisture availability due to rainfall and drought conditions. We use data from two transects with flux towers located along elevation gradients and quantify redundant, synergistic, and unique flow of information between lagged sources and targets to characterize joint asynchronous time dependencies. At the Reynolds Creek Critical Zone Observatory in Idaho, a dry-season rainfall pulse leads to increased connectivity from soil and atmospheric variables to heat and carbon fluxes. At the Southern Sierra Critical Zone Observatory in California, separate sets of dominant drivers characterize two sites at which fluxes exhibit different drought responses. For both cases, our information flow-based connectivity characterizes dominant drivers and joint variability before, during, and after disturbances. This approach to gauge the responsiveness of ecosystem fluxes under multiple sources of variability furthers our understanding of complex ecohydrologic systems.

process network | critical zone | ecohydrology | information decomposition

Ecohydrologic systems are complex networks where time-dependent interactions occur between and within atmosphere, vegetation, and soil subsystems. These interactions involve forcing and feedback that cause fluctuations in a single component to propagate through the entire network. This propagation and its attenuation or amplification can also be thought of as a flow of information between interacting network components. Together, these interactions dictate large-scale behaviors such as responses to drought or changes in climate. For example, in the recent drought in California, multiple time-varying processes influenced the impact of drought on streamflow (1). These included intensifying mechanisms, such as enhanced evapotranspiration due to warmer temperatures and increased allocation of rainfall to evapotranspiration over runoff, and mitigating mechanisms, such as redistribution of soil moisture and vegetation thinning. While these dependencies between landscape, climate, and ecohydrologic fluxes influence aggregate responses such as streamflows, changing moisture availability also influences ecohydrologic fluxes locally and on an individual-event time scale. For instance, rainfall pulses in semiarid regions impact soil moisture and consequently the energy balance due to dependencies involving altered surface albedo, emitted radiation, clouds, and surface temperature (2). Due to such complex and joint variability at both short and long time scales, we must quantify multivariate dependencies to understand how distur-

bances can cause changes in water and heat flux partitioning, ecosystem water use, and net carbon fluxes along elevation and climate gradients.

Eddy covariance flux tower measurements are valuable datasets with which to characterize states and fluxes and identify feedback between processes. The increasing availability of this type of data enables us to characterize connectivity between interacting components through their joint, contemporaneous or lagged, variability in many types of ecosystems. In this paper, we take a complex network perspective (3, 4) and define the set of time-dependent couplings between fluctuations in observed variables as process connectivity (5–8). We use information theory measures to show how connectivity within a process network of environmental variables (9–12) relates the sensitivity of energy and carbon fluxes to changes in moisture availability, as shaped by the propagation of fluctuations. We focus specifically on the disturbances of (i) dry-season rainfall pulses that occur on daily to weekly time scales and (ii) accumulating drought over annual time scales. We use observed time-series data of a range of variables along two transects with eddy covariance flux towers to (i) identify how process connectivity maps to ecosystem responses along an elevation gradient and (ii) characterize the relative sensitivity of different ecosystem fluxes to the altered conditions.

We hypothesize that changes in the partitioning of energy and water and production or uptake of CO₂ by the ecosystem due to altered moisture availability will be associated with

Significance

In the face of changing climate, weather variability, and land cover, it is important to understand how ecosystem components vary jointly to determine how the system responds as a whole. While previous works have identified thresholds along climate gradients regarding precipitation, soils, and vegetation, we relate these thresholds to shifts in connectivity between variables, captured through joint variability, to better understand whole-system attributes of resilience, sensitivity, and vulnerability. We use data from flux tower transects along elevation gradients to address the relationship between joint connectivity and energy, water, and carbon flux responses to changes in moisture availability. This analysis reveals differences in joint variability between locations that can help explain responses to disturbances such as rain events or drought.

Author contributions: A.E.G. and P.K. designed research; A.E.G. and P.K. performed research; A.W.F. and G.N.F. collected some of the data; A.E.G. and P.K. interpreted results; A.W.F. and G.N.F. contributed to interpretation of results; and A.E.G. and P.K. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

¹To whom correspondence should be addressed. Email: kumar1@illinois.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1800236115/-DCSupplemental.

Published online August 27, 2018.

changes in process network connectivity, and that these relations can reveal mechanisms behind ecosystem responses that are either site-specific or common across the elevation gradient. Previous works have identified thresholds for different ecosystems linking precipitation amount and seasonality, plant species dormancy, and soil properties along elevation and climate gradients based on in situ or remotely sensed measurements (13–18). Information theory (19, 20) and nonlinear methods have also been used to characterize dependencies between eddy covariance variables (9, 10, 21–25). This study is distinctive in that it relates behavioral thresholds to shifts in joint variability, or process connectivity, as forcing and feedback relations alter. This is based on an approach for using information partitioning to characterize the nature of joint dependencies before, during, and after environmental disturbances.

In our framework, information theory metrics, which quantify uncertainty (Shannon's entropy) and reductions in uncertainty (mutual information), are used to quantify and characterize nonlinear and multivariate dependencies between fluctuations in ecohydrologic variables. In a process network, connectivity is defined in terms of shared information between lagged "source" variables and current "target" variables. That is, when the knowledge of lagged sources reduces the uncertainty of a target variable, we say that the sources are connected to the target. Process networks have previously been constructed to analyze the influence of weather conditions on joint variability of atmospheric states (11, 12), seasonal connectivity between ecosystem fluxes (9, 10), atmosphere and biosphere elasticity to climate forcing (26), and spatial and temporal connectivity within a delta system (8, 27). In this work we use the recently developed Temporal Information Partitioning Network (TIPNet) approach (11, 12), which identifies multivariate asynchronous dependencies and their composition in terms of synergistic (S), unique (U), and redundant (R) information transfer from sources to target variables (28). Synergy is information provided to the target only when two sources act jointly, uniqueness is information that only one source provides individually, and redundancy is overlapping information that two or more sources provide (Fig. 1 *A* and *B*). While there are many ways to identify dependencies, this partitioning of multivariate shared information into S , U , and R components enables us to unambiguously characterize nonlinear and lagged dependencies and the extent to which drivers of variability are independent (unique), joint (synergistic), or overlapping (redundant) (Fig. 1 *A* and *B*).

We use the TIPNet framework to study data from eddy covariance flux towers along elevation transects at Reynolds Creek Critical Zone Observatory (RC-CZO) in Idaho and Southern Sierra Critical Zone Observatory (SS-CZO) in California (*SI Appendix, Figs. S3 and S4* and Table 1). These sites, particularly the lower-elevation sites along each transect, constitute water-limited ecosystems that can be particularly sensitive to variability in water and energy availability and exhibit nonlinear behaviors (29). At each site, we compare carbon and heat flux responses to changes in process connectivity measures before and after moisture-related disturbances. Specifically, we analyze changes in information transfer relative to fluxes during a dry-season rainfall pulse at RC-CZO (*SI Appendix, Fig. S3B*) and a multiyear drought at SS-CZO (*SI Appendix, Fig. S4 B and C*). Between two given time windows (e.g., T_1 and T_2 in Fig. 1), process connectivity and environmental indicators, such as time-averaged fluxes, may be linked indirectly or directly, or unrelated. For example, increased process connectivity and increased average carbon flux (F_c) may indicate that increasing outward carbon fluxes are associated with increased joint variability of F_c with source variables such as soil moisture, temperature, or wind. Alternately, a flux may exhibit a change in either magnitude or joint variability, but not both, indicating a disconnect between

Fig. 1. In TIPNets, time-series variables are considered as nodes, and information theory measures identify time-dependent links from sources X_{s1} , X_{s2} , X_{s3} , and so on, to target X_{tar} . (A) Time-series datasets are segmented into multiple windows, for example T_1 and T_2 , to capture dynamics before or after some disturbance. (B) Illustration of information transfer from three source nodes to a target node, where components shift in strength between two time windows. A single source may provide information uniquely (U), and pairs of sources may provide redundant (R) or synergistic information (S). (C and D) We compare changes in S , U , and R information transfer to a target to changes in the state of a target variable (e.g., a measured eddy covariance flux) between time windows to map the stability of a variable to a shift in connectivity. A target variable and its TIPNet characteristics may be inversely related ($-+$, $+ -$), directly related ($++$, $--$), disconnected ($0+$, $0-$, -0 , $+0$), or stable (00).

magnitude and process connectivity. This could occur if an external or unmeasured driver causes a flux to appear independent of other observed ecosystem components, or if source or target variability is highly constrained. This mapping of ecohydrologic fluxes to process connectivity allows us to understand how forcing and feedback are linked to ecosystem states under different types of disturbances.

2. Flux Tower Study Sites

In southwestern Idaho, the RC-CZO maintains a transect of four flux towers, WB (Ameriflux site US-Rws), LS (Ameriflux site US-Rls), PS, and MS (Ameriflux site US-Rms), along an elevation and climate gradient from north to south (14). Northern sites are at lower elevation and receive lower annual rainfall relative to the southern sites (Table 1 and [SI Appendix, section 2 and Fig. S1](#)). Along this transect, we analyze changes in process connectivity between net carbon flux (F_c), latent heat flux (LE), sensible heat flux (H), and ground heat flux (G), and atmospheric and soil conditions before and after a rainfall pulse in July 2015 ([SI Appendix, Fig. S3 B and C](#)). In California, the SS-CZO also maintains a transect of four flux towers along an elevation gradient. We focus on the middle two, Soaproot Saddle (SR, Ameriflux site US-CZ2) and Providence Creek (PC, Ameriflux site US-CZ3), due to longer-term data availability over the 6-yr

Table 1. Site details for RC-CZO and SS-CZO flux tower transects

Flux tower name	Short name	Elevation, m	Latitude	Longitude	Vegetation	Mean annual precipitation, mm	Study period
Wyoming Big Sage (Ameriflux US-Rws)	WB	1,425	43.1675	−116.7132	Wyoming sage	292	June–July 2015–2016
Lower Sheep (Ameriflux US-Rls)	LS	1,608	43.1439	−116.7356	Low sage	333	June–July 2015–2016
Upper Sheep (138h08ec)	PS	1,878	43.1207	−116.7231	Postfire sage	505	June–July 2015–2016
Mountain Big Sage (Ameriflux US-Rms)	MS	2,111	43.0645	−116.7486	Mountain big sage	800	June–July 2015–2016
Soaproot Saddle (Ameriflux US-CZ2)	SR	1,160	37.0306	−119.2562	Ponderosa pine and oak	805	June–August 2010–2015
Providence Creek P301 (Ameriflux US-CZ3)	PC	2,015	37.067432	−119.1935	Sierran mixed conifer	1,015	June–August 2010–2015

period before and during the recent California drought (Table 1 and *SI Appendix, section 2 and Fig. S2*). Here, we analyze process connectivity between measured fluxes and atmospheric and soil variables before and during the drought. Details on the SS-CZO and RC-CZO sites can be found in *SI Appendix, section 2, Table S1, and Figs. S2–S5*.

3. TIPNets

A. Information Partitioning Measures. In a network of interacting variables, a given variable may be considered as a “target” of information at a current time step ($X_{tar} = X(t)$) or a “source” at a lagged time step ($X_s = X(t - \tau)$). We use Shannon information theory (19) measures to characterize joint variability through the information transfer between source and target variables. The shared information between two time-lagged source variables X_{s1} and X_{s2} and one target variable X_{tar} is the mutual information:

$$I(X_{s1}, X_{s2}; X_{tar}) = \sum p(x_{s1}, x_{s2}, x_{tar}) \log_2 \left(\frac{p(x_{s1}, x_{s2}, x_{tar})}{p(x_{s1}, x_{s2})p(x_{tar})} \right). \quad [1]$$

We use measures based on information partitioning, or information decomposition (28, 30), to classify the nature of multivariate shared information in terms of synergistic (S) or joint, unique (U_1 , U_2) or individual from one of the two sources, and redundant (R) or overlapping, components. In this framework, information provided from any two lagged sources to a target can be defined as the sum of S , U_1 , U_2 , and R . For two sources X_{s1} and X_{s2} and one target X_{tar} , the mutual information $I(X_{s1}, X_{s2}; X_{tar})$, $I(X_{s1}; X_{tar})$, and $I(X_{s2}; X_{tar})$ can be partitioned as follows (28):

$$I(X_{s1}, X_{s2}; X_{tar}) = U_1(X_{s1}; X_{tar}) + U_2(X_{s2}; X_{tar}) + R(X_{s1}, X_{s2}; X_{tar}) + S(X_{s1}, X_{s2}; X_{tar}) \quad [2]$$

$$I(X_{s1}; X_{tar}) = U_1(X_{s1}; X_{tar}) + R(X_{s1}, X_{s2}; X_{tar}) \quad [3]$$

$$I(X_{s2}; X_{tar}) = U_2(X_{s2}; X_{tar}) + R(X_{s1}, X_{s2}; X_{tar}). \quad [4]$$

If one source provides a larger amount of information than another (e.g., $I(X_{s1}; X_{tar}) > I(X_{s2}; X_{tar})$), as reflected through a higher reduction in uncertainty of the target, it will have a higher uniqueness (U), indicating its dominant influence as an individual source. A high synergy (S) indicates that two sources provide information jointly, since both sources must be known together to reduce target uncertainty. In contrast, redundancy

(R) indicates an overlap in information due to lagged synchronization or correlation between sources, and the extent to which either source reduces the same target uncertainty.

Since mutual information quantities in Eqs. 2–4 are directly computable, one of the four components S , U_1 , U_2 , and R must be obtained independently to solve this underdetermined system. To address this, we perform information partitioning using a recently developed approach (11) where redundancy, R , is obtained based on scaling by source dependency $I(X_{s1}; X_{s2})$, such that independent sources are minimally redundant (maximally unique) and highly dependent sources are assumed to be maximally redundant (minimally unique). A TIPNet for a given time window is composed of all S , U , and R relations between all source pairs and a specified target or set of targets (Fig. 1B). We note that in the TIPNet framework a target variable that serves as a source for other variables could itself be considered as a target, enabling us to capture feedback dependencies. In this application, however, we specify nonoverlapping sets of source and target variables, such that only feedbacks between sources may be captured. For a given target variable, we denote Q as the sum of all information components, that is, $S + U_1 + U_2 + R$ from all pairs of sources, such that Q indicates total information flow to the target. Additional details on the TIPNet approach, probability density function estimation (9, 31–33), and statistical significance testing (9, 33) are provided in *SI Appendix, section 1*.

B. Data Preparation. We consider half-hourly time-series variables measured at the flux towers as nodes in a network, where measured fluxes of LE , H , G , and F_c are targets of information transfer from multiple source variables related to atmospheric and soil conditions (*SI Appendix, Table S1*). We construct process networks for different sites and time windows according to seasons and the timing of the drought in the case of SS-CZO and a dry-season rain pulse at RC-CZO. These selected time windows enable us to explore how network measures change with moisture availability under disturbances. We compute information theory measures using only daytime data, defined based on sunrise and sunset times, to omit differences between nighttime and daytime processes and to avoid eddy covariance errors common to nighttime measurements. We consider time lags from 30 min to 4 h (one to eight time steps of half-hourly data) to capture high-frequency joint variability as opposed to longer-term interactions that would span multiple days. Finally, we take the 5-d anomaly of variables that exhibit a diurnal cycle (*SI Appendix, Table S1*) to focus on fluctuations that occur on these short time scales, rather than magnitudes of variables or longer-term relationships. Details on data preparation are provided in *SI Appendix, section 1B*).

to T_a , since their variabilities are very low. In terms of joint sources, the prevalence of synergy, S , over redundancy, R , for all cases indicates the importance of considering multiple drivers of variability when analyzing ecohydrologic time-series data. As in the example of propagating waveforms, we find that the knowledge of combinations of source variables reduces more target uncertainty than would the knowledge of any single variable. In this study, we do not discuss specific time lags of dominant information transfer for each case, but note that any information measure is associated with a time lag of 4 h, the maximum time lag considered in this application, or fewer. As illustrated here, a TIPNet composed of individual S , U , and R information components between sets of sources and targets and the total information quantity Q characterizes aspects of complex dependencies that are not captured with traditional measures.

4. Results: Response to Rainfall Pulse at RC

A. Whole-Network Shifts over Monthly Time Windows. For the RC-CZO transect, we first study the relationship between target fluxes and process network connectivity on a monthly time scale. For each of the four sites, we define time windows for TIPNet analysis as follows: T_1 = DOY 152–180 (June) and T_2 = DOY 181–210 (July) for both 2015 and 2016 (*SI Appendix, Fig. S2*). We compare changes in fluxes to changes in process connectivity in the form of total information (illustrated in Fig. 1C and D) between time windows. This total information quantity, Q , for a given time window is the sum of S , U_1 , U_2 , and R information components that all pairs of lagged source variables (*SI Appendix, Table S1*) provide to carbon and heat fluxes. From this, we can identify shifts in ecosystem interactions associated with event dynamics, disturbance, or phenological transition. For both years, monthly average LE decreases (Fig. 3A) and F_c increases (Fig. 3D) from June to July, regardless of the rainfall conditions. For the two lower sites, H (Fig. 3B) and G (Fig. 3C) trends reverse in 2015 compared with 2016.

Across the sites, the increase in monthly average F_c from June to July is slightly stronger in 2015 relative to 2016 (larger positive ΔF_c), as outward carbon fluxes increased during and after the rainfall pulse (*SI Appendix, Fig. S3 C and D*). Process connectivity, in the form of total information Q to F_c , increases from June to July in 2015 and decreases in 2016 for all sites. From this we infer that, given a monthly time window, altered connectivity due to the July 2015 rainfall event was sufficient to slightly magnify the seasonal increase in carbon flux. Although the relationship between connectivity and F_c changes from direct in 2015 to inverse in 2016, the mitigated increase in monthly average F_c in 2016 confirms that lower process connectivity leads to lower net upward carbon fluxes, in the form of a mitigated seasonal increase. Similar to ΔF_c , the change in monthly average ground heat flux, ΔG , differs slightly between 2015 and 2016 (Fig. 3C). Meanwhile, total information transfer Q to G increases at all sites in 2015 and decreases at all sites in 2016. From this we infer that process connectivity to G varies due to the moisture availability, but these changes have a relatively weak influence on monthly average G .

Latent heat flux, LE , decreases from June to July for all sites and years to varying extents. However, the July 2015 rainfall pulse is associated with a pulse in LE and increased process connectivity to LE at lower-elevation sites, and a lesser effect at the higher elevations. For 2015, the trend between ΔLE and ΔQ (Fig. 3A) is nearly linear with elevation. Lower-elevation sites, WS and LS, show a small decrease in LE and an increase in Q , while the higher-elevation sites, PS and MS, show larger decreases in LE and a decrease in Q . In the context of the rainfall event in 2015, the added moisture caused a pulse in LE at the lower-elevation sites that was large enough to weaken the seasonal trend of decreasing LE relative to the

Fig. 3. Network analysis of RC flux tower sites for time windows June (T_1) and July (T_2) for 2015 (closed circles) and 2016 (open squares). Relationships between information transfer and state variables are as illustrated in Fig. 1C. The horizontal distance of a point from the origin indicates the change in average monthly LE , H , G , or F_c between June and July of 2015 or 2016. The vertical distance indicates the anomaly in total information transfer ($Q = S + U + R$) over the same time windows. Total information transfer, Q , to (A) LE , (B) H , (C) G , and (D) F_c versus the change in average monthly fluxes (e.g., $\Delta LE = LE_{July,avg} - LE_{June,avg}$) for each site for each year. The rainfall event occurs near the beginning of July in 2015. Colors indicate the site (blue is lower elevation, red is higher elevation). (E) Illustration of different behaviors between sites. High- and low-elevation sites differ in terms of fluxes, while extreme- and middle-elevation sites differ in terms of connectivity.

drier summer of the following year. This is similar to the magnifying effect of the rainfall on the monthly average F_c . At the higher-elevation sites, particularly site MS, the rainfall event did not have this influence. This could be related to the higher antecedent precipitation at MS in 2016 (*SI Appendix, Fig. S2C*) and a less intense July rainfall event relative to the other sites (*SI Appendix, Fig. S2B*). At MS, LE was already occurring at a high rate such that the rainfall did not significantly influence evapotranspiration.

In 2016, increased monthly average sensible heat flux, H , is always associated with decreased information transfer to H (Fig. 3B). This indicates that as conditions become drier and the magnitude of H increases, joint variability between atmospheric and soil states and H decreases. This inverse relationship between connectivity and H magnitude could be interpreted as H becoming increasingly constrained by variability in other sources. In other words, as conditions become drier, H increases regardless of the variability of sources which, during wetter periods, may constrain H in favor of LE . In 2015, H exhibits very diverse June-to-July behaviors for each site (Fig. 3B), indicating that the rainfall pulse in 2015 has a different effect on connectivity and H at each site.

Based on this monthly analysis, the RC-CZO flux tower sites can be grouped in two ways (Fig. 3E). First, the two lower-elevation sites can be separated from the higher-elevation sites in terms of flux responses, ΔLE , ΔH , ΔG , and ΔFc , for a given June-to-July period. This can be attributed to differences between vegetation and microbial activity at the higher- and lower-elevation sites (14). At the lower-elevation sites, WB and LS, vegetation is dormant or nearly dormant by the time of the rainfall event. Temperature and water availability drive microbial respiration, which in turn drive Fc . At PS and MS, vegetation is not dormant and both photosynthesis and respiration drive fluxes of water and carbon. A second grouping of sites can be observed in terms of process connectivity. While the middle-elevation sites tend to exhibit more moderate changes in process connectivity under the disturbance, the sites on the extreme ends of the elevation gradient behave similarly to each other in that they exhibit large changes in total information transfer. For most target fluxes, changes in total information transfer, ΔQ , are larger at sites WB and MS than those at the mid-elevation sites LS and PS. These two groupings of locations along the elevation gradient place each site in a unique position in terms of how flux magnitudes can relate to shifts in joint variability (Fig. 3E).

B. Driving Influences Change on Short Time Scales. The monthly time windows captured several changes in heat and carbon flux behaviors and process connectivity in relation to the rainfall event but also captured similarities between years that indicate seasonal trends during the dry season. An alternate definition of time windows enables us to focus more specifically on the effects of the July 2015 rainfall pulse. Here we define 10-d time windows of before rainfall (DOY 176–185), during rainfall (DOY 186–195), and after rainfall (DOY 196–205) periods (SI Appendix, Fig. S2 B–H) for 2015. Also in contrast to the previous analysis of total information transfer, Q , from many sources, we now focus on individual sources and source pairs that provide unique, synergistic, and redundant information within each time window. We consider information transfer from source combinations of water vapor density (ρ_v), soil water content (VWC), air tempera-

ture (T_a), and surface temperature (T_{surf}) to fluctuations in latent heat flux, LE , at the lower-elevation sites. A similar analysis for all sites and target fluxes is provided in SI Appendix, section 3 and Fig. S6.

For the time windows before and after the rainfall, sources and strengths of information transfer to LE are very similar, except that ρ_v is a stronger source before the rainfall and T_{surf} is a stronger source after the rainfall (Fig. 4). This could indicate an increased sensitivity of LE to soil conditions, although soil moisture does not vary enough during this window for a dependency to be detected. At both WB and LS sites, we find that information transfer to LE increases during the rainfall pulse (Fig. 4A), corresponding to a large peak in average LE during the period DOY 186–195. This indicates that the fluctuations triggered by the rainfall event lead to both increased magnitudes of LE and increased connectivity between fluctuations in LE and atmospheric and soil variables.

At site WB, the increase in process connectivity is attributed to information transfer from source pairs that include VWC (Fig. 4B). At site LS, the increased information transfer during the rainy time window is also due to increased information transfer from VWC, but a relatively higher proportion of this information is redundant. This indicates that the sources VWC, ρ_v , T_{surf} , and T_a are more tightly synchronized to each other at site LS compared with site WB. At WB, sources share similar quantities of information with LE but tend to provide information uniquely or synergistically. After the rainfall event at LS, the only two detected sources are ρ_v and T_{surf} . This indicates an enhanced joint variability between temperature, moisture, and LE that persists in the days after the rainfall event.

In most cases, the network connectivity trends between the 10-d windows differ from those detected for the monthly time windows. From this we infer that the rainfall event had some shorter-term influences that are better captured within an event-scale time window, while seasonal or more persistent influences can be assessed with longer time windows. As evident from similarities in total information transfer, Q , between 2015 and 2016, the 30-d windows also capture typical seasonal patterns of fluxes and process connectivity.

Fig. 4. Specific source pairs that shift in terms of their provision of information to LE before, during, and after the rainfall event in July 2015 at RC-CZO. (A) Total information (bits/bit, $Q = S + U + R$ relative to total information capacity, defined as the potential total information if all sources completely informed the target) to target LE at sites WB (Upper) and LS (Lower), respectively. For sites (B) WB and (C) LS, black, gray, and white links indicate synergistic information (S), unique information (U), and redundant information (R), respectively, to LE during the different 10-d windows. Sources considered here are air temperature (T_a), surface temperature (T_{surf}), water vapor density (ρ_v), and soil water content (VWC) as a representative subset of variables.

Fig. 6. TIPNet analysis of SS-CZO flux tower sites for summer (June–August) time windows from 2010 to 2015. (A and B) Total information (bits/bit, $Q = S + U + R$ relative to total information capacity, defined as the potential total information if all sources completely informed the target) to target node *LE* at lower-elevation site SR and higher-elevation site PC, respectively. (C and D) Specific sources of unique and synergistic information for summers of 2010–2015 at sites SR and PC, respectively. Gray links indicate unique information transfers from individual sources T_{surf} , VWC , T_a , RH , ρ_v , and WS , while colored links indicate synergistic information from combinations of these sources. Outer black curved segment lengths are proportional to the total amount of U and S provided to *LE* for each year.

sources. In the years before the drought, process connectivity is higher at site PC than site SR due to a larger number of detected sources. While ρ_v and T_a are dominant sources at SR, WS , T_{soil} , and RH are additionally detected as sources at PC. At the beginning of the drought in 2012–2013, process connectivity to *LE* increases for both sites, and many sources of information are detected. Additionally, a larger proportion of this information is synergistic. Increased synergy or redundancy is to be expected under an increased number of sources, since there are more possible pairs of sources that could either provide overlapping or joint information to a target. This increase in synergistic information transfer early in the drought, particularly at site SR, indicates an increased responsiveness of variability in *LE* to environmental fluctuations as conditions first become dry.

The last two years in this study, 2014 and 2015, are characterized by very low information transfer at both sites, and few statistically significant sources to *LE*. This indicates a disconnect between *LE* and atmospheric and soil processes as conditions become increasingly dry. Although both sites exhibit this decrease in process connectivity to *LE*, dominant sources of information differ between sites. Specifically, soil moisture, VWC , and soil temperature, T_{soil} , are the only sources to *LE* at the lower-elevation site SR, while air temperature, T_a , and relative humidity, RH , are the only sources at site PC (Fig. 6). This indicates that in the late years of the drought fluctuations in soil variables and atmospheric variables drive variability in *LE* at the lower- and higher-elevation sites, respectively. This

contrasts with the predrought years of 2010 and 2011, during which both atmospheric and soil variables provided information to *LE* at both sites. This separation of drivers between sites can be placed into the context of the different drought responses at each site. The higher-elevation site, PC, had a mitigated drought response due to higher soil moisture recharge and deep rooting depths, while the lower-elevation site maintained *ET* through 2012 but soil water was not recharged as the drought progressed in later years (1). At site PC, we infer that since soil water was more available, fluctuations in *LE* retained their connectivity to atmospheric processes. Meanwhile, *LE* was tightly constrained by soil moisture at the lower-elevation site, such that soil states were detected as the sole drivers of variability. Carbon flux, F_c , exhibits more joint variability with source variables at site SR compared with site PC (SI Appendix, section 4 and Fig. S7). Since changes in summertime average F_c are more mitigated at PC, we infer that F_c at this site is less responsive to altered variability in soil and atmospheric drivers.

From the above analysis, we can say that the combination of strengthening and weakening influences as moisture conditions change indicates a complex response of *LE* to moisture availability between one summer and the next. At SS-CZO sites, the multiyear drought is characterized by first increasing and then decreasing process connectivity of flux tower variables to *LE*. However, the higher-elevation site is less responsive in terms of magnitudes of ΔLE between years. At both sites, different sets of drivers were detected before the drought and during early and later drought periods.

6. Discussion

When ecohydrologic fluxes along climate gradients diverge in their responses to disturbances, an analysis of process connectivity can reveal drivers and influences behind these differences. Along both RC-CZO and SS-CZO transects, the varying relations between information transfer and ecohydrologic behaviors at neighboring sites indicate the significant influence of heterogeneity in soil characteristics, topography, vegetation, and soil microbial activity (29). An analysis of process connectivity, in the form of total information transfer or specific source–target dependencies, identifies nonlinear and asynchronous connectivity that could not be detected with traditional linear measures (22). Information partitioning further characterizes the nature of a given multivariate dependency as joint, overlapping, or individual. The additional consideration of ecohydrologic states, such as average heat or carbon fluxes during a time period of interest, relates process connectivity and observed ecosystem sensitivity to disturbances.

At RC-CZO, a process connectivity analysis reveals the relation between joint variability and changes in ecohydrologic fluxes before and after a rainfall pulse, relative to a drier period. Differences between nearby sites likely indicate heterogeneity in vegetation characteristics, antecedent moisture, and soils. At SS-CZO, differences in sources of information are associated with different drought responses at two study sites. At the onset of drought conditions, both sites exhibit increases in process connectivity in the form of total information transfer to LE , indicating some heightened responsiveness of fluxes to environmental variability as conditions initially become dry. Later in the drought, information transfer does exhibit a breakdown, and soil moisture and atmospheric variability influence LE at the lower- and higher-elevation sites, respectively, corresponding to more extreme and mitigated drought responses. Here, process connectivity, when considered along with ecohydrologic indicators, identifies how mechanisms driving variability change during drought conditions for different sites. This study of process connectivity during drought conditions can be compared with a previous study that detected a breakdown in connectivity between eddy covariance variables during a Midwestern drought (9) compared with a wetter growing season. This difference between regions could relate to the timing of drought onset and the different climatic regimes studied, in that the California drought occurred over several years and was more dependent on winter precipitation rather than precipitation during the crop growth period.

Although the two case studies span different ecosystems, time ranges, and types of moisture-related disturbances, important inferences can be made regarding how connectivity between variables impacts the sensitivity of fluxes to change. Ground heat flux G and carbon flux F_c are similar in that their sources and strengths of joint variability alter with conditions, but their average magnitudes are relatively stable. As these variables likely

respond to fluctuations in soil states rather than more quickly varying atmospheric states, the results suggest that fluctuations propagate to influence short-term variability, but this does not always translate into changes in longer-term average magnitudes. At SS-CZO, however, we do see generally increasing F_c and increasing information flow to variability in F_c as the drought progresses. Latent heat flux, LE , and sensible heat flux, H , show relatively more joint relationships between process connectivity measures and flux magnitudes. For SS-CZO and some RC-CZO cases at the monthly time scale, information flow to LE increases as average LE decreases, but for very dry conditions information flow and LE decrease together. Meanwhile, for short time windows at RC-CZO, a single rainfall pulse led to short-term increases in both LE and information flow. Together, these results indicate that information flow increases when LE is moderately constrained or when there is a sudden pulse of moisture. However, for very dry conditions LE is constrained such that it is not responsive to the variability of sources. H shows more variable relationships between process connectivity and average magnitudes, but we find that large changes in one aspect generally relate to large changes in the other, such as at SS-CZO where changes in information flow were mitigated at the less drought-sensitive site. This indicates that while H is not constrained by moisture availability in the same way as LE , the joint variability of environmental source variables does influence longer-term average fluxes.

The characterization of multivariate forcing and feedback relations in ecohydrologic systems is integral to better understanding and predicting whole-system attributes of resilience, sensitivity, and vulnerability. In most systems, it is generally not possible to perform manipulative experiments to identify causal drivers and feedback (25), and observed datasets, modeling, and multivariate statistical methods are necessary instead. Given the multiple intensifying and mitigating mechanisms that can influence a given ecosystem property (1), it is important to consider joint interactions to understand the overall response. Process connectivity in terms of synergistic, unique, and redundant information transfers could benefit studies of controls on ecosystem dynamics and elasticity to climate change (26), assessing types of information present and absent in models (34), or studies of spatial connectivity (35, 36).

ACKNOWLEDGMENTS. We thank Kathleen Lohse, Roger Bales, Mike Goulden, and Joe Rungee. This work was supported by NASA Earth and Space Science Fellowship NNX15AN55H (to A.E.G.); NSF Grant EAR-1331906 for the Critical Zone Observatory for Intensively Managed Landscapes, a multiinstitutional collaborative effort; and NSF Grants CBET 1209402, ACI 1261582, and EAR 1417444. The RC-CZO (NSF Grant EAR 1331872), Agricultural Research Service of the US Department of Agriculture, and SS-CZO (NSF Grant EAR-1331939) provided data collection and quality control. SS flux tower data can be obtained at <https://www.ess.uci.edu/~california/> or through Ameriflux. RC flux tower data can be obtained at doi.org/10.18122/B2TD7V or through Ameriflux. The MATLAB toolbox for computing TIPNet information transfer measures can be downloaded at <https://github.com/HydroComplexity/TIPNet>.

- Bales RC, et al. (2018) Mechanisms controlling the impact of multi-year drought on mountain hydrology. *Sci Rep* 8:1–8.
- Small EE, Kurc SA (2003) Tight coupling between soil moisture and the surface radiation budget in semiarid environments: Implications for land-atmosphere interactions. *Water Resour Res* 39:1–14.
- Kumar P (2007) Variability, feedback, and cooperative process dynamics: Elements of a unifying hydrologic theory. *Geogr Compass* 1:1338–1360.
- Balasis G, et al. (2013) Statistical mechanics and information-theoretic perspectives on complexity in the earth system. *Entropy* 15:4844–4888.
- Nadeau T, Rains MC (2007) Hydrological connectivity of headwaters to downstream waters: Introduction to the featured collection. *J Am Water Resour Assoc* 43:1–4.
- Chaoka S, Kumar P (2012) Connectivity dynamics and its impact on material flux and transformations in a watershed. Master's thesis (Univ of Illinois at Urbana–Champaign, Urbana, IL).
- Bracken L, et al. (2013) Concepts of hydrological connectivity: Research approaches, pathways and future agendas. *Earth-Sci Rev* 119:17–34.
- Sendrowski A, Passalacqua P (2017) Process connectivity in a naturally prograding river delta. *Water Resour Res* 53:1841–1863.
- Ruddell BL, Kumar P (2009) Ecohydrologic process networks: 1. Identification. *Water Resour Res* 45:1–22.
- Ruddell BL, Kumar P (2009) Ecohydrologic process networks: 2. Analysis and characterization. *Water Resour Res* 45:1–14.
- Goodwell AE, Kumar P (2017) Temporal Information Partition Networks (TIPNets): A process network approach to infer eco-hydrologic shifts. *Water Resour Res* 53:5899–5919.
- Goodwell AE, Kumar P (2017) Temporal information partitioning: Characterizing synergy, uniqueness, and redundancy in interacting environmental variables. *Water Resour Res* 53:5920–5942.
- Goulden ML, et al. (2012) Evapotranspiration along an elevation gradient in California's Sierra Nevada. *J Geophys Res* 117:1–13.
- Fellows AW, Flerchinger GN, Seyfried MS, Clark PE, Lohse K (2017) Data for partitioned carbon and energy fluxes within the Reynolds Creek Critical Zone Observatory. Available at <https://doi.org/10.18122/B2TD7V>.

15. Nayak A, Marks D, Chandler DG, Seyfried M (2010) Long-term snow, climate, and streamflow trends at the Reynolds Creek experimental watershed, Owyhee Mountains, Idaho, United States. *Water Resour Res* 46:1–15.
16. Blankinship J, Meadows M, Lucas R, Hart S (2014) Snowmelt timing alters shallow but not deep soil moisture in the Sierra Nevada. *Water Resour Res* 50:1448–1456.
17. Seyfried M, Chandler D, Marks D (2011) Long-term soil water trends across a 1000-m elevation gradient. *Vadose Zone J* 10:1276.
18. Tague C, Peng H (2013) The sensitivity of forest water use to the timing of precipitation and snowmelt recharge in the California Sierra: Implications for a warming climate. *J Geophys Res Biogeosci* 118:875–887.
19. Shannon C (1948) A mathematical theory of communication. *Bell Syst Tech J* 27: 379–423.
20. Cover T, Thomas J (2006) *Elements of Information Theory* (Wiley, New York), 2nd Ed.
21. Brunzell N, Wilson C (2013) Multiscale interactions between water and carbon fluxes and environmental variables in a Central U.S. Grassland. *Entropy* 15:1324–1341.
22. Sturtevant C, et al. (2016) Identifying scale-emergent, nonlinear, asynchronous processes of wetland methane exchange. *J Geophys Res Biogeosci* 121:188–204.
23. Stoy PC, et al. (2006) An evaluation of models for partitioning eddy covariance-measured net ecosystem exchange into photosynthesis and respiration. *Agric Meteorol* 141:2–18.
24. Katul GG, et al. (2001) Quantifying the complexity in mapping energy inputs and hydrologic state variables into land-surface fluxes. *Geophys Res Lett* 28:3305–3307.
25. Detto M, et al. (2012) Causality and persistence in ecological systems: A nonparametric spectral granger causality approach. *Am Nat* 179:524–535.
26. Ruddell BL, Yu R, Kang M, Childers DL (2016) Seasonally varied controls of climate and phenophase on terrestrial carbon dynamics: Modeling eco-climate system state using dynamical process networks. *Landscape Ecol* 31:165–180.
27. Sendrowski A, et al. (2018) Transfer entropy as a tool for hydrodynamic model validation. *Entropy* 20:58.
28. Williams PL, Beer RD (2010) Nonnegative decomposition of multivariate information. arXiv:1004.2515.
29. Jenerette GD, Ga B-G, Guswa AJ, McDonnell JJ, Villegas JC (2012) Organization of complexity in water limited ecohydrology. *Ecohydrology* 5:184–199.
30. Barrett AB (2015) Exploration of synergistic and redundant information sharing in static and dynamical Gaussian systems. *Phys Rev E* 91:052802.
31. Gong W, Yang D, Gupta HV, Nearing GS (2014) Estimating information entropy for hydrological data: One-dimensional case. *Water Resour Res* 50:5003–5018.
32. Silverman BW (1986) *Density Estimation for Statistics and Data Analysis* (Wiley, New York), Vol 26.
33. Goodwell A, Kumar P (2015) Information theoretic measures to infer feedback dynamics in coupled logistic networks. *Entropy* 17:7468–7492.
34. Nearing GS, Mocko DM, Peters-Lidard CD, Kumar SV, Xia Y (2016) Benchmarking NLDAS-2 soil moisture and evapotranspiration to separate uncertainty contributions. *J. Hydrometeorol* 17:745–759.
35. Boers N, Bookhagen B, Marwan N, Kurths J, Marengo J (2013) Complex networks identify spatial patterns of extreme rainfall events of the South American monsoon system. *Geophys Res Lett* 40:4386–4392.
36. Deza JJ, Barreiro M, Masoller C (2015) Assessing the direction of climate interactions by means of complex networks and information theoretic tools. *Chaos* 25:033105.