ANNUAL REVIEWS

Annual Review of Earth and Planetary Sciences

Instructive Surprises in the Hydrological Functioning of Landscapes

James W. Kirchner,[1,2,3] Paolo Benettin,[4] and Ilja van Meerveld[5]

[1]Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland; email: kirchner@ethz.ch

[2]Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland

[3]Department of Earth and Planetary Science, University of California, Berkeley, California, USA

[4]Laboratory of Ecohydrology, School of Architecture, Civil and Environmental Engineering, École Polytechnique Fédérale de Lausanne, Lausanne, Switzerland

[5]Department of Geography, University of Zurich, Zurich, Switzerland

Annu. Rev. Earth Planet. Sci. 2023. 51:277–99

First published as a Review in Advance on January 10, 2023

The *Annual Review of Earth and Planetary Sciences* is online at earth.annualreviews.org

https://doi.org/10.1146/annurev-earth-071822-100356

Keywords

hydrology, ecohydrology, isotopes, catchment, hillslope, runoff

Abstract

Landscapes receive water from precipitation and then transport, store, mix, and release it, both downward to streams and upward to vegetation. How they do this shapes floods, droughts, biogeochemical cycles, contaminant transport, and the health of terrestrial and aquatic ecosystems. Because many of the key processes occur invisibly in the subsurface, our conceptualization of them has often relied heavily on physical intuition. In recent decades, however, much of this intuition has been overthrown by field observations and emerging measurement methods, particularly involving isotopic tracers. Here we summarize key surprises that have transformed our understanding of hydrological processes at the scale of hillslopes and drainage basins. These surprises have forced a shift in perspective from process conceptualizations that are relatively static, homogeneous, linear, and stationary to ones that are predominantly dynamic, heterogeneous, nonlinear, and nonstationary.

- Surprising observations and novel measurements are transforming our understanding of the hydrological functioning of landscapes.
- Even during storm peaks, streamflow is composed mostly of water that has been stored in the landscape for weeks, months, or years.

- Streamflow and tree water uptake often originate from different subsurface storages and from different seasons' precipitation.
- Stream networks dynamically extend and retract as the landscape wets and dries, and many stream reaches lose flow into underlying aquifers.

INTRODUCTION

When rain falls or snow melts, water reaches the living skin of the Earth, the so-called critical zone comprising soil, bedrock, and life forms ranging from trees to microbes (Grant & Dietrich 2017). Some of this water evaporates from the surface, some eventually becomes streamflow, some is eventually taken up and transpired by vegetation, and in between most of it is transiently stored in the subsurface on timescales ranging from minutes to millennia. How landscapes store, transport, and partition water among its ultimate fates is consequential for Earth's climate, for terrestrial and aquatic ecosystems, for our vulnerability to natural hazards, and for agricultural sustainability and food security. Thus the hydrological functioning of landscapes has far-reaching implications.

It can also be surprisingly counterintuitive. We all observe precipitation and its consequences in everyday life, and thus we might assume that the dynamics of water in the terrestrial environment are straightforward and obvious. But much of the behavior that we observe at the surface is generated in the complex and spatially heterogeneous subsurface, where our intuition often fails us.

Here we review key discoveries that have challenged our preconceptions of how landscapes store and release water and how they partition it among its various fates. We begin by summarizing how isotopic and chemical tracers have led to a new appreciation of the contrasting timescales of hydrologic response and transport, and new insights into the heterogeneity of aquifer storage on timescales from days to millennia. We then outline recent evidence that reveals how landscapes partition precipitation between its ultimate fates as streamflow and evapotranspiration and that quantifies the seasonal origins of the water that is ultimately used by trees. Last, we summarize recent insights into connections between landscapes and stream networks, highlighting the dynamic extension and retraction of headwater stream networks and the widespread prevalence of losing stream reaches (which lose flow via seepage into underlying aquifers rather than gaining flow from them). These examples illustrate how surprising observations and novel measurements have driven advances in our understanding of the hydrological functioning of landscapes.

TIMESCALES OF HYDROLOGIC RESPONSE AND TRANSPORT

If we venture out into a forest or meadow shortly after a cloudburst, we can often observe streams surging with flow. It seems intuitively obvious that this rapid response must reflect rainwater flowing immediately to channels via overland flow or fast subsurface flowpaths. This may indeed be the case in urban settings, agricultural fields, or disturbed landscapes with limited infiltration capacity. But in most natural landscapes, contrary to our intuition, recent rainfall makes up only a small fraction of streamflow.

Instead, decades of studies with isotopes and other passive tracers have shown that streamflow, even during storm events, is usually composed mostly of rain that fell weeks, months, or even years ago and has been stored within the landscape ever since (e.g., Sklash & Farvolden 1979, Neal & Rosier 1990, Sklash 1990, Buttle 1994, Kirchner et al. 2000, McGuire & McDonnell 2006, Jasechko et al. 2016, Jasechko 2019). In other words, landscapes respond to recent rainfall by releasing stored water to streamflow much more rapidly than they transmit recent rainfall itself to streams [even in some catchments dominated by overland flow runoff (Lapides et al. 2022)].

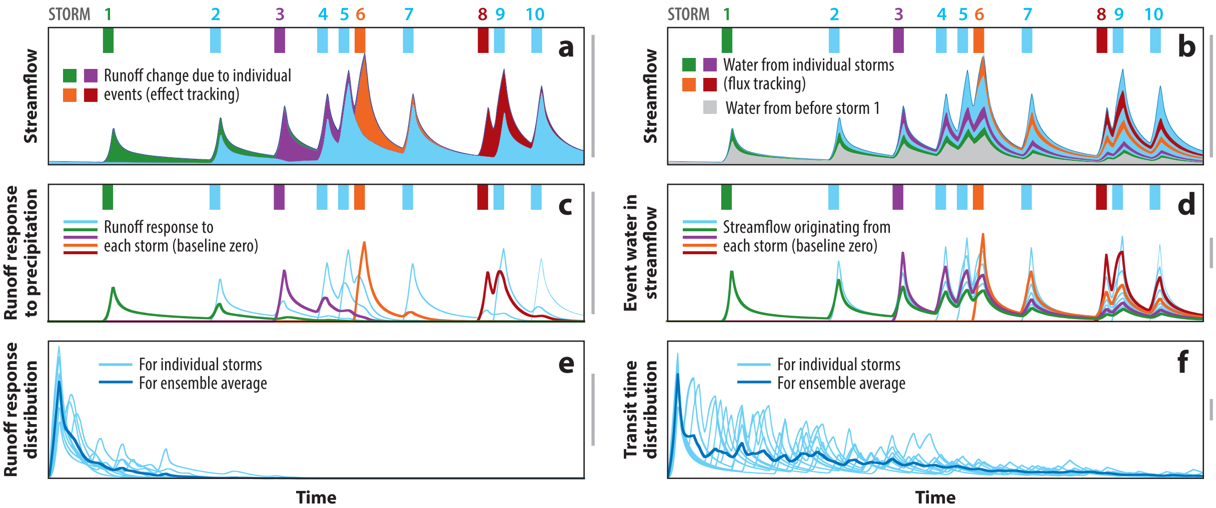


Figure 1

Effects of 10 simulated rainstorms on future stream discharge (*left panels*) and future streamflow composition (*right panels*) in the simple nonlinear two-box model of Kirchner (2019). The green, purple, orange, and red bands show the runoff response to storms numbered 1, 3, 6, and 8, respectively. Runoff response, shown in panel *a*, is measured by how much the discharge time series changes when individual storms are included/excluded from the precipitation time series. Transport response, shown in panel *b*, is measured by tracking the water flux that originated as precipitation during each storm; streamflow originating from precipitation before storm 1 is shown in gray. Panels *c* and *d* show runoff and transport response, respectively, for all 10 storms, plotted against a baseline of zero so that they can be more easily compared. Panels *e* and *f* show the runoff and transport responses from panels *c* and *d*, expressed in terms of lag time since the onset of precipitation; the dark blue lines show the ensemble averages of the 10 individual runoff response distributions and transit time distributions shown in light blue. Each horizontal axis shows the same time interval. The vertical scales are identical in panels *a*–*c* but differ among the remaining panels to show the behavior more clearly. The gray bars along the right edge of each panel show what the relative sizes of the vertical axes would be if the scales were consistent.

This decoupling of the timescales of hydrological response and transport has been recognized for at least half a century (e.g., Brown 1961, Hubert et al. 1969, Pinder & Jones 1969, Martinec 1975, Rodhe 1981), but understanding its underlying mechanisms remains a central challenge in hydrology (Kirchner 2003, McDonnell & Beven 2014).

A simple model of catchment behavior (**Figure 1**) illustrates the contrasting timescales of hydrologic response and transport for four individual storms highlighted in contrasting colors. The left-hand side of **Figure 1** shows how each rainstorm alters the total rate of stream discharge; the right-hand side, by contrast, shows how much each rainstorm's water contributes to future streamflow. In contrast to the short-lived runoff response (left-hand side of **Figure 1**), the same storms have much longer-lived effects on the composition of streamflow (right-hand side of **Figure 1**). The water from each storm persists in runoff throughout the whole storm sequence, with each storm mobilizing stored water that fell during previous storms.

Streamflow typically varies as a nonlinear function of catchment storage (Kirchner 2009). This implies that, as one can see from **Figure 1*c*,*d***, the response to each storm may depend on future precipitation (which spurs the release of water from subsurface storage), as well as on how wet the landscape already is (and thus on antecedent precipitation). Thus, each storm's distribution of response times [between when rain falls and when stream discharge subsequently rises (**Figure 1*e***)] and transit times [between when water enters the catchment and when it subsequently leaves (**Figure 1*f***)] will depend on the size and timing of both previous and subsequent storms. Nonetheless, the averages of these response time and transit time distributions (distributions of lag times between water entering the catchment as precipitation and leaving as streamflow) over many storm events (dark blue lines in **Figure 1*e,f***) can be considered as signatures of landscapes' hydrologic behavior.

Until recently, hydrology courses and rainfall-runoff models have mostly overlooked the contrast between the timescales of hydrologic response and transport, or, equivalently, between the celerity with which rainfall-induced perturbations are transmitted through the landscape and the velocity at which the water itself moves (Beven 2012, McDonnell & Beven 2014). One reason may be simple pragmatism: Applied hydrology is often concerned with forecasting and managing streamflow, and when a river creates havoc by overflowing its banks, questions about the age of the floodwaters will seem pedantic. Instead, the central questions for managing hydrologic hazards such as floods, landslides, and debris flows will focus on how meteorological conditions and catchment processes combine to create so much streamflow so quickly, no matter what its age might be.

But understanding and managing these natural hazards requires understanding their underlying mechanisms, which in turn requires understanding where, how, and how quickly water is mobilized from the landscape (Bogaard & Greco 2016). Conversely, understanding where and how water is retained within the landscape is crucial for understanding water availability for plants (Allen et al. 2019) and how soil drying amplifies heat waves (Mueller & Seneviratne 2012, Miralles et al. 2014). Water ages, and the tracers that we use to infer them, provide crucial information about subsurface hydrologic processes that would otherwise be invisible.

Many different mechanistic assumptions can be encoded in models that, given sufficient parameter flexibility, will reproduce the observed dynamics of soil moisture and streamflow rather well (Beven 2012). Thus, models based on these different mechanistic assumptions may all fit the data well, but they may also lead to divergent inferences about how these systems will behave in the future and how they should be managed. Tracers and water ages provide an important constraint that helps us test whether such models are getting the right answers (i.e., good fits to the observed data) for the right reasons (Kirchner 2006, McDonnell & Beven 2014). How quickly landscapes transport water and, conversely, how long they store it, are also important questions for their own sakes, as controls on the transport and release of nutrients and contaminants (Hrachowitz et al. 2016) and on rates of chemical weathering and thus long-term geochemical regulation of atmospheric CO_2 (Maher 2010, Maher & Chamberlain 2014).

Isotopic Indicators of Transport Timescales

The contrasting timescales of hydrologic response and transport can be inferred from hydrometric and isotopic time series, as shown in **Figure 2** for the Upper Hafren catchment in Wales. At Upper Hafren, as in many catchments, stream discharge responds quickly to rainfall, but isotopic tracers in rainfall are strongly damped in streamflow (**Figure 2*a***). The water isotopes ^{2}H and ^{18}O follow the water because they are part of the water molecule itself; thus, if peak flow were composed mostly of recent rainfall, its isotopic signature would also resemble recent rainfall. Instead, stormflow isotopic signatures typically deviate little from a relatively stable background value, implying that streamflow is a mixture of waters from months or even years of previous rain events.

The fraction of streamflow originating from recent rainfall can be estimated from the change in streamwater isotopic composition, relative to the prestorm baseline and the rainfall input [hydrograph separation (Klaus & McDonnell 2013)]. Tracer time series can also be used to estimate transit time distributions via many different approaches, including spectral methods and time-domain convolution fitting (McGuire & McDonnell 2006), as well as through calibration of catchment mixing models (e.g., Weiler et al. 2003, van der Velde et al. 2015) with their attendant problems of equifinality and epistemic uncertainty. In the past decade, a major effort has sought to

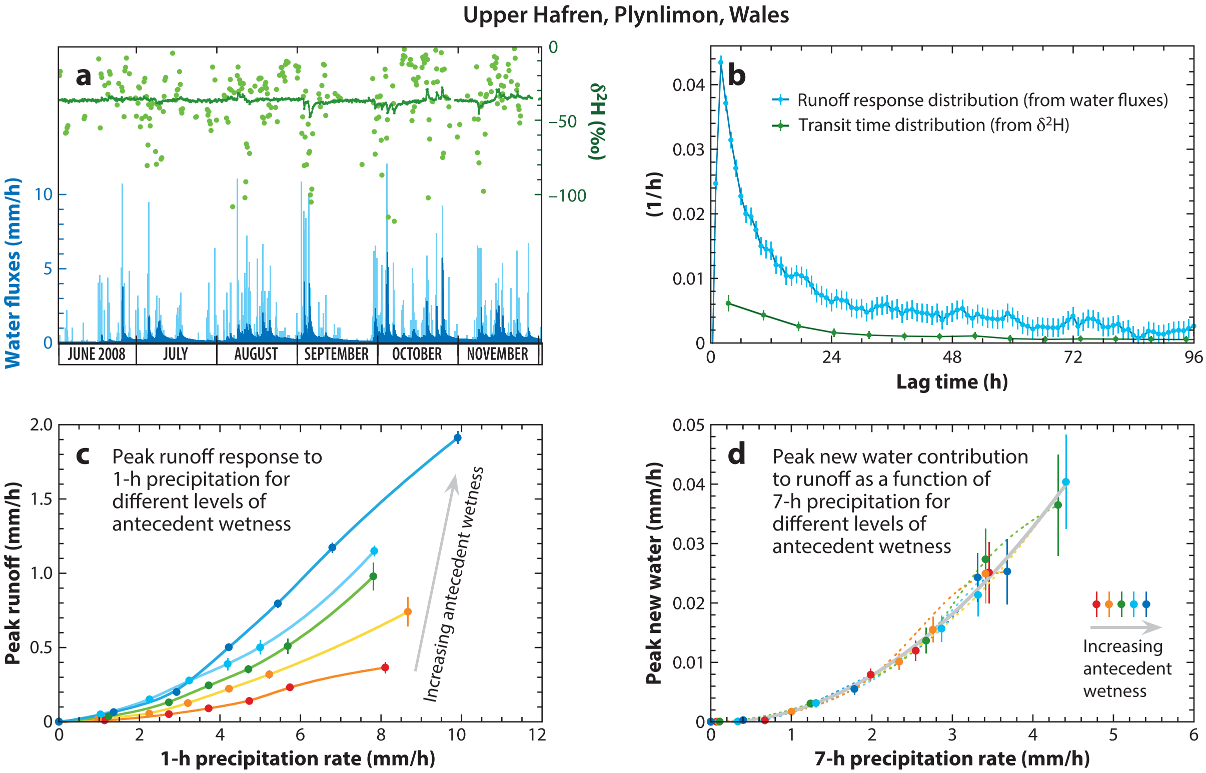


Figure 2

Hydrologic response and transport at Upper Hafren, Plynlimon, Wales, as reflected in hydrometric and isotopic time series (data from Knapp et al. 2019). (*a*) Hourly streamflow water fluxes respond quickly and sharply to precipitation inputs (*dark* and *light blue*, respectively; left scale), whereas 7-hour deuterium tracer fluctuations in streamflow are strongly damped relative to precipitation tracer fluctuations (*dark* and *light green*, respectively; right scale). (*b*) Ensemble-averaged runoff response distribution (*blue symbols*), calculated from precipitation and streamflow using nonlinear deconvolution (Kirchner 2022), shows that the hydrologic response is much larger and sharper than the transport behavior reflected in the ensemble-averaged transit time distribution (*green symbols*), calculated from tracer concentrations using ensemble hydrograph separation (Kirchner 2019, Knapp et al. 2019). (*c*) Peak runoff varies nonlinearly with precipitation intensity and with antecedent wetness; the colored curves (*red* to *blue* in order of pre-event discharge, as a proxy for wetness) show that the runoff response is stronger, and more nonlinear, under wetter conditions. (*d*) Transport of new water to runoff varies nonlinearly with precipitation intensity but not with antecedent wetness: curves of different colors (indicating different wetness conditions) lie on top of one another.

explain nonstationary transit time behavior in terms of storage selection functions, which quantify the relative mobility of waters of different ages stored within the catchment (Botter et al. 2010, van der Velde et al. 2012, Benettin et al. 2015, Harman 2015). A still more recent development is ensemble hydrograph separation, a model-independent, data-driven method for deconvolving transit time distributions directly from observational data (Kirchner 2019, Knapp et al. 2019). By analyzing data subsets reflecting different catchment conditions or meteorological forcings, ensemble hydrograph separation can quantify, directly from data, how transit time distributions and new water fractions vary with storm characteristics and ambient conditions such as antecedent wetness.

Amid the community's focus on quantifying timescales of catchment transport, the corresponding timescales of hydrologic response have received relatively little attention recently. For nearly a century, hydrologic response time distributions have primarily been estimated by unit hydrograph methods (Sherman 1932, Jakeman et al. 1990, Dooge & O'Kane 2003, Shaw et al. 2011). These methods assume linearity (outputs are proportional to inputs) and stationarity (precipitation has the same effect, no matter when it falls), whereas hydrological systems are typically nonlinear and nonstationary. However, new methods have recently been developed for quantifying landscapes' nonlinear, nonstationary response to precipitation directly from observational data using nonlinear deconvolution and demixing (Kirchner 2022), and the first hydrological applications are now underway.

These nonlinear deconvolution and demixing methods show that the runoff response distribution for Upper Hafren (blue symbols in **Figure 2*b***) has a much higher, sharper peak than the ensemble hydrograph separation estimate of the transit time distribution (green symbols in **Figure 2*b***), illustrating the contrast between the timescales of transport and hydrological response. Integrating under these curves reveals that for each additional millimeter of rain, on average 0.80 ± 0.02 mm of additional streamflow leaves the catchment within the following week [roughly equaling the long-term runoff ratio at this very wet site (Marc & Robinson 2007)], but that only 0.19 ± 0.02 mm of that streamflow is composed of the rainfall in question, with the rest being mobilized from storage.

The peak runoff response at Upper Hafren varies nonlinearly with precipitation intensity and antecedent wetness, becoming stronger and more nonlinear under wetter conditions (**Figure 2*c***). The peak new water contribution of recent rainfall to streamflow also varies nonlinearly with precipitation intensity but, in contrast to the peak runoff response, it is independent of antecedent wetness (**Figure 2*d***). Together, **Figures 2*c*** and ***d*** show that wetter conditions prime the landscape to more readily release old water from storage, but not to more readily transmit new water to streamflow. This surprising result is consistent with the findings of von Freyberg et al. (2018) for the Erlenbach catchment (Alptal, Switzerland) using different methods. Whether this is also true for other landscapes remains to be seen.

Many mechanisms have been proposed to explain the rapid mobilization of water from catchment storage during storm events, including kinematic waves (Beven 1989), fracture flow in bedrock aquifers (Worthington 2018), and transmissivity feedback, in which the water table rises into shallower, more permeable soil layers as the catchment wets up (Bishop et al. 2011). The challenge for theory, however, goes beyond simply devising hypotheses that can explain how rainfall-induced perturbations can propagate through the landscape faster than the water itself flows. An adequate theory needs to explain how landscapes can also retain water for months but then release it, in large volumes, within minutes or hours after rain falls (Kirchner 2003), promptly increasing stream discharge by large multiples. A complete theory will also need to explain the shapes of the response time and transit time distributions (e.g., **Figure 2*b***), and their nonlinear and nonstationary response to catchment conditions and rainfall intensity (e.g., **Figure 2*c*,*d***). Such a theory remains elusive at present.

Implications of Multiscale Subsurface Heterogeneity

Beyond the timescales of individual hydrologic events, analyses of multi-year tracer time series have revealed that their power spectra often exhibit fractal $1/f$ scaling on timescales from hours to decades. In $1/f$ time series, spectral power is inversely proportional to the frequency f, and thus each octave (halving or doubling of frequency) contributes equally to the total variance. Such $1/f$ time series are fractal, lacking a dominant characteristic timescale. This fractal scaling—which differs from the nonfractal scaling of stream discharge itself—holds both for passive tracers such as water isotopes or Cl^- and for reactive solutes spanning the periodic table (Kirchner et al. 2000, Godsey et al. 2010, Kirchner & Neal 2013, Aubert et al. 2014, Knapp et al. 2019). It can arise from chemical signals originating across the landscape and undergoing widely varying degrees of either Fickian or anomalous dispersion (including both shear dispersion arising from permeability gradients in the subsurface and effective dispersion arising from differing topographic slopes and transmissivities in different parts of the catchment) as they are transported toward the stream (Kirchner & Neal 2013). Other explanations have also been proposed, including velocity and path length distributions in groundwater flow nets (Kollet & Maxwell 2008), matrix diffusion in fractured bedrock aquifers (Rajaram 2021), and continuous time random walks, which mimic the important mechanism that parcels of water flowing slowly through low-permeability zones will also disperse slowly, making them particularly persistent (Scher et al. 2002). In-stream dispersion can also lead to additional spectral steepening at high frequencies, particularly in large basins (Hensley et al. 2018). Whatever its origins, the $1/f$ scaling observed in solute concentrations has the consequence that on timescales from hours to decades, water quality time series are non-self-averaging: Contrary to the assumptions underlying conventional statistics, averages taken over longer and longer intervals do not converge to stable long-term means. This implies that conventional trend analyses will overestimate the statistical significance of many water quality trends and greatly underestimate their uncertainties (Kirchner & Neal 2013).

Young Streamflow from Old Aquifers

Over still longer timescales, stable water isotopes become uninformative and one must rely instead on tracers such as ^{3}H, chlorofluorocarbons, and ^{14}C to estimate the long tail of groundwater and streamflow ages (e.g., Stewart et al. 2010, Frisbee et al. 2013, Cartwright & Morgenstern 2018, Jasechko 2019). Groundwater can be impressively old; in a global survey, Jasechko et al. (2017) showed that half or more of total aquifer storage in the upper 1 km of Earth's crust is significantly depleted in ^{14}C (half-life 5,730 years) and thus is thousands of years old. Surprisingly, roughly half of these "fossil groundwater" samples also have measurable levels of ^{3}H (half-life 12.3 years) and thus must also contain some water that is just a few years or decades old, implying that many aquifers contain strongly contrasting permeabilities.

This subsurface heterogeneity has the consequence that waters stored in aquifers are typically much older than the waters that drain from them (Berghuijs & Kirchner 2017). Although this behavior seems counterintuitive (and is inconsistent with typical modeling assumptions), its explanation is straightforward: High-conductivity flowpaths flow faster, so they transmit disproportionately more water and this water is disproportionately young. Conversely, the large volumes of water that are retained in aquifers (rather than transmitted through them) are typically very old, precisely because they are very slowly recycled to the surface. At the global scale, this mismatch in water ages is substantial. For example, Jasechko et al. (2016) used seasonal isotopic cycles in 254 global rivers to show that water younger than ∼70 days makes up roughly one-third of global streamflow but originates from less than 0.1% of global subsurface storage, which on average is thousands of years old (Jasechko 2019). As this example shows, streamflow ages cannot be directly inferred from groundwater ages or vice versa [although they are mathematically related (see Berghuijs & Kirchner 2017)].

DIFFERENT WATER SOURCES FOR TREES AND STREAMS

Landscape processes partition rainfall and snowmelt between two ultimate fates: "blue water" that is discharged to streamflow, and "green water" that is evaporated and transpired back to the atmosphere. Understanding this partitioning is essential to predicting how both blue and green water fluxes will respond to climate change. Green water fluxes account for about 60% of the total, but unlike streamflow, they are invisible, spatially dispersed, and difficult to measure and sample, so their sources and controlling mechanisms have been difficult to pin down.

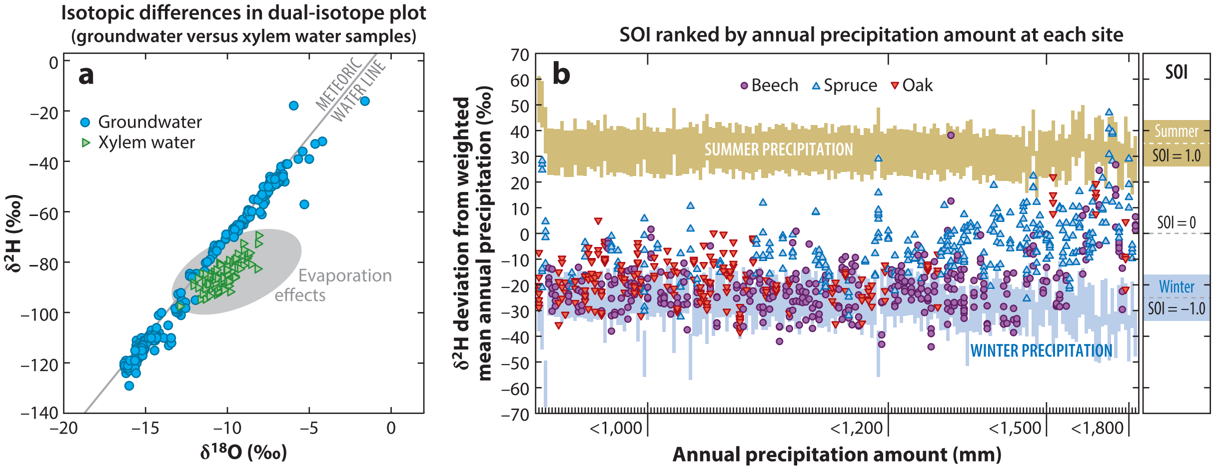


Figure 3

Examples of isotope data used to investigate plant water sources. (*a*) Groundwater and xylem water samples collected by Brooks et al. (2010), obtained from the database of Evaristo et al. (2015). Groundwater samples tend to plot along the meteoric water line that characterizes precipitation, while xylem samples plot below this line, indicating evaporative fractionation. (*b*) Seasonal origin index (SOI) computed by Allen et al. (2019) for 182 Swiss forest sites, plotted in order of annual precipitation. Isotope values in xylem samples lie much closer to winter than summer precipitation (shown by *blue* and *gold shading*, respectively), indicating that they are derived primarily from winter precipitation, except at the wettest sites. Panel *b* adapted from Allen et al. (2019) (CC BY 4.0).

For example, one might intuitively assume that trees growing directly adjacent to a perennial stream should be drawing on the same water that becomes streamflow. But already three decades ago, Dawson & Ehleringer (1991) used ^{2}H in xylem water of mature riparian trees to show that they did not obtain their water from the adjacent stream, nor from nearby soils, but most likely from groundwater flowing through the underlying bedrock. This study demonstrated that isotopic tracers could be used both to identify plant water sources and to overthrow our intuitive expectations of what those sources should be.

Two decades later, in two contrasting forest sites, Brooks et al. (2010) and Goldsmith et al. (2012) showed that soil and xylem samples exhibited clear isotopic evidence of evaporative fractionation relative to precipitation, whereas nearby streamwaters showed no such fractionation, again suggesting clear isotopic differences between the sources of blue and green water (see also **Figure 3*a***). A subsequent meta-analysis of 47 diverse forest ecosystems showed that this phenomenon is widespread (Evaristo et al. 2015). The isotopic differences between streams, soils, and xylem waters can vary with landscape and climate characteristics, and may be indistinct in some sites [e.g., the humid Scottish Highlands (Geris et al. 2015)].

These isotopic differences are often characterized as reflecting "ecohydrological separation" between "two water worlds" (e.g., McDonnell 2014, Berry et al. 2018). We should not take such terms too literally. Any water sample from a landscape reflects a mixture of waters with different origins, flowpaths, and histories. Thus, an isotopic difference between blue water and green water means only that their distributions of origins, flowpaths, and histories differ somewhat; they may still largely overlap (e.g., Dubbert et al. 2019). Ecohydrological separation is a question of degree, and landscapes will encompass not just two water worlds but rather a shifting continuum of water worlds across space and time.

There may be methodological complications as well. The procedures that are used to extract water from soils and xylem samples may themselves cause isotopic fractionation, which may mimic the effects of evaporation (e.g., Orlowski et al. 2016, Chen et al. 2020). Such artifacts do not necessarily invalidate the use of xylem water isotopes to infer plant water sources, however, as long as they are small compared to the real-world isotopic signals in the data (Allen & Kirchner 2022).

One might also intuitively assume that trees typically rely on rain that falls during the growing season (except, of course, in climates where summer precipitation is scarce). But by comparing the seasonal cycle in precipitation isotopes with xylem water samples from more than 900 trees across 182 Swiss forest sites (**Figure 3*b***), Allen et al. (2019; see also Goldsmith et al. 2022) showed that except at the wettest sites, trees primarily used water that had fallen as precipitation during the winter (despite the fact that at most of these sites, more precipitation falls during the summer). One consequence is that isotopic climate proxies in tree rings may not reflect growing-season conditions or even annual average conditions.

One might furthermore intuitively assume that trees get their water solely from the soil that surrounds their roots. But isotopic and ecophysiological data show that unsaturated rock moisture within bedrock pores and fractures (Rempe & Dietrich 2018) can be the dominant water source for many trees in climates subject to summer drying (Hahm et al. 2020) and may be essential for their survival during drought (McDowell et al. 2019). Plant communities that are seasonally reliant on rock moisture may be extensive. For example, McCormick et al. (2021) estimate that woody vegetation that accesses rock moisture accounts for more than half of California's aboveground carbon storage.

At first glance, the isotopic differences between waters found in trees, soils, and streams would appear to be paradoxical. How can rainfall get through the rooting zone to become streamflow without being taken up by trees? And conversely, if near-surface soil waters and xylem waters show the isotopic effects of evaporative fractionation, why aren't these same effects found in streamwaters and groundwaters, which once also flowed through those same shallow soils?

One possible explanation lies in the pervasive multiscale heterogeneity of the subsurface and the resulting dominance of preferential flow (**Figure 4**). Simply put, most of the water that drains through the soil infiltrates rapidly via highly permeable flowpaths and mixes relatively little with the less mobile water in the soil matrix. Vegetation, on the other hand, is likely to preferentially use this less mobile matrix water, precisely because it is less mobile and thus more reliably available throughout the growing season (compared to water in the more permeable flowpaths, which drain faster between storms, precisely because they are more permeable). Any isotopic evaporation signal in the shallow soil matrix may fade with depth if most of the near-surface matrix water is eventually taken up by vegetation or diluted by new rainfall events (Sprenger et al. 2016).

The apparent paradox of plants preferentially using tightly held matrix water (Berry et al. 2018) disappears when one considers the temporal context. Plants use highly evolved rooting strategies to get the water and nutrients they need (Fan et al. 2017), and they need a reliable source of water throughout the growing season, not just briefly after rain events, when it would be available in higher-permeability flowpaths.

An even simpler potential explanation for the isotopic differences between trees, soils, and streams may lie in seasonal variations in precipitation and evapotranspiration rates, and thus in the contrasting proportions of winter and summer precipitation that eventually become green and blue water (Kirchner & Allen 2020, p. 29). Consider a hypothetical—but not unrealistic—scenario in which precipitation rates do not vary seasonally, but evaporation and transpiration are more prominent during the summer growing season. If the landscape does not store enough water to average out the seasonal isotopic variations in precipitation, then xylem water will more closely resemble summer precipitation compared to average streamflow (and will also be more fractionated by evaporation) simply because precipitation is more likely to be evapotranspired in the summer than the winter and is more likely to become streamflow in the winter than

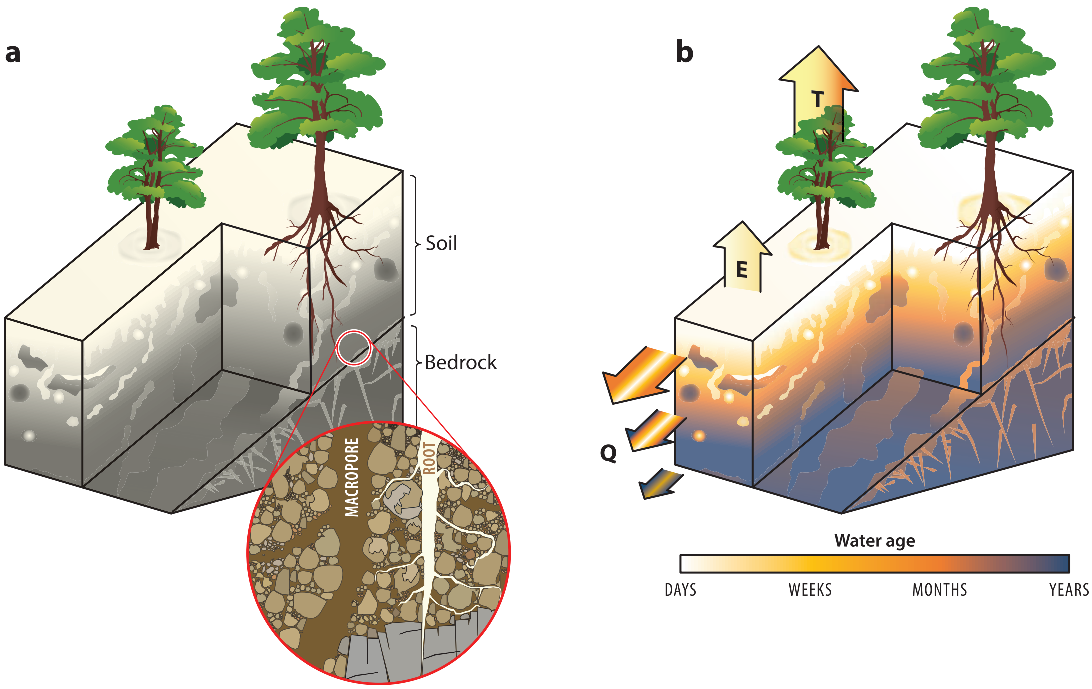


Figure 4

Conceptual illustration of the subsurface structure (*a*) and water age distribution (*b*) of a hillslope. (*a*) The subsurface environment is usually characterized by macropores and fractures that create heterogeneity at all scales; plants may not root in macropores if they are not a reliable source of water and nutrients. (*b*) Subsurface heterogeneity causes large spatial contrasts in water sources (here expressed through their age, i.e., the time since they entered the system as precipitation). Subsurface heterogeneity and plant rooting strategies are expected to generate differences in the isotope composition of evaporation (E), transpiration (T), and groundwater recharge/streamflow (Q). Panel *b* adapted with permission from Sprenger et al. (2019) (CC BY-NC-ND 4.0).

the summer. Note that this thought experiment does not require physically distinct storages or pathways for blue and green water. In particular, it does not require ecohydrological separation between matrix waters that supply vegetation and more mobile waters that supply streamflow.

A variant of this hypothesis may explain the summer use of predominantly winter water in Allen et al.'s (2019) Swiss forest plots. If interception and subsequent evaporation in the canopy, leaf litter, and forest floor consume a large enough fraction of summer precipitation, infiltration (and thus soil water storage in the rooting zone of trees) may be mostly derived from winter precipitation instead (Jasechko et al. 2014). This hypothesis is consistent with the trend toward less reliance on winter water at the wettest Swiss forest sites (**Figure 3*b***).

Several models are available that can simulate the transport and fractionation of water isotopes, but few of them have been tested on xylem isotope data (e.g., Knighton et al. 2019, Smith et al. 2022), and even fewer incorporate preferential flow explicitly (e.g., Sprenger et al. 2018). Dual-porosity or dual-permeability formalisms (e.g., Šimůnek et al. 2003) can partly account for preferential flow and isotopic variability in the subsurface, without explicitly representing subsurface spatial heterogeneity.

As an alternative to the complexity (and assumption-dependence) of simulation models, data-driven approaches can also be used to characterize plant water sources. For example, the seasonal origin index (Allen et al. 2019) quantifies the relative importance of winter versus summer precipitation as origins of soil water and xylem water. Bayesian mixing frameworks (e.g., Stock et al. 2018) based on isotope tracer data can help identify plant and stream water sources while handling the uncertainties that come from sparse and inconsistent tracer data.

Alternatively, instead of asking where blue and green water come from, one can ask where precipitation goes, using end-member splitting analysis (Kirchner & Allen 2020) to quantify how precipitation is divided between its ultimate fates as blue and green water. This can be done without measuring or sampling green water fluxes, so end-member splitting can be applied where flux measurements and isotopes are available only for precipitation and streamflow, and not for xylem water.

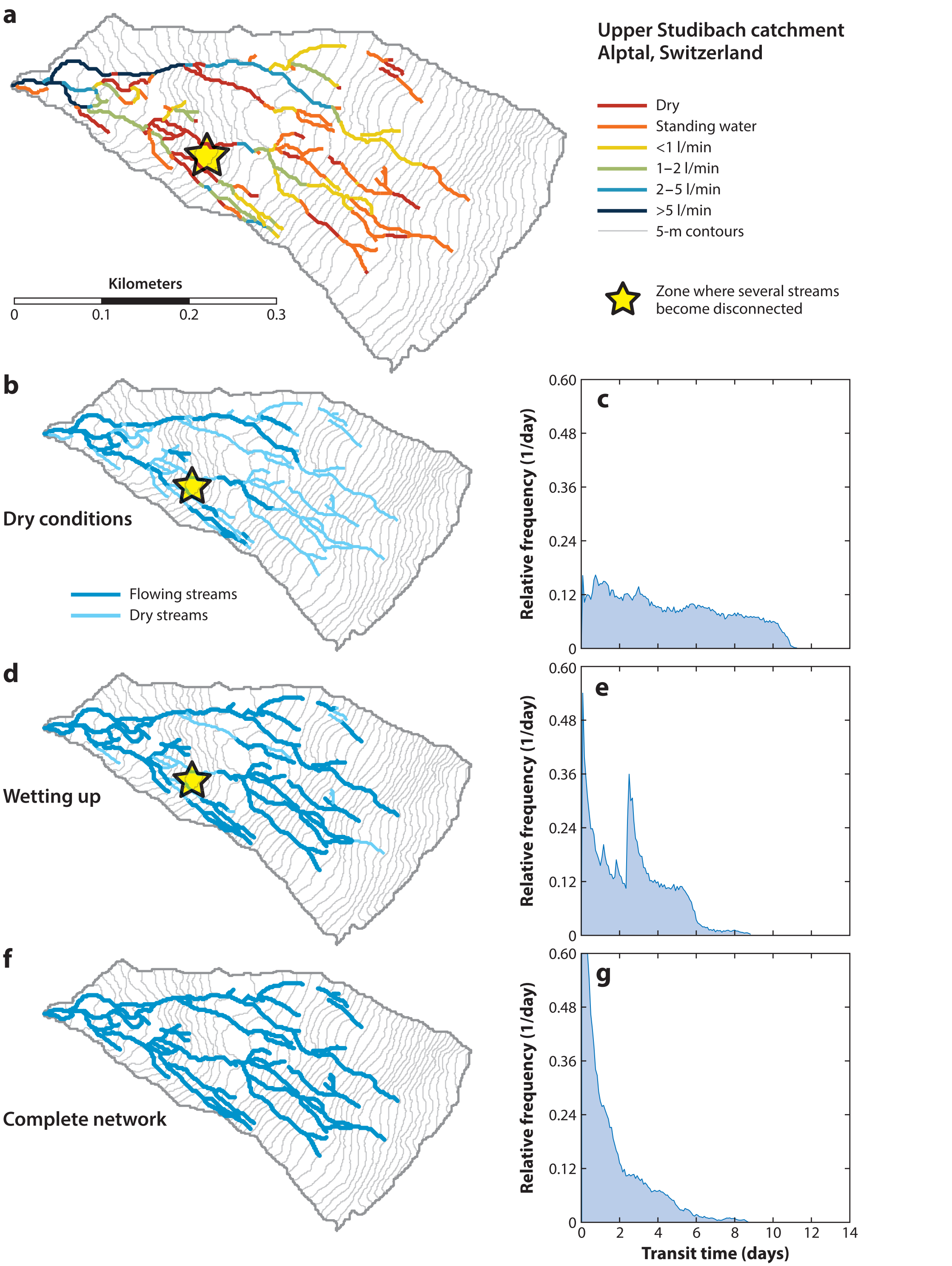
DYNAMIC CONNECTIVITY BETWEEN LANDSCAPES AND STREAM NETWORKS

Maps, and most hydrological theories, depict stream networks as static features. But in the real world, far from being the fixed blue lines that are shown on maps, stream networks dynamically extend and retract, and connect and disconnect, both seasonally and during storm events, as the landscape wets up and dries out. Although a few observations of this phenomenon reach back several decades (Gregory & Walling 1968, Blyth & Rodda 1973, Day 1978), more recent field mapping studies have highlighted how widespread and dynamic these nonperennial streams are (Wigington et al. 2005, Doering et al. 2007, Godsey & Kirchner 2014, Mutzner et al. 2016, Jensen et al. 2017, Zimmer & McGlynn 2018, Pate et al. 2020, Senatore et al. 2021). Far from being anomalies, nonperennial streams have been estimated to make up more than half of all channels on Earth by length (Hammond et al. 2021, Messager et al. 2021).

New low-cost sensors that continuously detect the presence of water (Blasch et al. 2002, Bhamjee & Lindsay 2011, Jaeger & Olden 2012) or streamflow (Assendelft & van Meerveld 2019) have revealed how quickly stream networks can expand during rainfall events. The drainage density (the length of flowing streams per catchment area) of headwater catchments can change by factors of 2–10 or more (Wigington et al. 2005, Godsey & Kirchner 2014) seasonally or during storm events. The flowing stream network can extend far beyond the geomorphic channel network, or contract to occupy only a small fraction of it (Godsey & Kirchner 2014). The total lengths of flowing stream networks typically vary as the 0.1–0.5 power of stream discharge (Godsey & Kirchner 2014, Prancevic & Kirchner 2019, Lapides et al. 2021), although they may remain nearly constant if stream heads primarily occur at perennial groundwater springs (e.g., Whiting & Godsey 2016).

Implications of Network Extension and Retraction

As the flowing stream network expands, it comes closer to each point on the landscape (van Meerveld et al. 2019). This accelerates the runoff response at the catchment scale because hydraulic signals propagate much faster (i.e., with higher celerity) along flowing channels than through hillslope soils or bedrock. The velocity of the water itself is also much higher in flowing channels, so network expansion also results in faster transport of nutrients and contaminants to the catchment outlet. Expansion of the stream network not only shortens the average transit time but also changes the shape of the transit time distribution, making it less uniform by multiplying the number of points on the landscape that are adjacent to a flowing channel (van Meerveld et al. 2019) (**Figure 5*b*–*g***). Stream network expansion can also bypass riparian buffer strips and has been linked to increases in nitrate concentrations (Wigington et al. 2005), changes in dissolved organic carbon (Hale & Godsey 2019), and accelerated release of CO_2 to the atmosphere (Marx et al. 2017, Duvert et al. 2018). The onset of flow in previously dry or disconnected stream sections can flush out sediment and organic material, leading to high sediment and nutrient fluxes to downstream rivers (Hladyz et al. 2011, Fortesa et al. 2021). Rewetting events are also hot moments for



(Caption appears on following page)

Figure 5 (*Figure appears on preceding page*)

Network contraction and disconnection in the Upper Studibach catchment, Alptal, Switzerland. (*a*) Map of flow states and estimated flow rates on November 2, 2016, highlighting the variability in flows across the stream network, including gaining and losing reaches, as well as the dry sections that cause disconnections. Data collected by Rick Assendelft. (*b–g*) Maps of the flowing stream network (*dark blue*) during contrasting wetness conditions (*left panels*), and calculated transit time distributions (*right panels*) assuming a subsurface velocity through the soil of 5×10^{-4} m s^{-1} and a surface velocity in the stream of 0.5 m s^{-1}. As the flowing stream network expands, the distances to the stream become shorter, resulting in a shorter transit time and a less uniform transit time distribution because many more points in the landscape are now close to a flowing stream. Figure adapted from van Meerveld et al. (2019) (CC BY 4.0).

biogeochemical reactions and significantly affect dissolved inorganic carbon and nitrogen fluxes (von Schiller et al. 2017, Gomez-Gener et al. 2021). Thus, changes in the flowing stream network can substantially alter both water quantity and quality.

Mechanisms Underlying Network Extension and Retraction

The emergence of surface flow in channels depends on whether the supply of water from upstream or upslope exceeds the capacity of the subsurface to transport this water downstream or downslope (Godsey & Kirchner 2014, Dohman et al. 2021, Warix et al. 2021). The supply of water varies across the landscape, reflecting both the upslope drainage area and its topographic convergence (Anderson & Burt 1978, Freer et al. 1997, Jencso et al. 2009). The subsurface transport capacity likewise varies across the landscape, depending on valley slope, cross-valley curvature, and subsurface transmissivity. These factors can be combined to estimate, directly from topographic characteristics, how dynamic (or, conversely, stable) stream networks are likely to be (Prancevic & Kirchner 2019). The spatial patterns of local drainage area and subsurface transport capacity are durable features of landscape organization, thus explaining headwater stream networks' hierarchical dynamics (Botter et al. 2021), in which more persistent stream segments begin flowing earlier and cease flowing later than less persistent channels.

Connectivity Between Surface and Subsurface Flow Networks

Much of the lateral drainage from hillslopes occurs through discrete preferential flowpaths, including old root channels, animal burrows, fracture networks, and zones with coarser, more permeable material (**Figure 4*a***). Large dye tracing experiments (Sidle et al. 2001, Anderson et al. 2009, Graham et al. 2010) and modeling studies (Weiler & McDonnell 2007, Nieber & Sidle 2010) have shown that although the individual preferential flow pathways are often short and physically disconnected, the water flowing through them will tend to create networks of preferential flowpaths. These subsurface seepage networks are analogous to surface stream networks and similarly expand and contract, depending on wetness conditions (Tsuboyama et al. 1994, Sidle et al. 2000). Flows through these subsurface seepage networks can have a different chemical composition from the rest of the subsurface (Burns et al. 1998, Welsch et al. 2001, Ploum et al. 2020), and their intersections with the surface stream network can lead to fine-scale patchiness in streamwater quality (e.g., Zimmer et al. 2013, McGuire et al. 2014).

Bidirectional Connectivity Between Surface Waters and Groundwaters

Textbooks mostly feature gaining streams, which receive flow from their surrounding groundwaters. Losing streams, which lose flow via seepage into underlying aquifers, are less commonly depicted. But in the real world, they are not rare; in a survey of 4.2 million wells across the United States, Jasechko et al. (2021) showed that two-thirds of them had water levels below adjacent streams, implying widespread potential for streamflow losses to groundwaters. Individual stream reaches can alternate between gaining and losing conditions, both seasonally and in response to

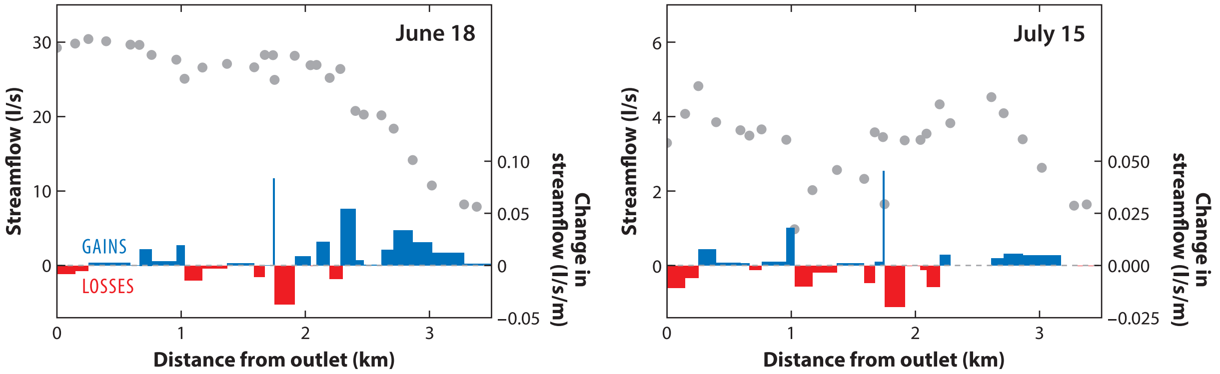


Figure 6

Measured streamflow (adjusted for diurnal streamflow variations) in Long Joe Creek, British Columbia, Canada, on June 18 and July 15, 2011 (*gray circles*), together with the change in streamflow per meter distance between successive measurement locations (*bars*). Repeated measurements throughout spring to fall 2011 showed that the patterns of gains (*blue bars*) and losses (*red bars*) remained stable, except that the major gains in the headwater area of the catchment (above km 2.4) decreased after the snowmelt period. Although the flow decreased by about a factor of five between the two selected dates (note the differences in the vertical axes), the major inflows and outflows decreased only by about a factor of two. Data collected by Emily Huxter.

hydrological events (e.g., Vidon & Hill 2004, Vidon 2012). Flow and tracer measurements have also shown that many streams are composed of alternating gaining and losing reaches (e.g., Covino & McGlynn 2007, Payn et al. 2009, Dohman et al. 2021) (see also **Figure 6**).

Many headwater streams can even disappear into the subsurface entirely, where they flow over coarse, highly permeable substrates or large bedrock fractures (Godsey & Kirchner 2014, Whiting & Godsey 2016) (for one example, see the red asterisks in **Figure 5**). This disconnects the upstream catchment from the downstream network, leading to fragmentation of the in-stream habitat (even if a subsurface flow connection remains). These disconnections may be persistent, or may transiently appear and disappear in response to seasonal or event-timescale changes in catchment wetness.

These dynamic and heterogeneous linkages between groundwater and surface water have important implications for modeling and managing water resources. Losing flow conditions are rarely represented in hydrological models. Most lumped conceptual (i.e., bucket-type) models cannot explicitly represent losing-gaining dynamics (but for important exceptions, see Brauer et al. 2014 and Staudinger et al. 2021). Some model studies, while not directly simulating the interaction between groundwater and streamwater, have allowed for intercatchment groundwater flow (Le Moine et al. 2007, Schwamback et al. 2022). Distributed physically based models can simulate these bidirectional fluxes and the flowing stream network explicitly (Querner et al. 2016, Gutierrez-Jurado et al. 2021), and their calibration can be improved by testing whether they correctly predict the presence and absence of surface flow (Stoll & Weiler 2010).

At the regional scale, hydrometric and isotopic data show that losing rivers can provide an important mountain-to-desert subsidy to dryland ecosystems, as they flow from humid headwaters to arid lowlands and recharge their aquifers (Jobbágy et al. 2011). A global mass balance study (Kuppel et al. 2017) shows that this lateral subsidy from humid uplands to arid lowlands supports a substantial fraction of annual evapotranspiration over large areas of the globe (Fan 2019). Conversely, the spatial correlation between groundwater pumping rates and the prevalence of losing streams (Jasechko et al. 2021) shows that our use of groundwater comes at a cost to surface flows, as we draw down water tables and convert gaining streams to losing ones.

SUMMARY AND OUTLOOK

We have briefly reviewed several surprising observations that have transformed, and continue to transform, scientific perspectives on the hydrological functioning of landscapes. These include the following:

- Streamflow—even during storm runoff—is typically dominated by water that has been stored in the landscape for weeks, months, or even years, rather than recent rainfall. This implies that landscapes transmit hydrological signals faster, and with higher fidelity, than they transmit water itself. Understanding the mechanisms by which landscapes retain water for so long, but then mobilize it so quickly, remains an important scientific challenge.
- Power spectra of solute time series exhibit $1/f$ fractal scaling for elements spanning most of the periodic table, contrasting with the nonfractal scaling of stream discharge itself. This implies that the subsurface is pervasively heterogeneous across multiple scales, including the widely varying path lengths connecting each point on the landscape to the nearest channel. It further implies that spurious and inconsistent, but visually convincing, trends can readily arise in water quality time series.
- Groundwaters can contain a wide spectrum of ages, even within individual samples, and streamwaters are much younger than the aquifers that feed them. This implies that many aquifers are dominated by strong permeability contrasts, such that even old groundwaters could be affected by modern contamination. Aquifer heterogeneity also implies that even in steady state, aquifers and the waters that flow from them should be expected to yield strongly contrasting water ages.
- Tree xylem waters are often isotopically distinct from streamwaters, indicating physical or seasonal differences in their dominant sources. This implies incomplete mixing between waters that become streamflow (flowing primarily via higher-permeability subsurface flowpaths) and those that become evapotranspiration (which are retained, and thus are more reliably available for plant uptake, in lower-permeability zones of the subsurface). It also highlights the importance of seasonal differences in the effective precipitation that remains available for infiltration and plant uptake after losses to interception and evaporation in the canopy and forest floor.
- Stream networks dynamically extend and retract, and connect and disconnect, resulting in nonperennial channels that account for over half of all streams on Earth. This implies dynamic variation in the extent and connectivity of aquatic habitats. Stream network extension also shortens hillslope flowpaths to the nearest stream, shortening timescales of hydrologic response and accelerating the transport of nutrients and contaminants. The presence or absence of surface flow reflects the balance between subsurface transport capacity and the delivery of water from upslope and upstream; thus the extension and retraction of stream networks dynamically maps out patterns of transmissivity in the subsurface.
- Losing streams are widespread, with two-thirds of measured groundwater levels lying below nearby rivers. Losing streams provide an important groundwater subsidy to many dryland ecosystems that lie downstream of more humid headwaters. The prevalence of losing streams is correlated with groundwater pumping rates, highlighting the importance of managing groundwater and surface water as interconnected resources (e.g., Winter et al. 1998).

To be clear, the surprises outlined above may not have surprised every hydrologist. With the benefit of hindsight, for example, one can find early work (e.g., Hewlett & Hibbert 1967) concerning translatory flow processes that transmit discharge perturbations faster than the water itself flows (see also the historical account of Beven 2004). But until recently, many hydrology students were taught that stormflow is derived from recent rainfall that reaches the stream by overland flow, and some are still taught this today. Similarly, 50 years ago Blyth & Rodda (1973) asked, "Why has it largely been ignored that natural drainage networks are dynamic rather than static phenomena?" But it has only recently become clear how much these networks extend and retract, and how widespread and consequential this phenomenon is. Thus, when we characterize these observations as surprises, we mean that they were surprising to (or overlooked by) substantial fractions of the research community, not that they were completely unknown.

Many of the surprises outlined above stand in particularly sharp contrast to conceptualizations of catchments as well-mixed boxes. Such well-mixed boxes may be a legacy of catchment science's original emphasis on mass balances (of both water and solutes), for which they provide a simple first-order framework. Such boxes are also often adopted as a mathematical convenience in hydrological modeling, but the fact that these box models can often be calibrated to perform rather well (particularly if they are only tested against stream discharge time series) should not be mistaken as confirmation that they are mechanistically realistic. At the same time, it would be a formidable challenge (and superfluous for many purposes) to explicitly model the multiscale subsurface heterogeneity that underlies many of the phenomena outlined above. Thus, an important challenge is to develop theoretical frameworks for characterizing this heterogeneity and quantifying its effects at larger scales, without needing to represent it explicitly.

What can be done to create favorable conditions for future instructive surprises? Tracers, particularly water isotopes, have spurred many of the surprises outlined above, and their potential to surprise us has probably not been exhausted. High-frequency tracer measurements, on similar timescales to the landscape's hydrological response, have an important role to play (Rode et al. 2016). Real-time in situ tracer measurements in soils and plants (Beyer et al. 2020) will aid us in seeing inside the whole-landscape black box, particularly when coupled with simultaneous in situ measurements of water fluxes and potentials. The black box can also be cracked open by tracer experiments targeting individual system components or processes (e.g., Benettin et al. 2021, Werner et al. 2021). Together with measurement and observation initiatives such as these, analysis and synthesis tools that can cope with—and even characterize and quantify—the nonlinearity and nonstationarity inherent in many hydrological systems (e.g., Kirchner 2022) will probably also play an important role in revealing future surprises.

We close by noting that every one of the surprises outlined here came primarily from observations and measurements, rather than from theoretical modeling, which tends to encapsulate our preconceptions rather than overthrow them. We belabor this point in view of hydrology's declining emphasis on field observations and growing reliance on models (Burt & McDonnell 2015), including the tracer-aided simulation models that are increasingly used to interpret the isotopic dynamics of streamflow, soils, and xylem water. The risk of model-based inference is that, because simulation models are inherently based on our conceptualization of a system, their behavior will rarely conflict with our intuition, limiting the chances for instructive surprises. Surprises—and the insights that come from them—can indeed arise from models, but only within a hypothesis-testing framework that is carefully designed to avoid confirmation bias (Pfister & Kirchner 2017). Maximizing the chances for future instructive surprises will require the thoughtful application of models but will also require adequate support for field measurements and experiments, and for data-driven analysis of the resulting observations.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

P.B. acknowledges financial support from the School of Architecture, Civil and Environmental Engineering at École Polytechnique Fédérale de Lausanne (EPFL). The authors thank Matthias Sprenger for help with **Figure 4**.

LITERATURE CITED

Allen ST, Kirchner JW. 2022. Potential effects of cryogenic extraction biases on plant water source partitioning inferred from xylem-water isotope ratios. *Hydrol. Process.* 36(2):e14483

Allen ST, Kirchner JW, Braun S, Siegwolf RTW, Goldsmith GR. 2019. Seasonal origins of soil water used by trees. *Hydrol. Earth Syst. Sci.* 23:1199–210

Anderson AE, Weiler M, Alila Y, Hudson RO. 2009. Dye staining and excavation of a lateral preferential flow network. *Hydrol. Earth Syst. Sci.* 13:935–44

Anderson MG, Burt TP. 1978. The role of topography in controlling throughflow generation. *Earth Surface Process.* 3:331–44

Assendelft RS, van Meerveld HJI. 2019. A low-cost, multi-sensor system to monitor temporary stream dynamics in mountainous headwater catchments. *Sensors* 19:4645

Aubert AH, Kirchner JW, Gascuel-Odoux C, Facheux M, Gruau G, Merot P. 2014. Fractal water quality fluctuations spanning the periodic table in an intensively farmed watershed. *Environ. Sci. Technol.* 48:930–37

Benettin P, Nehemy MF, Asadollahi M, Pratt D, Bensimon M, et al. 2021. Tracing and closing the water balance in a vegetated lysimeter. *Water Resour. Res.* 57:e2020WR029049

Benettin P, Rinaldo A, Botter G. 2015. Tracking residence times in hydrological systems: forward and backward formulations. *Hydrol. Process.* 29:5203–13

Berghuijs WR, Kirchner JW. 2017. The relationship between contrasting ages of groundwater and streamflow. *Geophys. Res. Lett.* 44:8925–35

Berry ZC, Evaristo J, Moore G, Poca M, Steppe K, et al. 2018. The two water worlds hypothesis: addressing multiple working hypotheses and proposing a way forward. *Ecohydrology* 11:e1843

Beven K. 1989. Interflow. In *Unsaturated Flow in Hydrologic Modeling*, ed. HJ Morel-Seytoux, pp. 191–219. Amsterdam: Kluwer

Beven K. 2004. Robert E. Horton and abrupt rises of ground water. *Hydrol. Process.* 18:3687–96

Beven KJ. 2012. *Rainfall-Runoff Modelling: The Primer*. Chichester, UK: Wiley-Blackwell

Beyer M, Kühnhammer K, Dubbert M. 2020. In situ measurements of soil and plant water isotopes: a review of approaches, practical considerations and a vision for the future. *Hydrol. Earth Syst. Sci.* 24:4413–40

Bhamjee R, Lindsay JB. 2011. Ephemeral stream sensor design using state loggers. *Hydrol. Earth Syst. Sci.* 15:1009–21

Bishop K, Seibert J, Nyberg L, Rodhe A. 2011. Water storage in a till catchment II: implications of transmissivity feedback for flow paths and turnover times. *Hydrol. Process.* 25:3950–59

Blasch KW, Ferre TPA, Christensen AH, Hoffmann JP. 2002. New field method to determine streamflow using electrical resistance sensors. *Vadose Zone J.* 1:289–99

Blyth K, Rodda JC. 1973. A stream length study. *Water Resour. Res.* 9:1454–61

Bogaard TA, Greco R. 2016. Landslide hydrology: from hydrology to pore pressure. *Wiley Interdiscip. Rev. Water* 3:439–59

Botter G, Bertuzzo E, Rinaldo A. 2010. Transport in the hydrological response: travel time distributions, soil moisture dynamics, and the old water paradox. *Water Resour. Res.* 46:W03514

Botter G, Vingiani F, Senatore A, Jensen C, Weiler M, et al. 2021. Hierarchical climate-driven dynamics of the active channel length in temporary streams. *Sci. Rep.* 11:21503

Brauer CC, Teuling AJ, Torfs P, Uijlenhoet R. 2014. The Wageningen Lowland Runoff Simulator (WALRUS): a lumped rainfall-runoff model for catchments with shallow groundwater. *Geosci. Model Dev.* 7:2313–32

Brooks JR, Barnard HR, Coulombe R, McDonnell JJ. 2010. Ecohydrologic separation of water between trees and streams in a Mediterranean climate. *Nat. Geosci.* 3:100–4

Brown RM. 1961. Hydrology of tritium in the Ottawa Valley. *Geochim. Cosmochim. Acta* 21:199–216

Burns DA, Hooper RP, McDonnell JJ, Freer JE, Kendall C, Beven K. 1998. Base cation concentrations in subsurface flow from a forested hillslope: the role of flushing frequency. *Water Resour. Res.* 34:3535–44

Burt TP, McDonnell JJ. 2015. Whither field hydrology? The need for discovery science and outrageous hydrological hypotheses. *Water Resour. Res.* 51:5919–28

Buttle JM. 1994. Isotope hydrograph separations and rapid delivery of pre-event water from drainage basins. *Prog. Phys. Geog.* 18:16–41

Cartwright I, Morgenstern U. 2018. Using tritium and other geochemical tracers to address the "old water paradox" in headwater catchments. *J. Hydrol.* 563:13–21

Chen Y, Helliker BR, Tang X, Li F, Zhou Y, Song X. 2020. Stem water cryogenic extraction biases estimation in deuterium isotope composition of plant source water. *PNAS* 117:33345–50

Covino TP, McGlynn BL. 2007. Stream gains and losses across a mountain-to-valley transition: impacts on watershed hydrology and stream water chemistry. *Water Resour. Res.* 43:W10431

Dawson TE, Ehleringer JR. 1991. Streamside trees that do not use stream water. *Nature* 350:335–37

Day DG. 1978. Drainage density changes during rainfall. *Earth Surf. Process. Landf.* 3:319–26

Doering M, Uehlinger U, Rotach A, Schlaepfer DR, Tockner K. 2007. Ecosystem expansion and contraction dynamics along a large Alpine alluvial corridor (Tagliamento River, Northeast Italy). *Earth Surf. Process. Landf.* 32:1693–704

Dohman JM, Godsey SE, Hale RL. 2021. Three-dimensional subsurface flow path controls on flow permanence. *Water Resour. Res.* 57:e2020WR028270

Dooge JCI, O'Kane JP. 2003. *Deterministic Methods in Systems Hydrology*. Lisse, Netherlands: A.A. Balkema

Dubbert M, Caldeira MC, Dubbert D, Werner C. 2019. A pool-weighted perspective on the two-water-worlds hypothesis. *New Phytol.* 222:1271–83

Duvert C, Butman DE, Marx A, Ribolzi O, Hutley LB. 2018. CO_2 evasion along streams driven by groundwater inputs and geomorphic controls. *Nat. Geosci.* 11:813–18

Evaristo J, Jasechko S, McDonnell JJ. 2015. Global separation of plant transpiration from groundwater and streamflow. *Nature* 525:91–94

Fan Y. 2019. Are catchments leaky? *Wiley Interdiscip. Rev. Water* 6:e1386

Fan Y, Miguez-Macho G, Jobbágy EG, Jackson RB, Otero-Casal C. 2017. Hydrologic regulation of plant rooting depth. *PNAS* 114:10572–77

Fortesa J, Ricci GF, Garcia-Comendador J, Gentile F, Estrany J, et al. 2021. Analysing hydrological and sediment transport regime in two Mediterranean intermittent rivers. *Catena* 196:105050

Freer J, McDonnell J, Beven KJ, Brammer D, Burns D, et al. 1997. Topographic controls on subsurface storm flow at the hillslope scale for two hydrologically distinct small catchments. *Hydrol. Process.* 11:1347–52

Frisbee MD, Wilson JL, Gomez-Velez JD, Phillips FM, Campbell AR. 2013. Are we missing the tail (and the tale) of residence time distributions in watersheds? *Geophys. Res. Lett.* 40:4633–37

Geris J, Tetzlaff D, McDonnell J, Anderson J, Paton G, Soulsby C. 2015. Ecohydrological separation in wet, low energy northern environments? A preliminary assessment using different soil water extraction techniques. *Hydrol. Process.* 29:5139–52

Godsey SE, Aas W, Clair TA, de Wit HA, Fernandez IJ, et al. 2010. Generality of fractal 1/f scaling in catchment tracer time series, and its implications for catchment travel time distributions. *Hydrol. Process.* 24:1660–71

Godsey SE, Kirchner JW. 2014. Dynamic, discontinuous stream networks: hydrologically driven variations in active drainage density, flowing channels, and stream order. *Hydrol. Process.* 28:5791–803

Goldsmith GR, Allen ST, Braun S, Siegwolf RTW, Kirchner JW. 2022. Climatic influences on summer use of winter precipitation by trees. *Geophys. Res. Lett.* 49:e2022GL098323

Goldsmith GR, Muñoz-Villers LE, Holwerda F, McDonnell JJ, Asbjornsen H, Dawson TE. 2012. Stable isotopes reveal linkages among ecohydrological processes in a seasonally dry tropical montane cloud forest. *Ecohydrology* 5:779–90

Gomez-Gener L, Siebers AR, Arce MI, Arnon S, Bernal S, et al. 2021. Towards an improved understanding of biogeochemical processes across surface-groundwater interactions in intermittent rivers and ephemeral streams. *Earth-Sci. Rev.* 220:103724

Graham CB, Woods RA, McDonnell JJ. 2010. Hillslope threshold response to rainfall: (1) A field based forensic approach. *J. Hydrol.* 393:65–76

Grant GE, Dietrich WE. 2017. The frontier beneath our feet. *Water Resour. Res.* 53:2605–9

Gregory KJ, Walling DE. 1968. The variation in drainage density within a catchment. *Int. Assoc. Sci. Hydrol. Bull.* 13:61–68

Gutierrez-Jurado KY, Partington D, Shanafield M. 2021. Taking theory to the field: streamflow generation mechanisms in an intermittent Mediterranean catchment. *Hydrol. Earth Syst. Sci.* 25:4299–317

Hahm WJ, Rempe DM, Dralle DN, Dawson TE, Dietrich WE. 2020. Oak transpiration drawn from the weathered bedrock vadose zone in the summer dry season. *Water Resour. Res.* 56:e2020WR027419

Hale RL, Godsey SE. 2019. Dynamic stream network intermittence explains emergent dissolved organic carbon chemostasis in headwaters. *Hydrol. Process.* 33:1926–36

Hammond JC, Zimmer M, Shanafield M, Kaiser K, Godsey SE, et al. 2021. Spatial patterns and drivers of nonperennial flow regimes in the continental United States. *Geophys. Res. Lett.* 48:e2020GL090794

Harman CJ. 2015. Time-variable transit time distributions and transport: theory and application to storage-dependent transport of chloride in a watershed. *Water Resour. Res.* 51:1–30

Hensley RT, Cohen MJ, Jawitz JW. 2018. Channel filtering generates multifractal solute signals. *Geophys. Res. Lett.* 45:722–31

Hewlett JD, Hibbert AR. 1967. Factors affecting the response of small watersheds to precipitation in humid regions. In *Forest Hydrology*, ed. WE Sopper, HW Lull, pp. 275–90. Oxford, UK: Pergamon

Hladyz S, Watkins SC, Whitworth KL, Baldwin DS. 2011. Flows and hypoxic blackwater events in managed ephemeral river channels. *J. Hydrol.* 401:117–25

Hrachowitz M, Benettin P, van Breukelen BM, Fovet O, Howden NJK, et al. 2016. Transit times—the link between hydrology and water quality at the catchment scale. *Wiley Interdiscip. Rev. Water* 3:629–57

Hubert P, Marin E, Meybeck M, Olive P, Siwertz E. 1969. Aspects hydrologique, gèochimique et sèdimentologique de la crue exceptionnelle de la Dranse du Chablais du 22 septembre 1968. *Arch. Sci.* 22:581–604

Jaeger KL, Olden JD. 2012. Electrical resistance sensor arrays as a means to quantify longitudinal connectivity of rivers. *River Res. Appl.* 28:1843–52

Jakeman AJ, Littlewood IG, Whitehead PG. 1990. Computation of the instantaneous unit hydrograph and identifiable component flows with application to two small upland catchments. *J. Hydrol.* 117:275–300

Jasechko S. 2019. Global isotope hydrogeology—review. *Rev. Geophys.* 57:835–965

Jasechko S, Birks SJ, Gleeson T, Wada Y, Fawcett PJ, et al. 2014. The pronounced seasonality of global groundwater recharge. *Water Resour. Res.* 50:8845–67

Jasechko S, Kirchner JW, Welker JM, McDonnell JJ. 2016. Substantial proportion of global streamflow less than three months old. *Nat. Geosci.* 9:126–31

Jasechko S, Perrone D, Befus KM, Cardenas MB, Ferguson G, et al. 2017. Global aquifers dominated by fossil groundwaters but wells vulnerable to modern contamination. *Nat. Geosci.* 10:425–29

Jasechko S, Seybold H, Perrone D, Fan Y, Kirchner JW. 2021. Widespread potential loss of streamflow into underlying aquifers across the USA. *Nature* 591:391–95

Jencso KG, McGlynn BL, Gooseff MN, Wondzell SM, Bencala KE, Marshall LA. 2009. Hydrologic connectivity between landscapes and streams: transferring reach- and plot-scale understanding to the catchment scale. *Water Resour. Res.* 45:W04428

Jensen CK, McGuire KJ, Prince PS. 2017. Headwater stream length dynamics across four physiographic provinces of the Appalachian Highlands. *Hydrol. Process.* 31:3350–63

Jobbágy EG, Nosetto MD, Villagra PE, Jackson RB. 2011. Water subsidies from mountains to deserts: their role in sustaining groundwater-fed oases in a sandy landscape. *Ecol. Appl.* 21:678–94

Kirchner JW. 2003. A double paradox in catchment hydrology and geochemistry. *Hydrol. Process.* 17:871–74

Kirchner JW. 2006. Getting the right answers for the right reasons: linking measurements, analyses, and models to advance the science of hydrology. *Water Resour. Res.* 42:W03S4

Kirchner JW. 2009. Catchments as simple dynamical systems: catchment characterization, rainfall-runoff modeling, and doing hydrology backward. *Water Resour. Res.* 45:W02429

Kirchner JW. 2019. Quantifying new water fractions and transit time distributions using ensemble hydrograph separation: theory and benchmark tests. *Hydrol. Earth Syst. Sci.* 23:303–49

Kirchner JW. 2022. Impulse response functions for nonlinear, nonstationary, and heterogeneous systems, estimated by deconvolution and demixing of noisy time series. *Sensors* 22:3291

Kirchner JW, Allen ST. 2020. Seasonal partitioning of precipitation between streamflow and evapotranspiration, inferred from end-member splitting analysis. *Hydrol. Earth Syst. Sci.* 24:17–34

Kirchner JW, Feng X, Neal C. 2000. Fractal stream chemistry and its implications for contaminant transport in catchments. *Nature* 403:524–27

Kirchner JW, Neal C. 2013. Universal fractal scaling in stream chemistry and its implications for solute transport and water quality trend detection. *PNAS* 110:12213–18

Klaus J, McDonnell JJ. 2013. Hydrograph separation using stable isotopes: review and evaluation. *J. Hydrol.* 505:47–64

Knapp JLA, Neal C, Schlumpf A, Neal M, Kirchner JW. 2019. New water fractions and transit time distributions at Plynlimon, Wales, estimated from stable water isotopes in precipitation and streamflow. *Hydrol. Earth Syst. Sci.* 23:4367–88

Knighton J, Souter-Kline V, Volkmann T, Troch PA, Kim M, et al. 2019. Seasonal and topographic variations in ecohydrological separation within a small, temperate, snow-influenced catchment. *Water Resour. Res.* 55:6417–35

Kollet SJ, Maxwell RM. 2008. Demonstrating fractal scaling of baseflow residence time distributions using a fully-coupled groundwater and land surface model. *Geophys. Res. Lett.* 35:2008gl033215

Kuppel S, Fan Y, Jobbágy EG. 2017. Seasonal hydrologic buffer on continents: patterns, drivers and ecological benefits. *Adv. Water Res.* 102:178–87

Lapides DA, Hahm WJ, Rempe DM, Dietrich WE, Dralle DN. 2022. Controls on stream water age in a saturation overland flow-dominated catchment. *Water Resour. Res.* 58:e2021WR031665

Lapides DA, Leclerc CD, Moidu H, Dralle DN, Hahm WJ. 2021. Variability of stream extents controlled by flow regime and network hydraulic scaling. *Hydrol. Process.* 35:e14079

Le Moine N, Andreassian V, Perrin C, Michel C. 2007. How can rainfall-runoff models handle intercatchment groundwater flows? Theoretical study based on 1040 French catchments. *Water Resour. Res.* 43:W06428

Maher K. 2010. The dependence of chemical weathering rates on fluid residence time. *Earth Planet. Sci. Lett.* 294:101–10

Maher K, Chamberlain CP. 2014. Hydrologic regulation of chemical weathering and the geologic carbon cycle. *Science* 343:1502–4

Marc V, Robinson M. 2007. The long-term water balance (1972–2004) of upland forestry and grassland at Plynlimon, mid-Wales. *Hydrol. Earth Syst. Sci.* 11:44–60

Martinec J. 1975. Subsurface flow from snowmelt traced by tritium. *Water Resour. Res.* 11:496–98

Marx A, Dusek J, Jankovec J, Sanda M, Vogel T, et al. 2017. A review of CO_2 and associated carbon dynamics in headwater streams: a global perspective. *Rev. Geophys.* 55:560–85

McCormick EL, Dralle DN, Hahm WJ, Tune AK, Schmidt LM, et al. 2021. Widespread woody plant use of water stored in bedrock. *Nature* 597:225–29

McDonnell JJ. 2014. The two water worlds hypothesis: ecohydrological separation of water between streams and trees? *Wiley Interdiscip. Rev. Water* 1:323–29

McDonnell JJ, Beven K. 2014. Debates—the future of hydrological sciences: a (common) path forward? A call to action aimed at understanding velocities, celerities and residence time distributions of the headwater hydrograph. *Water Resour. Res.* 50:5342–50

McDowell NG, Grossiord C, Adams HD, Pinzon-Navarro S, Mackay DS, et al. 2019. Mechanisms of a coniferous woodland persistence under drought and heat. *Environ. Res. Lett.* 14:045014

McGuire KJ, McDonnell JJ. 2006. A review and evaluation of catchment transit time modeling. *J. Hydrol.* 330:543–63

McGuire KJ, Torgersen CE, Likens GE, Buso DC, Lowe WH, Bailey SW. 2014. Network analysis reveals multiscale controls on streamwater chemistry. *PNAS* 111:7030–35

Messager ML, Lehner B, Cockburn C, Lamouroux N, Pella H, et al. 2021. Global prevalence of non-perennial rivers and streams. *Nature* 594:391–97

Miralles DG, Teuling AJ, van Heerwaarden CC, de Arellano JVG. 2014. Mega-heatwave temperatures due to combined soil dessication and atmospheric heat accumulation. *Nat. Geosci.* 7:345–49

Mueller B, Seneviratne SI. 2012. Hot days induced by precipitation deficits at the global scale. *PNAS* 109:12398–403

Mutzner R, Tarolli P, Sofia G, Parlange MB, Rinaldo A. 2016. Field study on drainage densities and rescaled width functions in a high-altitude alpine catchment. *Hydrol. Process.* 30:2138–52

Neal C, Rosier PTW. 1990. Chemical studies of chloride and stable oxygen isotopes in 2 conifer afforested and moorland sites in the British uplands. *J. Hydrol.* 115:269–83

Nieber JL, Sidle RC. 2010. How do disconnected macropores in sloping soils facilitate preferential flow? *Hydrol. Process.* 24:1582–94

Orlowski N, Pratt DL, McDonnell JJ. 2016. Intercomparison of soil pore water extraction methods for stable isotope analysis. *Hydrol. Process.* 30:3434–49

Pate AA, Segura C, Bladon KD. 2020. Streamflow permanence in headwater streams across four geomorphic provinces in Northern California. *Hydrol. Process.* 34:4487–504

Payn RA, Gooseff MN, McGlynn BL, Bencala KE, Wondzell SM. 2009. Channel water balance and exchange with subsurface flow along a mountain headwater stream in Montana, United States. *Water Resour. Res.* 45:W11427

Pfister L, Kirchner JW. 2017. Hypothesis testing in hydrology: theory and practice. *Water Resour. Res.* 53:1792–98

Pinder GF, Jones JF. 1969. Determination of the groundwater component of peak discharge from the chemistry of total runoff. *Water Resour. Res.* 5:438–45

Ploum SW, Laudon H, Tapia AP, Kuglerov L. 2020. Are dissolved organic carbon concentrations in riparian groundwater linked to hydrological pathways in the boreal forest? *Hydrol. Earth Syst. Sci.* 24:1709–20

Prancevic JP, Kirchner JW. 2019. Topographic controls on the extension and retraction of flowing streams. *Geophys. Res. Lett.* 46:2018GL081799

Querner EP, Froebrich J, Gallart F, Cazemier MM, Tzoraki O. 2016. Simulating streamflow variability and aquatic states in temporary streams using a coupled groundwater-surface water model. *Hydrol. Sci. J.* 61:146–61

Rajaram H. 2021. Matrix diffusion as a mechanism contributing to fractal stream chemistry and long-tailed transit time distributions. *Geophys. Res. Lett.* 48:e2021GL094292

Rempe DM, Dietrich WE. 2018. Direct observations of rock moisture, a hidden component of the hydrologic cycle. *PNAS* 115:2664–69

Rode M, Wade AJ, Cohen MJ, Hensley RT, Bowes MJ, et al. 2016. Sensors in the stream: the high-frequency wave of the present. *Environ. Sci. Technol.* 50:10297–307

Rodhe A. 1981. Spring flood—meltwater or groundwater? *Hydrol. Res.* 12:21–30

Scher H, Margolin G, Metzler R, Klafter J, Berkowitz B. 2002. The dynamical foundation of fractal stream chemistry: the origin of extremely long retention times. *Geophys. Res. Lett.* 29:5-1–5-4

Schwamback D, Gesualdo GC, Sone JS, Kobayashi ANA, Bertotto LE, et al. 2022. Are Brazilian catchments gaining or losing water? The effective area of tropical catchments. *Hydrol. Process.* 36:14535

Senatore A, Micieli M, Liotti A, Durighetto N, Mendicino G, Botter G. 2021. Monitoring and modeling drainage network contraction and dry down in Mediterranean headwater catchments. *Water Resour. Res.* 57:e2020WR028741

Shaw EM, Beven KJ, Chappell NA, Lamb R. 2011. *Hydrology in Practice*. New York: Spon

Sherman LK. 1932. Streamflow from rainfall by the unit-graph method. *Eng. News Record* 108:501–5

Sidle RC, Noguchi S, Tsuboyama Y, Laursen K. 2001. A conceptual model of preferential flow systems in forested hillslopes: evidence of self-organization. *Hydrol. Process.* 15:1675–92

Sidle RC, Tsuboyama Y, Noguchi S, Hosoda I, Fujieda M, Shimizu T. 2000. Stormflow generation in steep forested headwaters: a linked hydrogeomorphic paradigm. *Hydrol. Process.* 14:369–85

Šimůnek J, Jarvis NJ, van Genuchten MT, Gärdenäs A. 2003. Review and comparison of models for describing non-equilibrium and preferential flow and transport in the vadose zone. *J. Hydrol.* 272:14–35

Sklash MG. 1990. Environmental isotope studies of storm and snowmelt runoff generation. In *Process Studies in Hillslope Hydrology*, ed. MG Anderson, TP Burt, pp. 401–35. Chichester, UK: Wiley

Sklash MG, Farvolden RN. 1979. The role of groundwater in storm runoff. *J. Hydrol.* 43:45–65

Smith A, Tetzlaff D, Landgraf J, Dubbert M, Soulsby C. 2022. Modelling temporal variability of in situ soil water and vegetation isotopes reveals ecohydrological couplings in a riparian willow plot. *Biogeosciences* 19:2465–85

Sprenger M, Leistert H, Gimbel K, Weiler M. 2016. Illuminating hydrological processes at the soil-vegetation-atmosphere interface with water stable isotopes. *Rev. Geophys.* 54:674–704

Sprenger M, Stumpp C, Allen ST, Benettin P, Dubbert M, et al. 2019. The demographics of water: a review of water ages in the critical zone. *Rev. Geophys.* 57:800–34

Sprenger M, Tetzlaff D, Buttle JM, Laudon H, Leistert H, et al. 2018. Measuring and modeling stable isotopes of mobile and bulk soil water. *Vadose Zone J.* 17:1–18

Staudinger M, Seibert J, van Meerveld HJ. 2021. Representation of bi-directional fluxes between groundwater and surface water in a bucket-type hydrological model. *Water Resour. Res.* 57:e2020WR028835

Stewart MK, Morgenstern U, McDonnell JJ. 2010. Truncation of stream residence time: how the use of stable isotopes has skewed our concept of streamwater age and origin. *Hydrol. Process.* 24:1646–59

Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* 6:e5096

Stoll S, Weiler M. 2010. Explicit simulations of stream networks to guide hydrological modelling in ungauged basins. *Hydrol. Earth Syst. Sci.* 14:1435–48

Tsuboyama Y, Sidle RC, Noguchi S, Hosoda I. 1994. Flow and solute transport through the soil matrix and macropores of a hillslope segment. *Water Resour. Res.* 30:879–90

van der Velde Y, Heidbüchel I, Lyon SW, Nyberg L, Rodhe A, et al. 2015. Consequences of mixing assumptions for time-variable travel time distributions. *Hydrol. Process.* 29:3460–74

van der Velde Y, Torfs PJJF, van der Zee SEATM, Uijlenhoet R. 2012. Quantifying catchment-scale mixing and its effect on time-varying travel time distributions. *Water Resour. Res.* 48:W06536

van Meerveld HJI, Kirchner JW, Vis MJP, Assendelft RS, Seibert J. 2019. Expansion and contraction of the flowing stream network alter hillslope flowpath lengths and the shape of the travel time distribution. *Hydrol. Earth Syst. Sci.* 23:4825–34

Vidon P. 2012. Towards a better understanding of riparian zone water table response to precipitation: surface water infiltration, hillslope contribution or pressure wave processes? *Hydrol. Process.* 26:3207–15

Vidon PGF, Hill AR. 2004. Landscape controls on nitrate removal in stream riparian zones. *Water Resour. Res.* 40:W03201

von Freyberg J, Studer B, Rinderer M, Kirchner JW. 2018. Studying catchment storm response using event and pre-event water volumes as fractions of precipitation rather than discharge. *Hydrol. Earth Syst. Sci.* 22:5847–65

von Schiller D, Bernal S, Dahm CN, Marti E. 2017. Nutrient and organic matter dynamics in intermittent rivers and ephemeral streams. In *Intermittent Rivers and Ephemeral Streams*, ed. T Datry, N Bonada, A Boulton, pp. 135–60. London: Elsevier

Warix SR, Godsey SE, Lohse KA, Hale RL. 2021. Influence of groundwater and topography on stream drying in semi-arid headwater streams. *Hydrol. Process.* 35:e14185

Weiler M, McDonnell JJ. 2007. Conceptualizing lateral preferential flow and flow networks and simulating the effects on gauged and ungauged hillslopes. *Water Resour. Res.* 43:W03403

Weiler M, McGlynn BL, McGuire KJ, McDonnell JJ. 2003. How does rainfall become runoff? A combined tracer and runoff transfer function approach. *Water Resour. Res.* 39:1315

Welsch DL, Kroll CN, McDonnell JJ, Burns DA. 2001. Topographic controls on the chemistry of subsurface stormflow. *Hydrol. Process.* 15:1925–38

Werner C, Meredith LK, Ladd SN, Ingrisch J, Kübert A, et al. 2021. Ecosystem fluxes during drought and recovery in an experimental forest. *Science* 374:1514–18

Whiting JA, Godsey SE. 2016. Discontinuous headwater stream networks with stable flowheads, Salmon River basin, Idaho. *Hydrol. Process.* 30:2305–16

Wigington PJ, Moser TJ, Lindeman DR. 2005. Stream network expansion: a riparian water quality factor. *Hydrol. Process.* 19:1715–21

Winter TC, Harvey JW, Franke OL, Alley WM. 1998. *Ground Water and Surface Water: A Single Resource*. Denver, CO: USGS

Worthington SRH. 2018. How preferential flow delivers pre-event groundwater rapidly to streams. *Hydrol. Process.* 33:2373–80

Zimmer MA, Bailey SW, McGuire KJ, Bullen TD. 2013. Fine scale variations of surface water chemistry in an ephemeral to perennial drainage network. *Hydrol. Process.* 27:3438–51

Zimmer MA, McGlynn BL. 2018. Lateral, vertical, and longitudinal source area connectivity drive runoff and carbon export across watershed scales. *Water Resour. Res.* 54:1576–98