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Review

Ecohydrological decoupling under changing disturbances and climate

Nate G. McDowell,[1,2,*] Kristina Anderson-Teixeira,[3,4] Joel A. Biederman,[5] David D. Breshears,[6] Yilin Fang,[7] Laura Fernández-de-Uña,[8] Emily B. Graham,[9] D. Scott Mackay,[10] Jeffrey J. McDonnell,[11,12] Georgianne W. Moore,[13] Magali F. Nehemy,[11] Camille S. Stevens Rumann,[14] James Stegen,[15] Naomi Tague,[16] Monica G. Turner,[17] and Xingyuan Chen[1]

[1]Atmospheric Sciences and Global Change Division, Pacific Northwest National Lab, PO Box 999, Richland, WA 99352, USA
[2]School of Biological Sciences, Washington State University, PO Box 644236, Pullman, WA 99164-4236, USA
[3]Conservation Ecology Center, Smithsonian Conservation Biology Institute, Front Royal, VA 22630, USA
[4]Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Panama, Panama
[5]Southwest Watershed Research Center, Agricultural Research Service, Tucson, AZ 85719, USA
[6]School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721, USA
[7]Earth Systems Science Division, Pacific Northwest National Lab, PO Box 999, Richland, WA 99352, USA
[8]CREAF, Bellaterra (Cerdanyola del Vallés), 08193 Barcelona, Spain
[9]Earth and Biological Sciences Directorate, Pacific Northwest National Lab, PO Box 999, Richland, WA 99352, USA
[10]Department of Geography and Department of Environment and Sustainability, University at Buffalo, Buffalo, NY 14261, USA
[11]Global Institute for Water Security, School of Environment and Sustainability, University of Saskatchewan, Saskatoon, SK, Canada
[12]School of Geography, Earth & Environmental Sciences, University of Birmingham, Birmingham B15 2TT, UK
[13]Department of Biology, Georgia Southern University, PO Box 8042-1, Statesboro, GA 30460, USA
[14]Forest and Rangeland Stewardship, Colorado Forest Restoration Institute, Colorado State University, Mailstop 1472, Fort Collins, CO 80523, USA
[15]Ecosystem Sciences Team, Pacific Northwest National Lab, PO Box 999, Richland, WA 99352, USA
[16]Bren School of Environmental Science and Management, University of California, Santa Barbara, Santa Barbara, CA 93106, USA
[17]Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI 53706, USA
*Correspondence: nate.mcdowell@pnnl.gov
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SUMMARY

Terrestrial disturbances are increasing in frequency and severity, perturbing the hydrologic cycle by altering vegetation-mediated water use and microclimate. Here, we synthesize the literature on post-disturbance ecohydrological coupling, including the mechanistic relationship between vegetation and streamflow, under changing disturbance regimes, atmospheric CO_2, and climate. Disturbance can cause decoupling between transpiration and streamflow by altering the connectivity, size, availability, and spatial distribution of their source pools. Successional trajectories influence the dynamics of source water partitioning. Changing climate and disturbance regimes can alter succession and prolong decoupling. Increasing rates, severity, and spread of disturbances along with warming could promote greater decoupling globally. From this review emerges a framework of testable hypotheses that identify the critical processes regulating ecohydrological coupling and provide a roadmap for future research. Accurate prediction of post-disturbance coupling requires understanding the degree of hydraulic connectivity between source water pools and their response to succession under changing disturbance and climate regimes.

INTRODUCTION

Disturbances including drought, wildfire, and biotic agent outbreaks all cause ecohydrological impacts that are expected to increase in the future[1–5] (Figure 1). Vegetation growth, size, composition, and diversity can be altered for decades or even quasi-permanently after disturbance,[6–8] with similarly large impacts on the ecosystem energy budget and hydrologic stores and fluxes.[9–13] On top of these disturbances are the compounding impacts of rising atmospheric [CO_2] and vapor pressure deficit (*VPD*), the latter of which is a non-linear function of temperature that has strong impacts on vegetation growth and survival.[14] Chronic changes in CO_2 and *VPD* can accelerate or decelerate the rate of succession and associated species composition and can cause significant shifts in vegetation-mediated components of the hydrologic cycle.[7,8,15–20] The ecohydrological effects of these compounding disturbances with non-stationary atmospheric drivers are challenging to quantify and model.[20–23] These knowledge limitations hinder forecasts of ecohydrological function.[10,18,21–24]

The interdependency of vegetation and hydrology, which we refer to generally as ecohydrological coupling, mediates the outcomes of disturbances and climate upon plant communities and watershed hydrology (Figure 2). Ecohydrological coupling results from the degree of overlap between water pools that are the sources of hydrologic fluxes, the partitioning of which underlays responses that lead to changes in water provisioning for downstream use (see Box 1 for term definitions). A particularly

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Figure 1. Disturbed landscapes have altered physical and ecological properties

(A) Eucalyptus tree death from wildfire in Australia.
(B) Wildfire-induced conifer tree mortality in New Mexico, USA.
(C) Drought- and insect-induced conifer tree mortality in Colorado, USA.
(D) Wildfire-induced conifer tree mortality in New Mexico, USA.
Each site shown here is experiencing a vegetation-type conversion due to disturbance. Photos are from L.F.-d.-U. (A), C.D. Allen (B and D), and N.G.M. (C).

important ecohydrological coupling is that of canopy transpiration (T) with streamflow (Q; referred to herein as T/Q coupling). In the simplest form of the hydrological budget, Q results from precipitation minus T and surface evaporation (E_s), and assuming minimal variation in E_s, an increase in T should lead to lower Q. There are other fluxes that can influence Q in conjunction with E_s and T, which we detail in later sections. The dynamics of T/Q coupling have large implications for post-disturbance water and vegetation resources. T represents ~70% of precipitated water to the land-surface globally; thus, small shifts in T have large possible impacts on watershed hydrology, including upon Q.[25] A mechanistic understanding of T/Q coupling is critical to forecasting the impacts of changing disturbance regimes and climate on carbon and water cycles, including the provision of water for human uses. Understanding the mechanistic regulation of such coupling in relation to these drivers is a grand challenge for ecohydrological research.[26]

Significant advances in understanding of post-disturbance ecohydrological coupling have arisen from evidence-based frameworks,[20,21,26–28] observations,[29–32] and model simulations.[10,18,19,23] However, from this large increase in post-disturbance ecohydrological research has emerged the discovery that there is much greater variation in post-disturbance vegetation succession, hydrologic fluxes, and T/Q coupling than previously expected.[17,20,30,33,34] This is evidenced through our global review of Q response to disturbance (Figure 3). Across biomes, Q exhibits a significant correlation with forest cover such that decreases in cover result in increases in Q ($p < 0.05$). There were no differences in the slope of the relationship between the identified vegetation types that had sufficient data for analyses (conifer forests, broadleaf forests, and mixed forests; $p = 0.07$), and the overall regression is of low predictive power ($R^2 = 0.11$). This large variability results from the complex interaction between disturbance characteristics, vegetation community and physiological ecology, edaphic factors, weather, and climate. Poor understanding of the controls over post-disturbance T/Q coupling challenges understanding and prediction of the relationships between vegetation and Q. Prediction is further challenged by our limited understanding of how post-disturbance ecohydrological coupling responds to rising [CO_2] and *VPD,* which could also influence the variability in the response of Q to forest cover (Figure 3).

The prediction of disturbance-induced changes in water availability through Q is critical if we are to manage water resources under changing disturbance regimes.[37] Shifts in water yield have large implications for the sustainability of freshwater availability for agricultural use and human consumption.[38,39] The growing global population is driving increased agricultural demands that are dependent on freshwater availability, the provision of which is tenuous under climate change.[40] Likewise, Q is critical to support water availability for conservation of aquatic resources.[41,42] Thus, disturbance-induced hydrologic shifts impact many resources required by human society, including reservoir and fisheries management,[43] food security,[44] and power production.[45] With increasing demands for freshwater consumption, reservoir management becomes a primary means for mitigating variation in water availability, and such management requires predictive understanding of Q.[46] Disturbances can result in large hydrologic changes,[34,44] and they are growing in frequency and severity,[16] leading to concerns that unpredictable variation in water yields is impacting the provision of water for human consumption.[46,47]

The objective of this review is to improve predictive understanding of post-disturbance ecohydrological coupling under changing disturbance regimes and climate. We synthesize the state of knowledge of vegetation-hydrology coupling and their interdependencies post-disturbance, with a focus on T/Q coupling. We bring together evidence from theory, observations, and simulations to generate a framework of testable hypotheses that identifies key potential processes and thresholds, along with critical unknowns and challenges. The proposed framework provides a road map for future empirical and numerical research into the mechanisms of T/Q coupling under changing disturbance regimes and climate. We focus on the watershed-scale disturbances that occur throughout much of Earth, droughts, wildfires, and biotic agent attacks (e.g., insect outbreaks), and utilize literature associated with storms, land clearing, and/or rotational tree harvesting to highlight key mechanisms where appropriate. We consider changing CO_2 and *VPD* as compounding influences upon disturbances rather than disturbances per se.

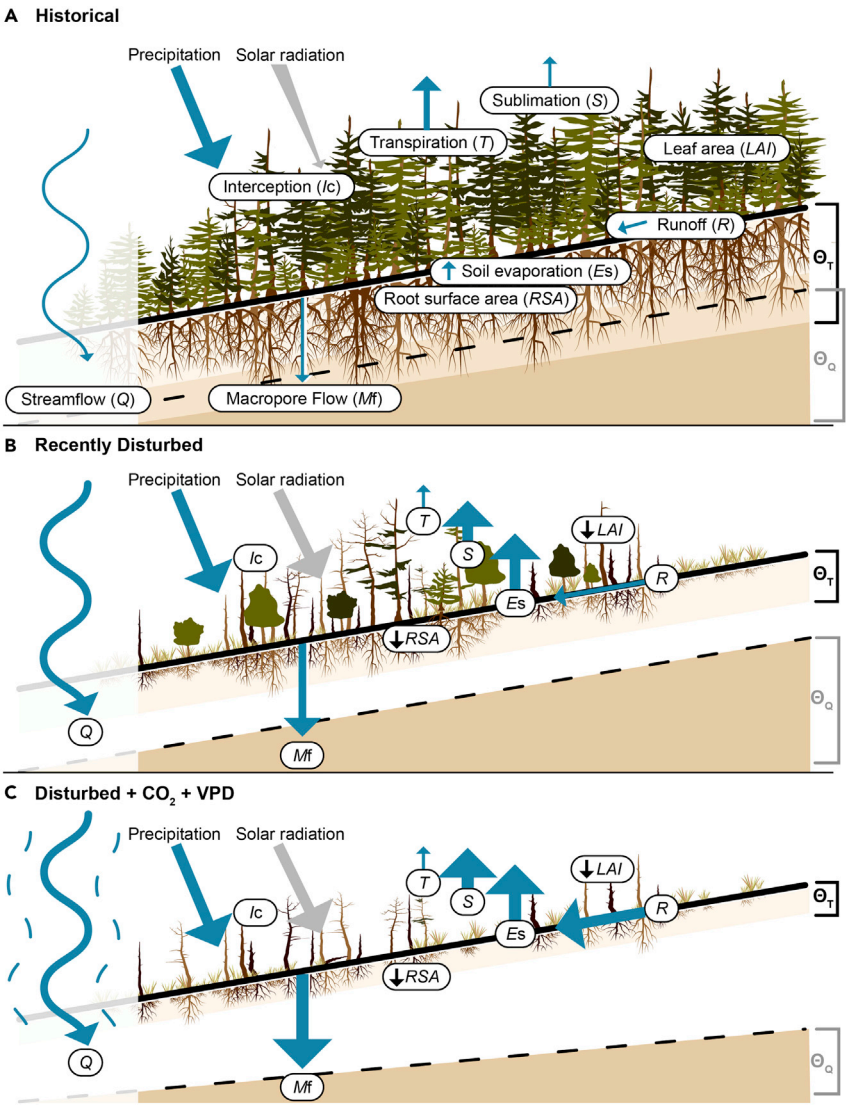

Figure 2. A schematic of the key mechanisms underlying the degree of *T*/*Q* coupling

(A) Plant mortality from disturbances leads to shifts in vegetation leaf and root area that subsequently alter streamflow via shifts in the rate and location of plant water acquisition from the belowground water pools, along with alterations of biophysical properties such as precipitation interception, macropore flow, runoff, sublimation, and soil evaporation.

(B and C) These shifts are expected to be different under current (B) and elevated CO_2 and VPD (C) conditions. Note that Θ_T (source water pool for transpiration) and Θ_Q (source water pool for streamflow) may have less physical separation than presented; however, they are shown with more distinct spatial differences to highlight the possible shifts in Θ_T and Θ_Q separation.

Before proceeding, we highlight some working definitions used for three key terms in this paper. We consider coupling to refer to the mechanistic interdependence between *T* and *Q* wherein a change in one causes a change in the other due to shared water pools. Decoupling, in contrast, is the partial or complete loss of the interdependency of *T* and *Q*. Correlation between *T* and *Q* can indicate mechanistic coupling, e.g., *T*-induced shifts in source water partitioning, or correlation can result from *T* and *Q* exhibiting independent responses to a driver, e.g., precipitation inputs driving individual increases in both *T* and *Q*.[48] Thus, care must be taken when inferring coupling from observations of *T*/*Q* correlations. The belowground water pool (Θ) includes the water sources to *T* and to *Q* (Θ_T and Θ_Q, respectively). The hydraulic connectivity of these pools refers to the interdependence of Θ_T and Θ_Q due to shared water at the pore-space to watershed scales. Partitioning refers to the flux of water from Θ_T and Θ_Q to *T* and *Q*. Definitions for these and additional terms are provided in Box 1.

DISTURBANCE TRENDS AND CONSEQUENCES

Watershed-scale disturbances are anticipated to increase in frequency and severity in the future.[4] The global wildfire risk has grown significantly over recent decades and is expected to worsen, in part, due to rising temperature and *VPD*.[2,3] Long-term records of insect and pathogen outbreaks are scant, but existing evidence suggests they are also increasing in frequency due to their frequent co-occurrence with droughts,[47] which weakens tree defense systems against attack.[49,50] Future outbreaks are expected to cause higher mortality rates along with greater return frequency and areal spread.[47] Droughts are becoming more severe because rising atmospheric *VPD* drives plant and soil water content to anomalously low values.[14] In addition to increasing severity, drought may also increase in frequency due to climate warming.[51] Watershed-scale destruction of trees via storms with high winds and precipitation inputs are also prevalent in some regions of the world and may be increasing in both frequency and intensity of wind speeds and precipitation amounts.[4]

Terrestrial ecosystem disturbances cause vegetation mortality through physical impacts[4] (Figure 1). There are numerous consequences of disturbances.[52] Disturbance to vegetated systems reduces standing biomass and thus carbon storage, until biomass stocks recover as succession progresses.[53] The loss of canopy leaf area and rooting surface area, referred to herein as *LAI* (leaf area index) and *RSA* (root surface area), respectively (both in units of m^2 surface area per m^2 ground area; Figure 2) significantly alter *T* and microclimate. Changes in ecosystem energy balance through altered surface heat flux and other radiative shifts can lead to significant regional warming.[54] Soil processes such as nutrient cycling, microbial activity, and erosion can all be affected by disturbances.[55,56] The loss of vegetation significantly impacts forestry, tourism, biodiversity, and other ecosystem services.[57]

Box 1. Glossary

Coupling: the interdependency between *T* and *Q* due to shared water pools.
Disturbance: destruction of live plant biomass in a discrete event.
Hydraulic connectivity: the degree of connectedness and interaction between Θ_T and Θ_Q.
Interception (I_c): the capture of precipitation on the canopy surface and subsequent evaporation.
Leaf area index (*LAI*): the area of canopy foliage per unit ground area.
Macropore flow (M_f): movement of water via gravity through non-capillary soil channels.
Partitioning: the flux of water from Θ_T and Θ_Q to *T* and *Q*.
Runoff (*R*): flow of water on the soil surface.
Root surface area (*RSA*): the surface area of roots per unit ground area.
Streamflow (*Q*): flow of water in stream channels.
Streamflow source water pool (Θ_Q): the pool that supplies water to streamflow.
Soil evaporation (E_s): evaporative water loss from the soil surface.
Sublimation (*S*): the loss of snow and ice through evaporation.
Succession: time-dependent changes in vegetation composition and structure after disturbance.
Transpiration (*T*): the flow of water from the soil through to evaporation from leaf surfaces.
Transpired source water pool (Θ_T): the pool that supplies water for transpiration.

Disturbance consequences include shifts in hydrologic pools and fluxes. Changes in *T, Q,* Θ, canopy interception (I_c), snow sublimation (*S*), surface runoff (*R*), E_s, and macropore flow (M_f) can all occur[10,20,29,30,32,33,57–60] (Figure 2). These responses occur through changes in the structure and function of the vegetation, and changes to the energy budget. Shifts in latent and sensible heat fluxes alter the energy balance of ecosystems, providing an overall constraint on the degree of hydrologic shifts.[61] Similar to vegetation successional trajectories after disturbance, components of the water cycle may or may not recover to pre-disturbance states, with the time frame, trajectories, and absolute magnitudes dependent, in part, upon the frequency and severity of disturbances.[62–66] These processes are reviewed further below in the section on decoupling under disturbances.

Disturbances induce *Q* changes that are consistent with a significant influence of vegetation water use upon *Q*, particularly in wetter regions.[6,9,17,20,67,30,50,68–73] In cases of watershed scale loss of vegetation, evidence suggests that there is a strong relationship between vegetation cover and *Q*. For example, a comparison of paired harvested and control watersheds in the Pacific Northwest and New England (n = 6 pairs per region) were monitored before and after forest loss[73] (Figure 4). *Q* was initially much higher in the denuded watersheds but subsided back toward no net change in later years, as vegetation succession led to greater *LAI* and *RSA*. Consistent with this, a global review found that changes in forest cover due to deforestation and afforestation lead to changes in *Q* that also suggest a strong role of plants on *Q*, with elevated *Q* occurring with less forest cover.[30] These patterns are not always observed, however, as drier and smaller catchments can show less responsiveness of *Q* to vegetation cover change,[20,30,34,66] a phenomenon we review below in the section on post-disturbance coupling.

MECHANISMS REGULATING ECOHYDROLOGICAL COUPLING PRE-DISTURBANCE

Here, we describe the known mechanisms regulating *T/Q* coupling in undisturbed systems because they are the reference point from which changes in ecohydrological coupling occur post-disturbance. We address the dominant role of weather and climate, at hourly to multi-annual scales, on *T/Q* coupling in steady-state systems, e.g., old growth. The section on decoupling under disturbances subsequently brings the knowledge on pre-disturbance *T/Q* coupling together with what is known regarding post-disturbance coupling and decoupling and identifies key ecohydrological mechanisms that are shared pre- and post-disturbance as well as those that diverge. Our hypothesis framework of mechanisms underlying *T/Q* coupling incorporates disturbance-induced changes in vegetation, soils, and the associated energy budget while considering local and regional climate.

Our emergent hypothesis framework suggests the critical hinge-point underlying *T/Q* coupling is the partitioning of Θ into Θ_T and Θ_Q; (hypothesis i; see Table 1 for a list of emergent hypotheses from this review). Potential Θ_T and Θ_Q are the total amounts of water in each pool that are available to *T* and *Q,* the actual amount of which (the partitioning) can be smaller than the potential pool size due to variation in hydraulic connectivity between pore spaces, *Q*, and *T*. (Figure 2). Existing evidence from both model[74,75] and empirical results[76,77] is consistent with the hypothesis that the hydraulic connectivity between Θ_T and Θ_Q, or their degree of sharing, underlies *T/Q* coupling. *T* and *Q* can respond both independently and in a coupled manner to precipitation events,[78–81] and they can exhibit strong coupling, on diel to seasonal periods[48,82–84] (Figure 5). This evidence of *T/Q* coupling across temporal scales highlights the likely role of vegetation in driving *Q*, while both can respond to seasonal variation in water inputs[48,83] (Figure 5). Understanding the controls over the degree of hydraulic connectivity between Θ_T and Θ_Q is therefore necessary to understand the mechanisms regulating *T/Q* coupling.[26]

A testable hypothesis from our emergent framework is that the degree of *T/Q* coupling increases with rooting zone Θ to a point, which is consistent with the hypothesis that the degree of hydraulic connectivity between Θ_T and Θ_Q underlies *T/Q* coupling[78,82–84] (hypothesis i; Table 1). Specifically, one can expect particularly low coupling when Θ_T is comprised of

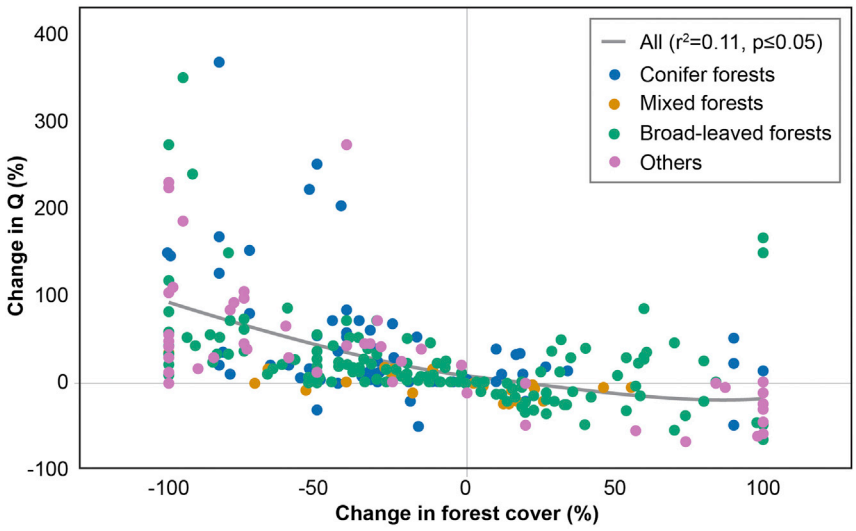

Figure 3. A global summary of the response of streamflow (*Q*) to changes in forest cover
Data sources are Adams et al.,[20] Zhang et al.,[30] Li et al.,[35] and Manning et al.[36]

unsaturated soil moisture no longer gravitationally linked to Θ_Q or when precipitation is so high that *Q* derives directly from input water. Thus, *T*/*Q* coupling should show a unimodal relationship with Θ. The dependence of the Θ_T/Θ_Q connectivity on total soil column Θ depends in part on the dynamics of the water distribution within the soil matrix. During dry periods, the impacts of *T* upon *Q* decline as roots acquire more tightly bound water in the soil pores than that which supplies *Q*.[31,85–87] Hence, under dry conditions, there should be less hydraulic connectivity between Θ_T and Θ_Q and hence reduced *T*/*Q* coupling. As total Θ increases in response to storm events or at seasonal or regional scales, the *T*/*Q* coupling increases due to dynamic processes that ensue with water input.[88,89] Depending in part on soil pore structure, significant new moisture inputs from precipitation or snowmelt initially infiltrate soil macropores at larger rates than at the rate they are absorbed by micropores, and as precipitation amounts increase, water is transported through progressively narrowing pores within the soil matrix, and hence pore structure and M_f are regulators of coupling.[89,90] This can initially promote a greater rise in Θ_Q than Θ_T, but with continued water input and subsequently increased continuity of the soil water potential through matric flow, Θ_T becomes more spatially homogenous.[91] As the hydraulic connectivity increases across pore sizes, the separation between Θ_T and Θ_Q decreases.[82–84] Consistent with this, the degree of *T*/Q coupling depends on the interaction between precipitation or snowmelt event size and soil infiltration rates, with the greatest decoupling occurring during particularly small and large events via bypassing of Θ_Q and Θ_T, respectively.[31,90] Notably, changes in *T*/*Q* coupling due to disturbance are most observable during periods of high Θ, again suggesting that coupling is enhanced by higher Θ.[92,93]

Evidence of *T*/*Q* decoupling has been shown using isotopic tracing approaches[31,76,77] and modeling analyses.[23] Θ_T can be dominated by younger, relatively more available water, with Θ_Q derived from water with a longer residence time in the watershed,[23,94] consistent with at least partially differing water sources for *T* and *Q*. Likewise, Θ_Q can often encompass a larger belowground volume than Θ_T, underlying reduced hydraulic connectivity between Θ_Q and Θ_T[95,96] (Figure 2). Edaphically, the degree of decoupling is influenced in part by the maximum depth of roots relative to the bedrock interface, which can decrease hydraulic connectivity between Θ_T and Θ_Q.[96,97] With a greater distance between the bottom of the rooting zone and the bedrock layer, changes in vegetation water uptake can have less influence over *Q* (though there is evidence of water uptake by roots penetrating bedrock[98]). Decoupling might also occur in systems with potential Θ_T distributed over a large soil depth but with flashy precipitation events that create significant *R*, such as in more arid environments.[99] This is consistent with a global analysis that found that most watersheds increase *Q* in response to deforestation, with this response becoming weaker in more arid locations.[30] This contrasts with wet, low-energy environments where large overlap exists between Θ_T and Θ_Q and stronger coupling can be expected.[100] Finally, site aspect and steepness influence Θ_T and *T* with more sun exposed and steeper slopes having lower *LAI* and less I_c, leading to greater E_s, *S*, and *R*[101] that again leads to reduced total Θ and should reduce hydraulic connectivity between Θ_T and Θ_Q. Based on this review, we hypothesize that conditions of higher Θ lead, to a point, to greater Θ_T/Θ_Q coupling, with drivers of total Θ spatial variation resulting from regional climatic variation to sub-meter resolution variation in soil pore matric potential and temporally from multi-decadal climate to daily precipitation events (hypothesis ii; Table 1).

The partitioning of Θ_T and Θ_Q to *T* and *Q* and hence the degree of *T*/*Q* coupling is also a function of vegetation traits that regulate *T*, with greater *T* leading to greater partitioning of Θ_T and Θ_Q, partially because high rates of *T* are coincident with high Θ.[102,103] Higher watershed-scale *T* should maximize *T*/*Q* coupling through a magnitude effect wherein larger *T* requires a larger Θ_T and hence greater Θ_T/Θ_Q hydraulic connectivity, creating greater sensitivity of Θ_Q to changes in Θ_T. However, elevated *T* will eventually deplete the Θ_T pool, causing a temporally hysteretic decline in Θ_T/Θ_Q coupling. Empirical data as well as models originating from a plant-hydraulic corollary to Darcy's law[83,103–105] provide guidance on some critical plant traits that regulate *T*. These traits include maximum stomatal conductance, hydraulic conductance of the entire plant, plant height, sapwood area, leaf area, and *RSA*. These traits vary significantly across plant functional types; thus, changes in plant species composition can lead to significant changes in potential *T*.[106–109] These changes in *T* are constrained by incoming precipitation, *VPD*, and the energy budget.[110,111] *RSA* provides the hydraulic supply capacity to convert potential Θ_T into actual Θ_T, and thus as *RSA* increases with *LAI*,[108,109] plants have greater water-foraging capacity and can thus increase their Θ_T pool size. Plant hydraulic conductance mediates the temporal dynamics of water flux

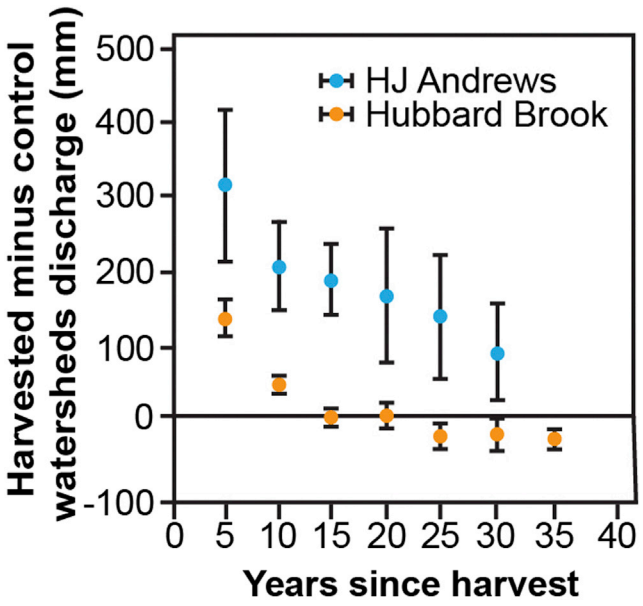

Figure 4. Streamflow increases after disturbance and decreases as succession proceeds

The mult-decadal response of streamflow to forest removal in six watersheds located in the Pacific Northwest (HJ Andrews Experimental Forest) and six watersheds located in New England (Hubbard Brook Experimental Forest). Results shown are the differential in streamflow (mm) between pairs of harvested and control watersheds. Error bars are standard errors for the six pairs per region. Data from Table 5 in Jones and Post.[73]

from roots to foliage and can decouple *T* from *Q* due to differences in water transit times within plants relative to the residence times of Θ_Q.[32,110] Thus, plant traits that increase watershed-scale *T* should lead to greater potential connectivity between Θ_T/Θ_Q and subsequent *T*/*Q* coupling, at least during periods of sufficiently abundant Θ (hypothesis iii; Table 1).

ECOHYDROLOGICAL DECOUPLING POST-DISTURBANCE

Ecohydrological changes post-disturbance

Ecohydrological impacts from vegetation disturbance include immediate decreases in ecosystem-scale *LAI*, *T*, and I_c, increased E_s, and positive, negative, or no changes in *S*, *R*, Θ, and *Q*[10,11,17,20,33,63,35,112–114] (Figures 6 and 7). Hypotheses regarding ecohydrological coupling post-disturbance typically revolve around vegetation dynamics[20,30,35,111–114] because *T* is the dominant terrestrial hydrological flux[25,29] and due to the frequent observation of higher *Q* with forest loss (Figure 3).[30] The recruitment rate of seedlings and their survival and growth and the hydraulic traits of the vegetation community that regulate *T* (Figure 2) all can influence Θ and *Q*.[6,10,115] In cases of severe, stand-clearing disturbances, e.g., clear-cut harvest or severe wildfire, *Q* can increase quickly, only to decline as plants reoccupy the site and watershed-scale *LAI* and *T* increase[6,10,30,115,116] (Figures 4 and 6). This is consistent with a global analysis of water yields in response to deforestation in large watersheds (>1,000 km^2), which showed that decreases in forest cover resulted in increases in *Q*.[30] Increased *T* per unit leaf area of the surviving vegetation can buffer disturbance impacts on coupling; however, this mechanism requires significant vegetation survival to mitigate changes in watershed-scale *T*.[59] *LAI* increases to a maximum as the stand regrows, with the rate of recovery a function of disturbance severity, frequency, and size[116] (Figure 6A). If the ecosystem returns to the same vegetation composition as pre-disturbance, then as the plants approach their maximum height, *Q* can again increase due to hydraulic limitations imposed by increasing path-length through the stem, which can limit *T*[6,63,113] (Figure 6B). Thus, an emergent hypothesis is that ecosystems experiencing more severe, frequent, and spatially extensive disturbances should incur greater *T*/*Q* decoupling through reduced *LAI* for *T*, *RSA* for extracting Θ_T, and hence reduced hydraulic connectivity between Θ_T and Θ_Q (hypothesis iv; Table 1; Figures 6 and 7).

Disturbance impacts on the physical environment and the energy budget promote *T*/*Q* decoupling by altering the magnitude and timing of inputs to Θ_T and Θ_Q.[11,33] I_c is reduced with forest disturbance due to decreased *LAI* (Figure 5D), thereby allowing increased precipitation to reach the soil surface and greater snowpack accumulation.[11,117–119] However, increased E_s (Figure 5C) and *S* (in snow-dominated watersheds) can result from greater exposure of the sub-canopy to wind and solar radiation.[11,33,61,120,121] The balance of reduced I_c and greater snowpack accumulation with increased E_s and *S* can drive increases or decreases in hydraulic connectivity between Θ_T and Θ_Q, respectively. *R* can increase due to lowered infiltration capacity and increased hydrophobicity after wildfires[121] but can decline in cases where downed necromass is abundant, leading to shifts in the hydraulic connectivity between Θ_T and Θ_Q.[122] Increased macropore abundance due to decaying roots can allow greater M_f to deeper depths,[123,124] potentially bypassing or slowing water flux into the smaller micropores where roots predominantly forage for water,[125] thus decreasing hydraulic connectivity between Θ_T and Θ_Q (Figure 6). M_f should decline from its peak in early succession due to vegetation growth and to soil compaction, though observations of M_f in relation to non-mechanical disturbance are limited. Ultimately, total soil-column Θ can increase following disturbance due to reduced *T*,[126] or it may decrease due to increased E_s and *S*,[33,120] or it may not change at all due to the balance of changes in *T*, E_s, *S*, and *R*. Thus, decoupling of Θ_T to Θ_Q, and *T* to Q, should generally occur from pre- to post-disturbance due not only to ecological but also biophysical drivers, with the rate and trajectory of biophysical changes during succession playing a decisive role in the degree of hydraulic connectivity between Θ_T and Θ_Q and hence the dynamics of *T*/*Q* coupling (hypothesis v; Table 1; Figure 7).

Watershed disturbances typically increase *Q* in cooler, wetter regions and result in no changes or decreases in warmer, more arid regions,[21,33,63,100,127] especially if successional growth is rapid.[128] In energy-limited systems, a larger fraction of precipitation reaches Θ_Q due to lower E_s, thus providing a larger relative input to *Q* than in more arid systems. Furthermore, energy- and water-limited systems may differ in the relative increase in *Q* post-disturbance resulting from the relative changes in E_s and *T*[20,129] due to the lower maximum *LAI* in arid systems and the non-linear relationship between canopy penetration of solar radiation and *LAI*.[130] Canopy light interception is relatively constant for *LAI* values >3 (m^2 leaf area per m^2 ground area) but shows a non-linear, steep decrease for *LAI* values <3. Because

Table 1. Some emergent hypotheses and associated understanding needs regarding disturbance and climate impacts on *T/Q* coupling

Key hypotheses	Critical understanding needs
i. Θ_T/Θ_Q overlap drives *T/Q* coupling	partitioning of total Θ to Θ_T and Θ_Q and *T, Q*
ii. Decreasing total Θ decouples *T/Q*	abiotic/biotic mechanisms regulating Θ_T, Θ_Q
iii. Vegetation traits impact *T/Q* coupling	impacts of vegetation on I_c, E_s, *T*, Θ_T
iv. Transpiration loss decouples *T/Q*	disturbance impacts on *T*, Θ_T, Θ_Q, *Q*
v. Biophysical features impact *T/Q* coupling	disturbance impacts on M_f, *R*, I_c, E_s
vi. Increasing disturbance decouples *T/Q*	disturbance-regimes impact on Θ_T, Θ_Q
vii. *T/Q* decoupling is increasing globally	global-scale changes in disturbances and *T/Q*
viii. Rising CO_2 (de)couples *T/Q*	interactions of total Θ, rising CO_2, and *T*
ix. Rising *VPD* (de)couples *T/Q*	*VPD* impacts on *LAI*, E_s, *T*, Θ_T, Θ_Q
x. Rising drought (de)couples *T/Q*	drought impacts on *LAI*, *T*, Θ_T, Θ_Q
xi. Succession regulates the *T/Q* trajectory	succession impacts on M_f, *R*, I_c, E_s, *T*, Θ_T, Θ_Q

These are testable hypotheses, with the critical understanding needs guiding the parameters requiring measurement and model examination. Note that hypotheses viii–x suggest that CO_2, *VPD*, and drought can both couple and decouple *T/Q* dependent on multiple interacting factors. Hypotheses viii–x propose that either decoupling or coupling may occur.

arid systems have lower pre-disturbance *LAI* than mesic systems, relatively smaller declines in their *LAI* due to disturbance will have large impacts on the penetration of solar radiation to the forest floor and hence higher E_s and *S*, whereas high *LAI* systems must lose a larger fraction of canopy surface area to exhibit the same increase in E_s (Figure S1). For example, in a mesic system with an *LAI* of six, a 50% reduction still leaves an *LAI* of three, resulting in small changes in E_s because an *LAI* of three still captures most incoming light[130] (Figure S1). Furthermore, *T* on an individual plant basis can increase when *LAI* declines, thus maintaining significant watershed-scale *T*.[60,131,132,133] Thus, in mesic systems, the surface hydrologic response to disturbance is dominated by the change in *T* and not E_s. In contrast, in arid systems with open canopies and low *LAI,* a 50% reduction of *LAI* from two to one results in much larger absolute changes in E_s due the much higher light (and wind) penetration (Figure S1). Furthermore, there is less response of *T* to disturbance in arid systems due to the already low stem density in these systems, thus disturbance induces less change in *T* pre- to post-disturbance.[120] Therefore, the relative ratio of E_s/T post-disturbance, as driven by the energy budget and shifts in *LAI*, is a critical determinant of *Q* responses, with larger post-disturbance values in this ratio (e.g., more arid systems) leading to reduced *Q*.[134] This theory also suggests that *T/Q* coupling should be stronger in mesic systems due to the greater importance of *T* than E_s or I_c with lower incoming solar radiation and increasing *LAI*, which scales with aridity (consistent with hypothesis ii; Table 1).

On the role of novel disturbance regimes

Successive disturbances with return intervals that are shorter than successional recovery times can lead to more extreme shifts in ecohydrological parameters, delaying or even quasi-permanently altering the trajectory of hydrologic pools and fluxes (Figure 7). An increasing frequency of disturbances could promote species replacements through repeated destruction of pre-disturbance vegetation types, allowing successful invasion by vegetation types that have shallower rooting depths and lower *LAI* (Figure 7). Species replacements can occur through the repeated destruction of *LAI* and the removal of deep-rooted species and through the continued alteration of microclimate.[134] The increasing frequency of disturbances can lead to persistent reductions in plant biomass through hampered succession,[67] with larger impacts expected in the future due to the increasing frequency of disturbances and changing climate.[4,5,7,8,135,133] Therefore, shifts in succession, in the degree of hydraulic connectivity between Θ_T and Θ_Q, and in *T*/Q coupling may be exacerbated by successive disturbances (hypothesis iv; Table 1; Figures 7 and 8).

Disturbance-driven changes in species composition (e.g., broadleaf to conifer trees, or trees to shrubs to grass; Figure 1), which are being observed more frequently in recent years,[136–139] can also have quasi-permanent impacts on watershed ecohydrology. Large changes in species composition post-disturbance can occur in response to an increasing frequency, severity, and size of disturbances. Large, severe disturbances can be particularly strong drivers of vegetation-type changes and hence *T/Q* decoupling (Figure 7) through large reductions in recruitment of pre-existing vegetation via destruction of reproductive sources.[140,141] Vegetation-type shifts are exacerbated in cases where reproductive sources are few or dependent on slower dispersal mechanisms.[78,139–142] These altered trajectories can lead to significant changes in the vegetation type such as from conifers to broadleaf species and from large-statured to smaller-statured species with lower *LAI* and *RSA*.[4,7,104,141] Vegetation types have significantly different *T* responses to changing *LAI* and *VPD* and large differences in rooting depths,[108,109] both of which can drive large changes in M_f, I_c, *S*, and *R*, so vegetation-type changes can drive large and long-term changes in the hydraulic connectivity between Θ_T and Θ_Q and, subsequently, in *T/Q* coupling.

An emergent hypothesis from the framework is that the disturbance type, size, severity, and frequency can be primary drivers of the impacts upon *T/Q* coupling through differences in their initial impacts, the rate of succession, and on the vegetation-type that recolonizes the watershed (hypothesis vi; Table 1; Figure 8). Disturbances with greater areal spread and loss of plant biomass, and more frequent return intervals, should cause larger and longer-lasting ecohydrological impacts.[23,31,143]

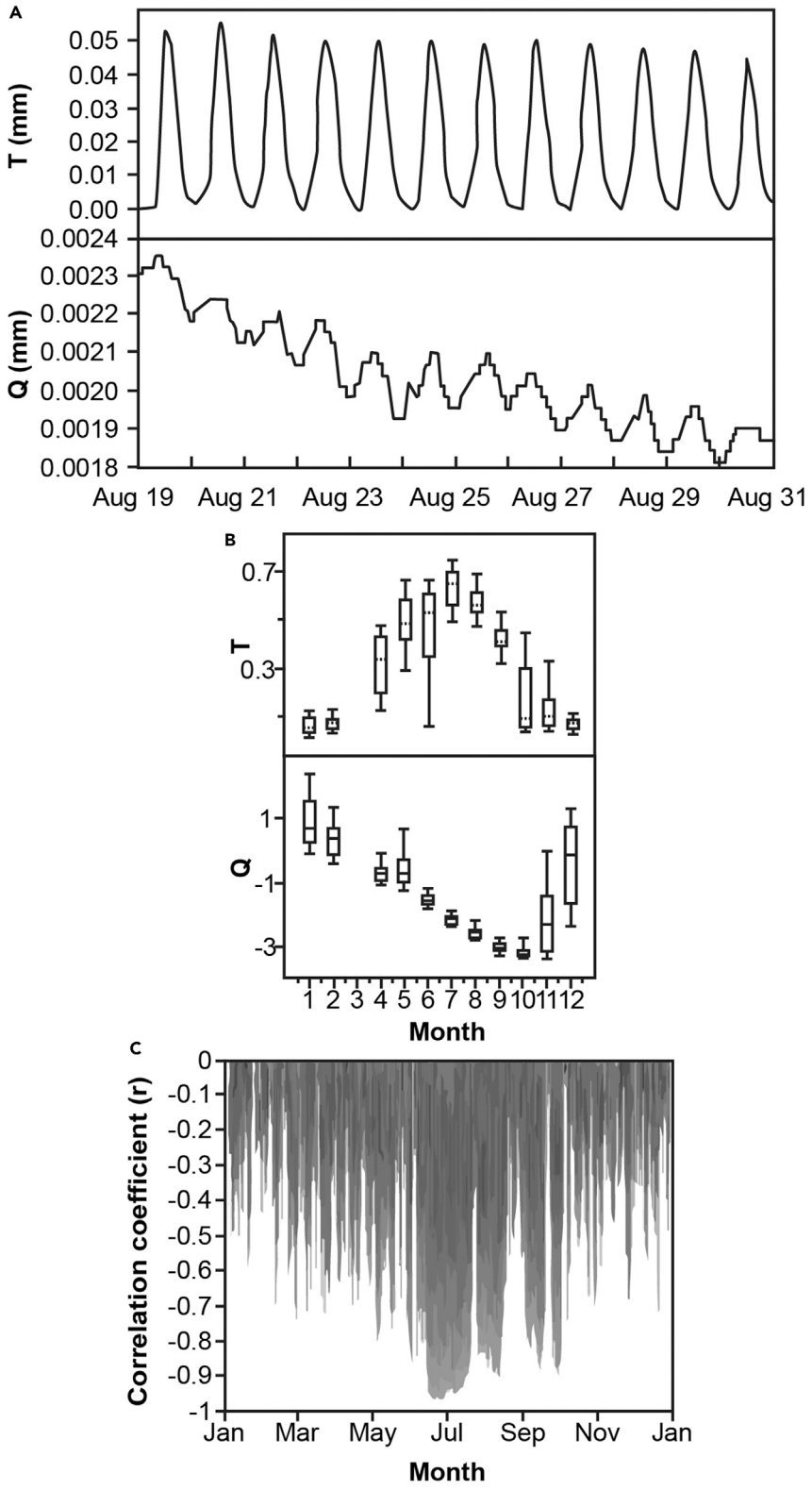

Figure 5. *T* and *Q* coupling across a range of time scales

(A and B) *T* and *Q* coupling in a moist, temperate, old-growth forest on diel (A) and seasonal (B) time periods. On seasonal periods (B), log-transformed mean monthly *Q* and *T* are shown with standard error bars. Note the lag between *T* and *Q* in (B).

(C) Correlation coefficients of the relationship between *T* and *Q* from a semi-arid forest in the intermountain western USA. The data were collected in gauged watersheds with co-located sapflow measurements. The data in (C) were generated from hourly fluxes, similar to those shown in (A).

Data from Moore et al.[83] (A and B) and Graham et al.[48] (C).

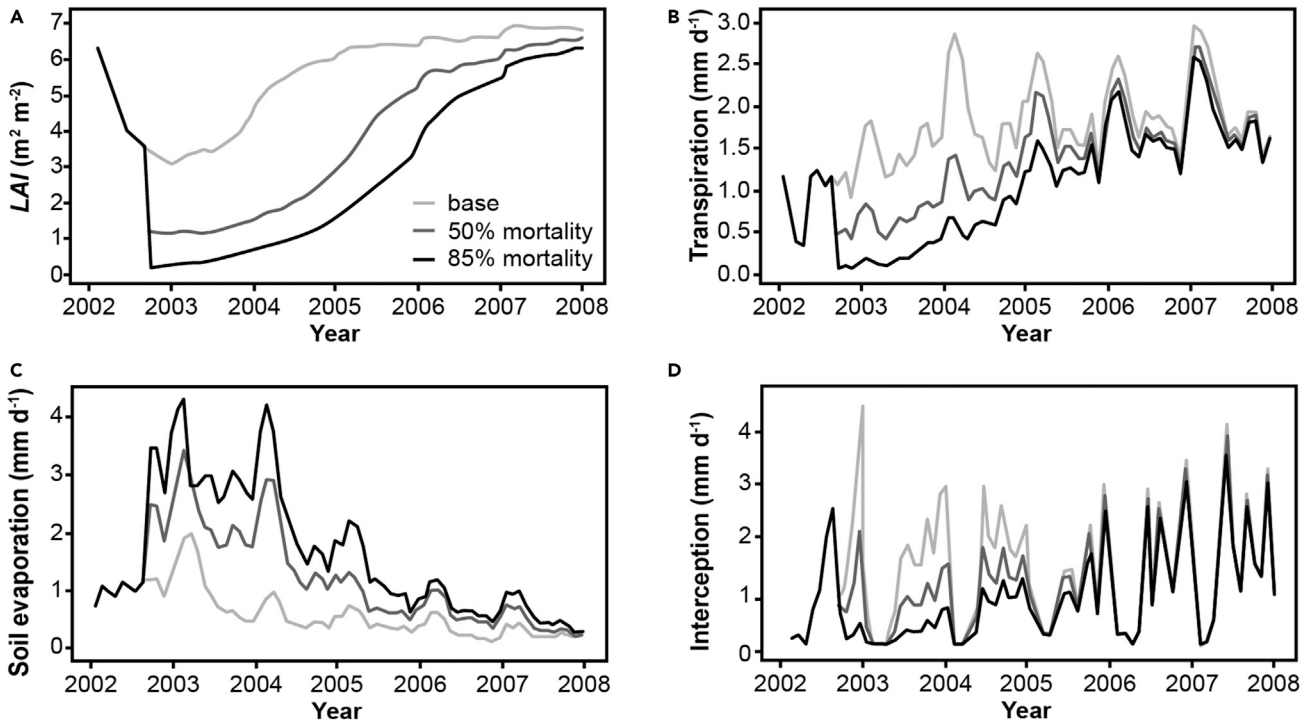

Figure 6. Disturbance alters structural and functional watershed attributes

Modeled monthly (A) leaf area index, (B) transpiration, (C) soil surface evaporation, and (D) canopy interception responses to simulated tree mortality in a moist tropical forest on Barro Colorado Island, Panama. The simulations represented tree mortality (number of of individuals killed) at 0%, 50%, and 85%. Simulations were done using FATES-Hydro (Functionally Assembled Terrestrial Ecosystem Simulator; see Note S1 for more information on FATES-Hydro).

Because the watershed-scale disturbances of drought, wildfire, insect outbreaks, and extreme storms are all anticipated to increase in severity and frequency in the future,[4] a subsequent logical hypothesis is that disturbance impacts will affect *T*/*Q* across larger areas globally, with more severe and frequent impacts in the future (hypothesis vii; Table 1).

POST-DISTURBANCE COUPLING UNDER CHANGING CO_2 AND CLIMATE

Atmospheric CO_2, *VPD*, and drought are rising rapidly and are expected to continue rising for the foreseeable future.[5] Manipulative experiments, observations, and models have demonstrated that CO_2 and *VPD* can impact plant- and ecosystem-scale Θ and *T*.[144] Subsequently, the degree of *T*/*Q* coupling could vary if the chronic rises in CO_2, temperature, and *VPD* affect the magnitude of *T* and E_s and the subsequent sharing of Θ_T and Θ_Q. There is substantial indirect evidence to support this hypothesis; however, direct tests are limited, and thus the role of changing CO_2 and climate upon the partitioning of Θ_T and Θ_Q to *T* and *Q* is a major uncertainty in predictive ecohydrological models.

Most documented CO_2 fertilization responses are seen in young, relatively mesic forests, with less responsiveness observed in dry and/or older forests.[144] In these younger, wetter systems, rising CO_2 can impact *T* at the leaf level through reductions in stomatal aperture, with such reductions in *T* expected to result in water savings that increase Θ.[144] However, these potential water savings can be counteracted by multiple processes. Any "extra" Θ may be unavailable to vegetation if it goes predominately into Θ_Q through M_f or *R*.[18] Physiologically, there are many counteracting forces that may drive *T* up, rather than down, with increasing CO_2. CO_2 fertilization can increase root biomass, rooting depths, and plant leaf area.[135,144] Such whole-plant responses raise whole-plant *T*, thus compensating for leaf-level *T* reductions due to stomatal closure.[145,146] These shifts increase *T* through increasing *LAI* and *RSA*, hence increasing Θ_T and subsequently increasing hydraulic connectivity between Θ_T and Θ_Q. Thus, our literature view supports the hypothesis that in relatively wet sites dominated by young, small-statured vegetation, i.e., systems most likely to respond to CO_2 fertilization, biomass succession and hence the temporal trajectory of *T* and *T*/*Q* coupling may accelerate under elevated CO_2 (hypothesis viii; Table 1).

Rising *VPD* can couple or decouple *T*/*Q* with the net impact unknown. *VPD*, which represents the atmospheric demand for water from the land surface, is an exponential function of temperature and is rising rapidly as temperature increases.[14] Rising *VPD* exacerbates water loss from ecosystems, which increases E_s and *T* and hence depletes Θ, therefore decoupling *T*/*Q*. However, such a rise in *T* should act to couple *T*/*Q* over the short term through greater influence on the hydraulic connectivity between Θ_T and Θ_Q, leading to uncertainty as to the net impacts of rising *VPD* on coupling. Indeed, *T* has increased globally over the last two decades in response to land-surface warming[20,147] which should lead to reduced *Q* at the global scale.[19] However, negative *VPD* impacts on growth have been rising in recent years,[148] which could lead to decoupling

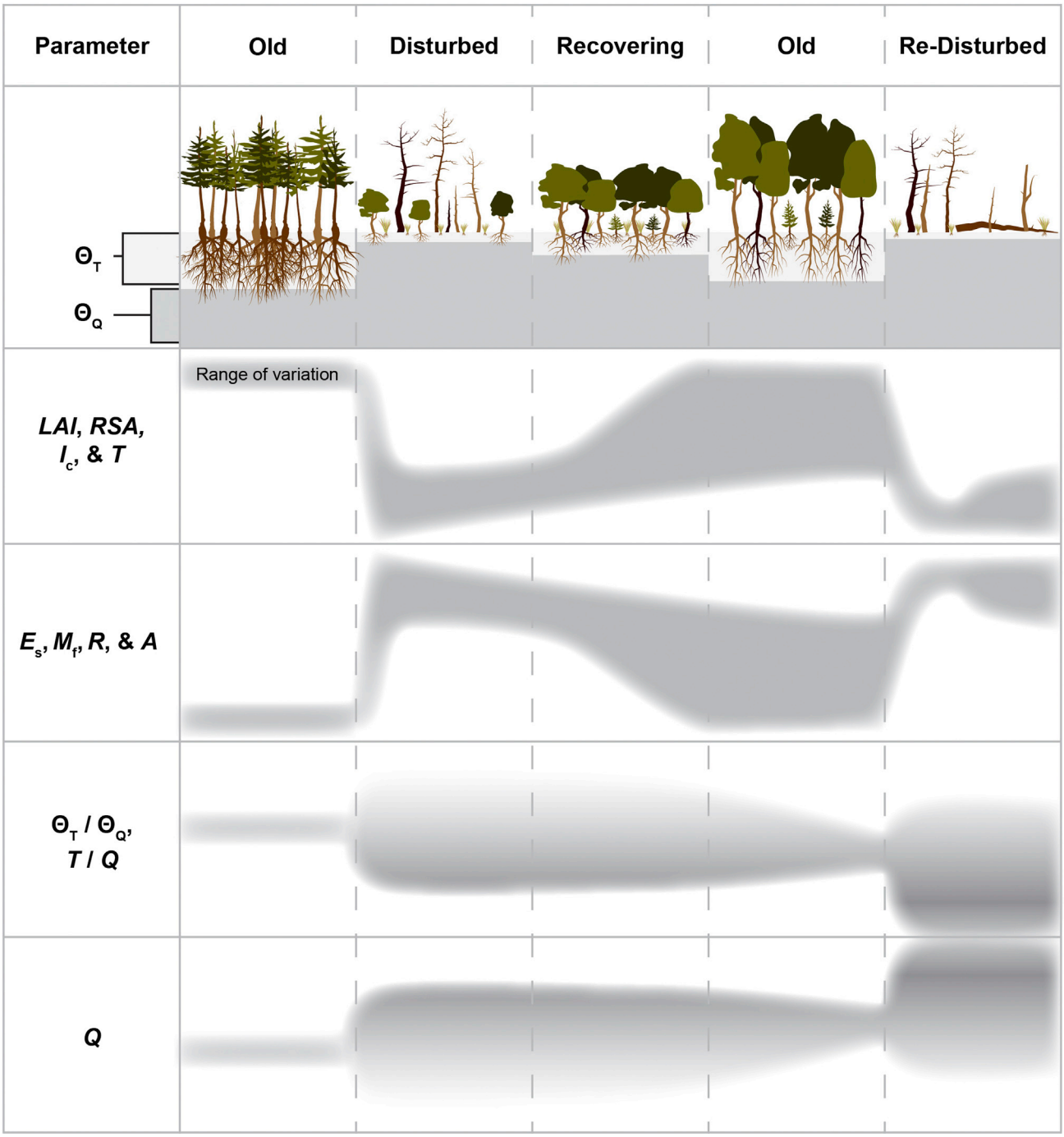

Figure 7. Hypothesized trajectories of key mechanisms underlying *T*/*Q* coupling in relation to successional states before, during, and after disturbance

Also shown is the scenario in which a subsequent disturbance occurs prior to vegetation recovery to the pre-disturbance state. The redisturbed ecosystem was disturbed prior to complete resuccession to an old-growth or quasi-steady-state condition and thus has altered values for the key parameters and ultimately lower *T*/*Q* coupling relative to the first disturbance. The hypothesized range of trajectories of each parameter are shown with the gray shaded area. In some cases, the parameters do not fully respond despite a long return interval due to warming and rising vapor pressure deficit. Key parameters are leaf area index (*LAI*), root surface area (*RSA*), canopy interception (I_c), transpiration (*T*), soil evaporation (E_s), macropore flow (M_f), runoff (*R*), sublimation (*S*), streamflow (*Q*), source water pools coupling (Θ_T/Θ_Q), and *T*/*Q* coupling.

through loss of *LAI* and *RSA* via *VPD*-driven leaf loss or whole-plant mortality. Under conditions of high *VPD*, drought, or when trees become large statured, the benefits of acclimation to CO_2, such as reduced stomatal conductance and increased photosynthesis, decline significantly, and mortality becomes more likely.[104] Seedlings are particularly vulnerable to high

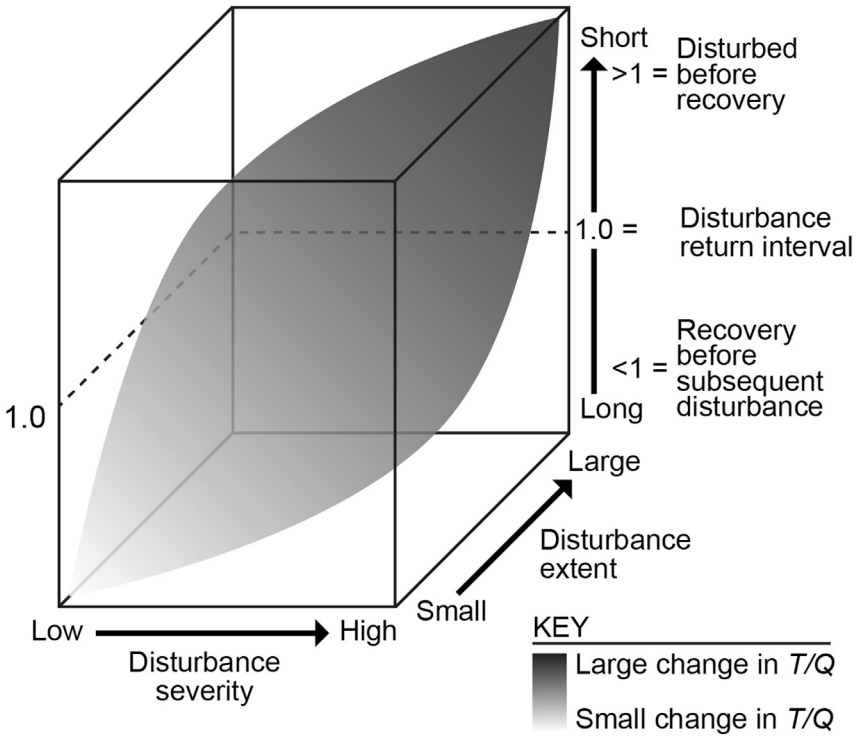

Figure 8. The hypothesized response of watershed *T*/*Q* coupling to disturbance severity, extent, and frequency

The shaded region shows the anticipated *T*/*Q* response to these disturbance characteristics, with light shading representing relatively minor disturbance impacts on *T*/*Q* coupling and dark shading representing significant impacts on *T*/*Q* coupling. Disturbance severity can be considered the degree of leaf area removed from the watershed, while extent represents the areal spread of the disturbance. Disturbance frequency (also known as disturbance return interval) values >1 indicate the watershed was disturbed before vegetation had recovered from the previous disturbance, whereas values <1 represent watersheds in which the vegetation composition and structure have fully recovered prior to a subsequent disturbance. Expectations of increasing severity, extent, and frequency of future disturbances lead to the hypothesis that *T*/*Q* decoupling should increase globally in the future.

VPD[149]; thus, compounding drivers of disturbance, drought, and rising *VPD* may cause recruitment failure of pre-disturbance vegetation, resulting in critical shifts, e.g., from forest to shrubland or grassland[7,8,149] (Figure 1), with associated shifts in *T* and *T*/*Q* coupling. Under warming conditions with increased *VPD*, the rate of succession can slow down leading to a system dominated by new, smaller-statured species with lower *LAI* and *RSA* and less *T*[7] and thus reduced hydraulic connectivity between Θ_T and Θ_Q (Figure 2). Thus, rising *VPD* can increase *T*/*Q* coupling through increasing *T* on a short-term basis or can decrease coupling longer term by reducing Θ and through negative impacts on growth (i.e., reduced *LAI*); hence, the net impact of rising *VPD* on *T*/*Q* coupling is uncertain (hypotheses ix and x: Table 1).

Rising frequency and severity of meteorological droughts (periods of anomalously low precipitation) should result in *T*/*Q* decoupling. This decoupling follows from the reduction in Θ and the subsequent reduction in *T*, both of which lead to less hydraulic connectivity between Θ_T and Θ_Q as described above. Exceptions to this expectation should occur in particularly energy-limited systems, where drought can actually lead to higher *T* and possibly greater *T*/*Q* coupling. Additionally, if drought leads to reduced *LAI* and *RSA* through leaf loss and plant mortality, this will act to reduce *T*/*Q* coupling over the long term (Figures 2 and 7). This leads to the hypothesis that increasing drought can decouple *T*/*Q* through impacts of decreasing Θ and lower hydraulic connectivity between Θ_T and Θ_Q (hypothesis x; Table 1). Thus, increasing droughts could lead to decreased *T*/*Q* coupling over longer-term periods in which vegetation structure and composition is influenced. The impact of these changing atmospheric drivers on *T*/*Q* coupling is a grand challenge for ecohydrology.

OUTLOOK AND CONCLUSIONS

The emergent hypotheses regarding the mechanisms underlying *T*/*Q* coupling post-disturbance revolve around how structural changes in the watershed, e.g., *LAI*, *RSA*, I_c, and M_f, lead to changes in the sharing of water fluxes that regulate Θ_T and Θ_Q (Table 1). Evidence from the literature leads to many hypotheses regarding the mechanisms driving the degree of *T*/*Q* coupling (Figures 2, 3, 4, 5, 6, and 7; some of which are highlighted in Table 1). Among the hypotheses that emerge, a logical one is that disturbances will decrease the hydraulic connectivity between Θ_T and Θ_Q, and, consequently, *T*/*Q* coupling should decline due to decreased *T* and increases in E_s, M_f, and *R* that allow incoming water to bypass Θ_T and go toward Θ_Q (hypothesis vi; Table 1). These hypotheses are time and climate dependent: as succession occurs, so will recovery of the system toward the original or new trajectory, with short- and long-term dynamics imposed by daily to multi-annual variation in precipitation, *VPD*, and other climatic drivers. We hypothesize further that post-disturbance *T*/*Q* coupling will be stronger under mesic conditions when soil hydraulic connectivity is high and weaker under more arid conditions.[21] Thus, as *VPD* and *T* rise, so will Θ_T/Θ_Q connectivity over the short term, but as ecosystems dry, we can expect less *T*/*Q* coupling. Predictions of increasing disturbance frequency, spread, and severity suggest greater ecohydrological impacts in upcoming decades, with the hypothesis that ecohydrological decoupling of many watersheds will be more dynamic, and may change quasi-permanently, in response to altered disturbance and climatic regimes. Shifts in coupling also result from changes in vegetation as succession progress, with traits changing over time and when species composition is quasi-permanently altered.[7,24]

These emergent hypotheses (Table 1) point to a research agenda that should be undertaken if we are to better predict hydrologic fluxes and stores under changing disturbance regimes and non-stationary climates. Simulating *T*/*Q* coupling ultimately requires improved understanding of the Θ_T/Θ_Q connectivity and

the dependence of that connectivity on soil characteristics, on hourly to multi-annual climatic variation in water inputs, and on regional climate variation. The subsequent partitioning of water to *T* and *Q* as a function of vegetation characteristics is critical to understand the link between soil hydraulic connectivity and the allocation of water to *T* and *Q*. Advances in our understanding of Θ_T/Θ_Q connectivity and partitioning need to be placed in the context of disturbances to better predict how changing disturbance regimes will lead to altered *T*/*Q* coupling. We need to find the dependence of Θ_T/Θ_Q connectivity and partitioning under a range of disturbance types, e.g., wildfire and insect outbreaks, across a range of disturbance frequencies, severities, and areal spread across watersheds. Thus, the use of paired watershed studies that compare disturbed and undisturbed systems (e.g., Figure 4), chronosequences that capture post-disturbance trends as succession advances, and long-time series datasets that include disturbance events should all be utilized to most effectively advance our understanding.

Maximal progress toward a better predictive understanding of *T*/*Q* coupling requires using all of the tools at our disposal. Efforts that integrate both models and measurements are likely to most rapidly advance our understanding, through the use of empirical data for hypothesis testing and model benchmarking and subsequent model analyses of alternative hypotheses.[10,12,150] Models can be further used for prediction of what could happen under different disturbance, management, and climate scenarios,[5,10,22] thus enabling mitigation and planning for *Q* responses to future disturbances. Efforts that integrate many measurement approaches, i.e., hydrometric, isotopic, and remote sensing methods,[21] are of greatest value, as they enable independent verification of results while also allowing scaling of detailed process measurements to the watershed.

Models allow investigation of processes that are difficult to measure as well as enabling experimental analyses of how processes interact and lead to variation in *T*/*Q* coupling. Such modeling efforts must be done in conjunction with empirical information such that the model outcomes are trustworthy. To achieve believable outcomes requires model benchmarking against observations of the key hydrologic pools and fluxes, as well as accounting for the factors that control them, such as soil and vegetation characteristics. Models require development, however, to best enable them to provide mechanistically realistic results. Models are currently challenged in the representation of dynamic hydraulic connectivity between Θ_T and Θ_Q and the in representation of vegetation characteristics such as acclimation to changing CO_2 and climate, carbon allocation, and recruitment, all of which regulate the rate and sources of *T*[151–154] (Figure 7).

The magnitude of potential changes in ecohydrology that can result from the interactions among multiple and compound disturbances may lead to positive feedbacks that push ecosystems and their water services to new, evolving states. Prediction of these changes is essential for informed water management under changing climate and disturbance regimes. Enhanced understanding and prediction will require integrated observational, experimental, and numerical approaches to understanding the degree of *T*/*Q* coupling post-disturbance and under a changing climate. Improved and validated models can inform prevention and mitigation strategies to avoid undesirable consequences for water cycling in the future. The emergent hypotheses can form the basis for a research agenda that quantifies the drivers and mechanisms regulating *T*/*Q* coupling after disturbances, thereby enabling improved anticipation of future impacts.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2023.02.007.

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AUTHOR CONTRIBUTIONS

N.G.M. drafted the manuscript and led the literature review. Y.F. conducted the modeling and created the global review figure. All authors contributed to the literature review and to the editing of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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