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Advancing Ecohydrology in the Changing Tropics: Perspectives from Early Career Scientists

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Running Header: EARLY CAREER PERSPECTIVES ON TROPICAL ECOHYDROLOGY

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Abstract

Tropical ecosystems offer a unique set of natural laboratories for investigating ecohydrological processes, but to date such investigations have been limited. The purpose of this paper is to highlight the importance of studying these processes—specifically, how they are being affected by the transformative changes taking place in the tropics—and to offer an agenda for carrying out such research to develop sound management strategies and policies. At present, changes in land use and land cover are major issues in tropical regions. The ongoing loss of native ecosystems is largely due to agricultural expansion, but parallel processes of afforestation are also taking place, leading to shifts in ecohydrological fluxes. Similarly, shifts in water availability due to climate change will affect both water and carbon fluxes in tropical ecosystems. A number of methods exist that can help us better understand how changes in land use and climate affect ecohydrological processes; these include stable isotopes, remote sensing, and process-based models. Still, our knowledge of the underlying physical mechanisms, especially those that determine the effects of scale on ecosystem processes, remains incomplete. We assert that development of a knowledge base concerning the effects of transformative change on ecological, hydrological, and biogeochemical processes at different spatio-temporal scales is an urgent need for tropical regions, and should serve as a compass for emerging ecohydrologists. To reach this goal, we advocate a research agenda that expands the number and diversity of ecosystems targeted for ecohydrological investigations and connects researchers across the tropics. We believe that the use of big data and open source software—already an important integrative tool/skill for the young ecohydrologist—will be key in expanding research capabilities.

1. Introduction

The tropics provide a unique, high-value natural context for ecohydrologic investigations (the study of how hydrological mechanisms drive—and are driven by—ecological patterns and processes) (Rodriguez-Iturbe, 2000). Located between approximately 23°28'N and 23°28'S, this region encompasses a remarkable diversity of terrestrial ecosystems, which are undergoing transformative changes that ultimately jeopardize the ecosystem services on which society depends. As young scientists working in the tropics, we recognize the importance of not only gaining a better understanding of how these transformative changes affect ecohydrological processes, but also determining how we can predict and mitigate those effects.

Despite the wealth of opportunities offered by tropical ecosystems, ecohydrological research has been limited. A literature search of published ecohydrological studies (Web of Science, since 1945) done in dry, northern, temperate, and tropical environments shows that less than 10% of the total number (404) report on work conducted in tropical regions (Figure 1). Using the keywords “ecohydrology,” “water isotopes” (selected as representative of relatively new methodologies) + “ecology,” and “water isotopes” + “hydrology” for each of the four environmental categories, we found that the majority of ecohydrologic studies have focused on dry environments (>50%), and twice as many (>20%) have been done in temperate and northern ecosystems as in the tropics. Only 21% of the total ecology publications and 17% of the total hydrology publications deal with research in tropical environments.

In addition, literature searches on ecohydrology-related keywords reveal very few publications conducted by researchers from tropical countries (Figure 2). Of the 37,293 articles containing the keywords “plant,” “soil,” and/or “water” (Web of Science, since 1997), only 14% were authored by researchers affiliated with organizations based in tropical countries. Of tropical affiliates, 57% are from the Americas, 23% from Asia, 18% from Africa, and about 2% from other regions. This information evidences the disproportionately small amount of research dedicated to the tropics—an alarming reality given that some 40% of the world’s population presently inhabit tropical areas, and that the population is projected to increase by as much as 50% by 2050. The highest population growth rate is projected for Africa, which is also the region least represented in terms of research organization affiliations (United Nations, 2016; <https://esa.un.org/unpd/wup/Maps/citygrowth/citygrowth.aspx>). Moreover, the literature search shows that only a small number of researchers based in tropical countries are actively

participating in ecohydrology research. As early-career scientists, we emphasize the urgent need for current and upcoming generations of tropical researchers in ecohydrology to work to close this critical knowledge gap. This gap is costing us a deeper understanding of ecohydrological processes in a diversity of tropical biomes, and thus is limiting our ability to sustainably manage natural resources such as water, soil, and vegetation, and the ecosystem services they provide including provisioning of clean water, food, and fuel; erosion control; carbon sequestration; and nutrient cycling.

In this paper, we focus on ecohydrological processes as a function of the transformative changes occurring in the tropics. Specifically, we propose to improve our understanding of ecohydrological processes—as a means of predicting and managing *ecohydrologic* change—by extending our monitoring and data analysis capabilities to a diverse set of ecosystems (Montanari *et al.*, 2013). The ultimate goal is effective management, conservation, and sustainability of ecosystems (Montanari *et al.*, 2013; Thompson *et al.*, 2013), which will lead to an improved quality of life for the people inhabiting the region.

Against this backdrop—the importance of stepping up ecohydrological research in the tropics—the objective of our paper is to highlight how transformative change in the tropics is driving ecohydrological change and how we might best understand and confront these changes in the coming decade. In section 2 we summarize the unifying and differentiating features that characterize tropical ecosystems, creating a complex of settings and conditions that are interesting, important, and challenging for ecohydrological research. In section 3, we discuss the main drivers of transformative change in the tropics: changes in land use and climate, both of which have anthropogenic origins and which often initiate ecological, hydrologic, and biogeochemical responses. In section 4 we highlight recently developed field-based and modeling approaches that can help us understand these changes, and we point out some of the remaining gaps in our knowledge. Finally, in section 5 we summarize the current state of ecohydrological research in the tropics, and we offer a direction for advancement to which we, as early-career ecohydrologists, feel we can most effectively contribute.

2. Biomes of the Tropics

Tropical ecosystems possess both unifying and differentiating features, thereby providing a unique set of natural laboratories for investigating ecohydrological processes. Unifying features

across tropical latitudes include relatively high insolation and temperatures, which mean that precipitation rather than energy often shapes ecosystem and hydrological seasonality. Hence, the role of hydrology in the tropics is potentially magnified. Tropical terrestrial ecosystems are also known for their complex vegetation configurations, rapid nutrient cycling, high productivity, and exceptional biodiversity—characteristics due in part to their long evolutionary history as well as the more recent development of drier tropical ecosystems (Kellman and Tackaberry, 1997). Finally, and critically, the tropics are perhaps the most rapidly changing terrestrial ecosystems of the Anthropocene (Hansen *et al.*, 2013), allowing for opportunities to investigate ecohydrological responses to land use and climate change (further discussed in section 3).

By differentiating features, we mean that the tropics encompass a variety of terrestrial biomes: deserts and xeric shrublands; lowland savannas and shrublands; dry/coniferous/Mediterranean forests; montane grasslands and shrublands; and humid forests, including tropical montane cloud forests (Figure 3; TNC, 2009). Their distribution is influenced by climate, elevation (ranging from 0 to ca. 6,000 m.a.s.l and atmospheric circulation patterns, including the Intertropical Convergence Zone (ITCZ), the El Niño Southern Oscillation (ENSO), monsoonal circulation, and frontal systems (Kellman and Tackaberry, 1997).

Deserts and xeric shrublands, typically classified as arid and semiarid ecosystems, are defined by low precipitation. These biomes typically occur at low elevations near subtropical high-pressure zones. They include the Caatinga in northeast Brazil, where annual precipitation ranges from 300 to 1000 mm (Sampaio, 1995), and the hyper-arid Atacama Desert in Chile, where precipitation reaches a maximum of 300 mm and some areas receive less than 1 mm (Houston, 2006). This biome type also includes the Sahara Desert and the Kalahari Savanna in Africa, much of the Middle East and Australia, and the Sonoran and Chihuahuan deserts of Mexico. The vegetation is generally resistant to drought conditions, exhibiting characteristics such as waxy cuticles to reduce evapotranspiration, phenology driven by rainfall, and ability to extract water at high matric potentials or taproots capable of reaching deeper water reserves.

Tropical lowland savannas and shrublands are generally categorized as semiarid to subhumid. This biome receives more rain, has a pronounced dry season, and is characterized by herbaceous vegetation. Examples include the Cerrado and Chaco savannas of South America and much of Africa. In the Chaco, precipitation ranges from 450 mm to 1200 mm (Fehlenberg, *et al.*, 2017). Often associated with lowland savannas and shrublands are dry forests. These biomes are

defined by their floristic composition as well as their distinct and often prolonged dry season. Annual rainfall can be up to 2,000 mm, including a 4- to 6-month period with less than 100 mm (Dirzo *et al.*, 2011), although this definition varies (see Bullock *et al.*, 1995). Depending on specific classifications, the Caatinga and parts of the Chaco and Cerrado are considered dry forests (Fehlenberg *et al.*, 2017). Other dry forests are found throughout Mexico, the Hawaiian Islands (not shown in Fig. 3), and much of India. Coniferous and Mediterranean forests, although areas of high endemism also found in the tropics, are relatively limited in extent (WWF 2017; <https://www.worldwildlife.org/biomes>); these forests are not discussed in detail in this paper.

The most celebrated biome of the tropics is the humid forests, which are distributed along the equator and are characterized by high rainfall and complex floristic composition and structure. Nutrient cycling in these systems is rapid, given the immensity of the biomass and the constant high temperatures and humidity. Notable tropical humid forests include the Amazon Rainforest in South America, the Congo Rainforest in Africa, and much of Oceania. Annual rainfall in the Amazon can be as high as 4000 mm (Sombroek, 2001). Often found associated with both humid rainforest and montane biomes are tropical montane cloud forests. In this ecosystem, fog is captured by vegetation through cloud water interception and can be an important water input (Marzol-Jaén, 2010; Hutley *et al.*, 1997)—as much 40% of total precipitation (rainfall + fog), as in the case of the Kilauea Volcano in Hawaii (DeLay and Giambelluca, 2010). Total annual precipitation ranges from 2,000 to 8,000 mm (Teodoro *et al.*, in review).

At higher elevations, at or above the tree line, are the montane grasslands and shrublands, whose defining characteristics include colder temperatures and high radiation. This biome includes the Andean Páramos, the headwaters of rivers feeding Pacific coastal regions and the Amazon Basin, and high-elevation savannas in Ethiopia, Angola, and the Tibetan plateau. Annual precipitation can range from lows of 100–500 mm in the Tibetan plateau (Xu *et al.*, 2008) to higher constant inputs of 700 to 3,000 mm in the Páramos (Luteyn, 1992).

3. Transformative Change in the Tropics

Transformative change refers to the “profound or radical changes to the earth’s surface that fundamentally alter ecosystem processes” (Wilcox, 2010). In this section we highlight the main ecohydrological processes affected by transformative changes occurring in the tropics—and

which are, respectively, direct and indirect results of human activity: (1) changes in land use and land cover, and (2) climate change.

3.1 Changes in Land Use/Land Cover

Land use drives global land cover change, and rapidly developing tropical regions present some of the most dynamic examples of this (Lambin *et al.*, 2003). The high rates of change in tropical landscapes are shaped by global markets and state/local policies that in turn shape rural population growth, migration, resource availability, and economics (Bonell and Bruijnzeel, 2005; Lambin *et al.*, 2003). Changes in land use are important because they ultimately change the structure and composition of vegetation cover, leading to different ecological, hydrological, and biogeochemical dynamics than those of the tropical ecosystems they replace (Jones *et al.*, 2017; Bruijnzeel, 2004). In many cases these new dynamics have detrimental consequences for ecosystem services—for example, lower water quality and reduced water supply for municipal and agricultural use.

3.1.1 Conversion of native ecosystems

Recent global analyses show that net deforestation continues across the tropics (Hansen *et al.*, 2013). Closer examination reveals that clearing of primary forest results in net losses, even as local forest cover may increase where there is afforestation and secondary growth (Hansen *et al.*, 2013; Keenan *et al.*, 2015). Hence, deforestation and degradation of native ecosystems remains the biggest threat to the ecohydrological integrity of tropical landscapes.

The dramatic conversion of humid forests to agricultural lands—as seen in Southeast Asia, Latin America, and Central Africa in the 1990s (Drigo, 2005; Bonell and Bruijnzeel, 2005)—is a process that continues even today. Between 2007 and 2012, Southeast Asia experienced the greatest proportional (38%) loss of intact primary forest: 4.9 Mha/yr (Tyukavina *et al.*, 2016). Even so, this region continues to be logged or converted to cash-crop plantations and oil palm estates (Stibig *et al.*, 2014; Margono *et al.*, 2014). During the same period, Latin America saw the greatest absolute loss of primary forest area (9.3 Mha/yr), with most of the land converted to livestock-based agriculture; and in Africa the expansion of smallholder croplands contributed most to deforestation, which amounted to 8.2 Mha/yr of primary forest (Tyukavina *et al.*, 2016).

Although generally overlooked, an accelerated rate of deforestation has also been spurred by agricultural activities in other biome types. Such is the case for tropical dry forests (Miles *et al.*, 2006; Baldi and Jobbágy, 2012; Fehlenberg *et al.*, 2017); in Latin America, losses of land in this biome have been proportionally greater than those in humid forests (Salazar *et al.*, 2015). Agricultural expansion is affecting large areas of native savanna in the Andean Páramos (Buytaert *et al.*, 2006) and in the Brazilian Cerrado (Brannstrom *et al.*, 2008).

The removal of vegetation has several ecohydrological consequences. For one, deforestation can decrease infiltration and increase runoff, leading to higher rates of erosion and a rapid loss of nutrients into streams. This is seen in humid forests (Bonell and Bruijnzeel, 2005; Malmer *et al.*, 2005), Páramos (Buytaert *et al.*, 2006), and likely also dry forests (Farrick and Braunfireun, 2015). Burning and grazing diminish infiltration, not only by contributing to the formation of soil crusts (Poulenard *et al.*, 2001) but also by facilitating the development of soil hydrophobicity (Golchin *et al.*, 1997). When deforested lands are grazed, the animals' trampling of the soil destroys roots and causes loss of macroporosity, loss of topsoil organic matter and associated soil fauna, and exposure of the surface to erosive precipitation (Bonell, 2010; Ghimire *et al.*, 2014). These alterations of vegetation and soil properties lead to greater water losses, by reducing infiltration into the vadose zone and increasing runoff. In addition, such alterations can decrease the amount of water stored in the soil after the rainy season, which is particularly detrimental for tropical ecosystems dependent on dry-season flow or stored water (Bruijnzeel, 1989, 2004).

Deforestation can also alter evapotranspiration (ET) fluxes. When canopy cover is reduced through deforestation or fire, the greater exposure of the soil means higher evaporation of soil water; and although total ET losses are initially lower because of the decreased canopy interception and transpiration, this effect is transient and ET subsequently increases with vegetation regrowth (Bruijnzeel, 2004; Buytaert *et al.*, 2006). An important exception to this pattern may be found in ecosystems with persistent fog, such as tropical montane cloud forests. Reduction of vegetation cover and simplification of vegetation structure in these systems may reduce fog interception and decrease net precipitation (Gomez-Peralta *et al.*, 2008). In other words, the net effect of vegetation conversion on the water budget components of infiltration, ET, and soil water storage is context-dependent, and at the catchment scale is shaped by spatial heterogeneity and extent of disturbance.

At large enough scales, deforestation can alter fire regimes (Nepstad *et al.*, 2008, Alencar *et al.*, 2015). While natural and anthropogenic fire regimes have long been part of the ecological histories of tropical regions, wildfires are on the rise because of human ignition and fire-favoring climatic conditions such as drought (Morton *et al.*, 2013; Alencar *et al.*, 2015; Taufik *et al.*, 2017). This increase in fire frequency is most pronounced in disturbed forests of the Amazon, but affects even dense forests during drought years (Alencar *et al.*, 2015). Additionally, grassfires may facilitate subsequent invasion of burned areas by non-native C4 pasture grasses (D'Antonio and Vitousek, 1992; Silvério *et al.*, 2013).

In tropical regions, nutrient cycling and water fluxes are tightly coupled (Manzoni and Porporato, 2011). But given the scarcity of studies assessing the dynamics and feedbacks between these important processes, the effects of deforestation and degradation on biogeochemistry are not well understood. It is known that intact tropical humid forests tend to exhibit high decomposition rates, high root/shoot ratios, and efficient nutrient cycling, which effectively minimize the loss of nutrients via leaching (Vitousek and Sanford, 1986), and that deforestation disrupts this efficient nutrient cycling. Evidence from a paired catchment study in humid forests of Costa Rica indicates that conversion of forests to pastures increases wet season runoff, resulting in losses of nitrogen and phosphorus (Bringhurst and Jordan, 2015). For other tropical ecosystems, however (such as dry forests and high-elevation Páramos), we know little about how changes in plant functional composition and water budgets—brought about by changes in climate and land use—will affect sediment yield and nutrient fluxes. Given the rapidity with which tropical landscapes are experiencing changes in land cover, it is critical that we fill these knowledge gaps (Hamilton, 2010).

3.1.2 Afforestation: recovery of ecohydrological function?

While clearing of primary forest continues, forest cover is increasing in some areas through both natural and managed afforestation (Hansen *et al.*, 2013). Still, it is unclear how long it takes for a secondary forest to recover the function of a more mature forest (Chazdon, 2008) since the effects of deforestation and afforestation depend not only on the initial ecosystem state but also on how much time has elapsed since disturbance (Jones *et al.*, 2017).

In general, natural succession and some planting interventions can contribute to the recovery of ecohydrological function. In the lowland tropics of Latin America, for example,

natural succession now accounts for about 28% of forest and farmland cover (Chazdon *et al.*, 2016). With increases in vegetation and root biomass come other changes, such as reduced erosion, deeper root water uptake, and higher rates of ET. In the Rift Valley of Ethiopia, human-assisted interventions in the 1980s improved vegetation cover and helped reduce erosion (Asfaha *et al.*, 2014). Early research with paired catchments demonstrated that afforestation reduces water yields by increasing canopy interception and transpiration losses (Bosch and Hewlett, 1982). At the same time, afforestation can increase soil water storage and yields by improving infiltration capacity (Bruijnzeel, 1989; 2004; Giambelluca, 2002; Ilstedt *et al.*, 2007). However, degraded or plantation forests having ET levels comparable to those of natural primary forest may not recover their original infiltration capacity (Bonell, 2010). In these cases, lower field-saturated hydraulic conductivity can contribute to increased quickflow during storms and to decreased runoff in the dry season (Krishnaswamy *et al.*, 2013; Ghimire *et al.*, 2014). The net effects of both increased ET and increased infiltration with afforestation can depend on variables such as soil texture and geology, which have yet to be explored empirically across tropical landscapes (Malmer *et al.*, 2010).

Although secondary forest can resemble more mature forest, areas dominated by plantation trees or invasive species likely have different influences on ecohydrological processes. Among plantation species, *Eucalyptus sp.* and *Pinus sp.* may have significant hydrological impact because of their rapid growth and shorter cultivation rotations (van Dijk and Keenan, 2007). Invasions of non-native species, especially in insular ecosystems, can result in monotypic growth that changes vegetation structure and thereby affects ET, rainfall partitioning, and soil processes. Early successional invasive plants often have higher stomatal conductance than native plants of the same growth form (Cavaleri and Sack, 2010), which—if leaf area also increases—could scale up to ecosystem-level differences in ET especially if leaf area also increases (Huxman *et al.*, 2005; Asner *et al.*, 2008). In fog-affected forests of Hawaii, the invasive species *Psidium cattleianum* Sabine (Myrtaceae) develops a uniform canopy structure with a high density of small stems, smooth bark, and low epiphyte biomass; this trait contributes to lower cloud water interception and canopy storage (Takahashi *et al.*, 2011). At a drier site, the same species generates higher stemflow than other invasive tree species (Safeeq and Fares, 2014), which may accelerate nutrient leaching. Similarly, the invasive species *Miconia calvescens* DC (Melastomataceae) creates erosive conditions by suppressing understory vegetation and

facilitating the formation of large throughfall water drops with high kinetic energy (Nanko *et al.*, 2015). These observations highlight the need for ecohydrologists to better understand the function of lower-diversity degraded/invaded forests, which are an increasing proportion of tropical landscapes, and how the broad range of different forest covers affect ecosystem services.

3.2 Climate Change

At global scales, atmospheric warming due to anthropogenic climate changes increases atmospheric moisture levels to rise, causing intensification of the water cycle (Huntington, 2006). This intensification is expected to mean increased total rainfall (P) across the tropics (Chou *et al.*, 2009), but regional precipitation changes within the tropics are less predictable (Chadwick *et al.*, 2016). Recent evidence from ground-based stations confirms that rainfall patterns are already changing. For example, from 1930 to 1990, West Africa experienced decreased rainfall seasonality with lower rainfall and a shortened wet season. During the same period, northeastern Brazil experienced increases in rainfall magnitude and variability with a later and longer wet season (Feng *et al.*, 2013). In southern Amazonia, however, dry season length has increased since 1979 (Fu *et al.*, 2013) and this trend is expected to continue (Malhi *et al.*, 2009). Recent CMIP5 GCM simulations (RCP 8.5 scenario) are projecting net drying in both the Amazon Basin (due to $-P$ and $+PET$ on an annual basis) and the Congo Basin ($+P \leq +PET$), limited drying on the Pacific side of the Andes ($+P \leq +PET$), and net wetting ($+P \geq +PET$) in maritime and mainland Southeast Asia (Cook *et al.*, 2014). Changes in atmospheric circulation also influence the timing of rainfall and rainy seasons. For example, the inter-annual El Niño/Southern Oscillation (ENSO) is associated with extreme events such as droughts and floods in the tropics (Christensen *et al.*, 2013), and at least one recent CMIP5 analysis projects future increases in both El Niño and La Niña extreme events (Cai *et al.*, 2015).

Shifting water availability is the principal climate-change-related variable affecting the carbon regime of tropical forests (Guan *et al.*, 2015; Nobre *et al.*, 2016). Understanding regional hydroclimate and present vegetation–water relationships is important for predicting how changes in the water balance will influence tropical ecosystems with respect to water stress and mortality (Bonal *et al.*, 2016; Corlett, 2016), ecosystem productivity, and carbon balance (Zhang *et al.*, 2015; Jung *et al.*, 2017). Plants under water stress alter their stomatal closure to reduce transpiration and CO₂ uptake (Buckley, 2005). Furthermore, many woody species—including

many trees of the wet tropics—function within narrow hydraulic safety margins (Choat *et al.*, 2012), suggesting that even wet forest species are vulnerable to drought. When drought causes extensive tree mortality, the decomposing organic matter releases large amounts of carbon (Rowland *et al.*, 2015), converting tropical forests from net carbon sinks (Osborne, 2012) to net carbon sources (Guan *et al.*, 2015). Drought also contributes to wildfire expansion as dead vegetation biomass augments fuel loads and low humidity creates conditions conducive to fire (De Faria *et al.*, 2017; Taufik *et al.*, 2017). At the ecosystem scale, the inter-annual variability of tropical gross primary production, terrestrial ecosystem respiration, and net ecosystem exchange are all strongly controlled by the availability of water (Jung *et al.*, 2017). Hence, climate-change-induced alterations in rainfall patterns can dramatically affect global greenhouse gas levels and have lasting effects on landscape-scale ecology, hydrology, and biogeochemistry.

While the water and carbon dynamics of the lowland forests have been well studied, less is known about these processes in other tropical ecosystems. For example, changing fog, precipitation, and evaporative regimes can have important ecohydrological implications for tropical montane headwater ecosystems adapted to frequent fog immersion (Hu and Riveros-Iregui, 2016). During fog immersion, canopy interception of fog can contribute to net precipitation (Bruijnzeel *et al.*, 2011): with the low solar radiation and high humidity, water films form on leaves, reducing CO₂ uptake and transpiration (Alvarado-Barrientos *et al.*, 2014; Oliveira *et al.*, 2014a) while facilitating foliar water uptake (FWU). A high FWU capacity improves plant water status (Goldsmith, 2013; Gotsch *et al.*, 2014), increases water use efficiency, decreases xylem embolism (McDowell *et al.*, 2008), and even facilitates hydraulic redistribution under soil drought (Eller *et al.*, 2013, 2016; Oliveira *et al.*, 2014a; Cassana *et al.*, 2016). While high FWU capacity improves survivability for some species in tropical montane cloud forests (Eller *et al.*, 2013; Gotsch *et al.*, 2014; Oliveira *et al.*, 2014a), it also renders these species more vulnerable to decreases in fog frequency (Eller *et al.*, 2016). For tropical dry forests, where drought is already pronounced, increasing drought intensity could further push these ecosystems into biological impoverishment—especially where there are acute and chronic anthropogenic disturbances (Rito *et al.*, 2017).

Climate change associated warming will also influence ecohydrological processes. Unlike the projections regarding precipitation, those regarding air temperature trends are generally in good agreement: warming is expected to exceed the historical range of variability

sooner in the tropics than elsewhere (Mora *et al.*, 2013). This scenario significant in the tropics because temperatures exceeding the thermal optimum of photosynthesis may decrease gross primary productivity, increase terrestrial ecosystem respiration, and lead to reduced net carbon uptake (Jung *et al.*, 2017). Furthermore, observational data indicate that warming is enhanced at high elevations (Bradley *et al.*, 2009; Mountain Research Initiative EDW Working Group, 2015), which will negatively affect tropical montane ecosystems and headwaters that support large downstream populations (Viviroli *et al.*, 2011). Predicted changes in hydroclimate, particularly those related to rainfall patterns and temperature, can have significant ecohydrologic consequences that will need to be addressed in the coming decades.

4. Integrating Field- and Modeling-Based Methods

In order to better understand the implications of changing tropical landscapes, we must develop a solid knowledge base of ecohydrological patterns and processes. One approach is to more tightly integrate field and modeling-based methods across scales. Field data is collected to augment, confirm, and elucidate our understanding of ecohydrological processes, and can form the basis of empirical, mathematical, and process-based models. The modeling of ecohydrological processes requires an understanding of links across scales; for instance, strong linkages between small-scale disturbances and large-scale consequences have been demonstrated in a variety of contexts, including land use and climate change (Stark *et al.*, 2015; Ochoa-Tocachi *et al.*, 2016). Scale differences are especially significant in tropical ecosystems because of their greater heterogeneity compared with temperate ecosystems. Hence, effectively predicting ecohydrological change depends on our ability to understand and model ecohydrological linkages across scales. In the following sections we describe some of the emerging field-based and modeling methods relevant to the tropics, while acknowledging that scale-related challenges still remain.

4.1 Stable isotopes of water

Since the 1970s, stable isotopes of water have been used for investigating hydrological processes in humid environments (Dinçer *et al.*, 1970; Sklash and Farvolden, 1979; McDonnell *et al.*, 1990). This field-based method, using in particular the naturally occurring stable isotopes of the water molecule (^2H and ^{18}O), provides valuable information on the history of water (Kendall and

McDonnell, 1998), and in combination with other hydrometeorological and hydrogeochemical measurements has helped elucidate the age, origin, and fate of water (Tetzlaff *et al.*, 2014; Hu *et al.*, 2015; Klaus *et al.*, 2015). Although most water isotope studies have been conducted in temperate and Mediterranean ecosystems, a few have been carried out in tropical regions to (1) estimate mean transit times of water (Timbe *et al.*, 2014; Muñoz-Villers *et al.*, 2015; Mosquera *et al.*, 2016a), (2) explore the influence of topographic and weather patterns on the isotopic composition of precipitation (Vimeux *et al.*, 2011; Windhorst *et al.*, 2013; Sánchez-Murillo *et al.*, 2016), and (3) calibrate hydrological models (Windhorst *et al.*, 2014; Birkel and Soulsby, 2016). Moreover, as methods are developed for monitoring stable isotopes of water at finer spatial and temporal resolutions (Herbstritt *et al.*, 2012; Volkmann *et al.*, 2016), we will gain better insights into processes occurring over short time spans at different scales, which has not been possible with the sole use of hydrometric measurements (e.g., rainfall, streamflow, and sap flow).

Stable isotopes also play an important role as tracers in ecology, because the chemical and physical processes occurring within plants affect the ratio of heavy to light isotopes of water (Dawson *et al.*, 2002). These small differences in isotope ratios are used to study plant water sources (Jackson *et al.*, 1995) and the partitioning of ecohydrological fluxes (Martinelli *et al.*, 1996; Villegas *et al.*, 2014). For example, Eller *et al.* (2013) used stable isotopes to understand the importance of fog water subsidies in *Drimys brasiliensis* Miers (Winteraceae), a prolific woody species of the Atlantic cloud forests of Brazil. They found that this species not only is capable of utilizing fog water from the surface of its leaves, but also can redistribute absorbed fog water to lower branches. In another study (Hu and Riveros-Iregui, 2016), stable isotopes of oxygen and carbon in tree rings were used to look at long-term effects of climate change on the physiology and water sources of plants in tropical montane cloud forests. Another promising application is the tracking of fog through the soil–plant–atmosphere continuum, made possible by the marked differences in isotopic composition between fog water and rain water (Scholl *et al.*, 2011). However, despite these promising advances, obtaining accurate and representative measurements of fog water inputs remains challenging (Giambelluca and Gerold, 2011).

Regarding links between ecology and hydrology, the application of dual water isotope tracers could improve our understanding of plant water uptake, soil water dynamics, and streamflow generation (Sprenger *et al.*, 2016; Mosquera *et al.*, 2016b; Farrick and Branfireun,

2015). Findings from recent studies (Bowling *et al.*, 2016; Hervé-Fernández *et al.*, 2016; Goldsmith *et al.*, 2012; Evaristo *et al.*, 2015; Evaristo *et al.*, 2016) suggest an ecohydrological separation between an immobile pool of water that is tightly bound to the soil matrix and is used by trees, and a mobile pool of water that infiltrates through soils and feeds streams and groundwater (the so-called “Two Water Worlds hypothesis”—Brooks *et al.*, 2010; McDonnell, 2014). But this hypothesis is controversial (Berry *et al.*, 2017), given discrepancies in soil water extraction techniques (Orlowski *et al.*, 2013, 2016; Oerter *et al.*, 2014; Sprenger *et al.*, 2015) and an incomplete understanding of the ecophysiological processes (Dawson *et al.*, 2002; Ellsworth and Williams 2007; Mamonov *et al.* 2007; Ellsworth and Sternberg 2015; Volkmann *et al.*, 2016). We believe that investigating the Two Water Worlds hypothesis in the tropics can contribute significantly to clarifying the ecophysiological processes that drive the suggested separation, and help reconcile the discrepancies, if carried out in (1) tropical dry forests and savannas during both the wet season, when primary productivity and precipitation are in phase, and the dry season, when water stress is higher; and (2) tropical wet environments, such as rainforests and Páramos, where precipitation seasonality is relatively low.

4.2 Remote and Environmental Sensing

Remote and environmental sensing products are important as data input for model development, calibration, validation, and upscaling (Anderson *et al.*, 2007). One of the first and most important applications of aerial and satellite remote sensing imagery has been the monitoring of changes in land cover, an application especially important for the rapidly changing landscapes of the tropics. Since 1972, Landsat has offered a continuous dataset of Earth imagery via satellite (Loveland and Dwyer, 2012)—data that is especially valuable for studying tropical ecosystems that are secluded or difficult to access (Nerini *et al.*, 2015). In 2008, access to Landsat data became open-source, after which usage by the research community increased dramatically (Woodcock *et al.*, 2008). For example, Hansen *et al.* (2013) used Landsat data to construct high-resolution maps of forest change. These maps have since been used by policy-makers (Gaveau *et al.*, 2016) and by governments to track illegal deforestation (Moonen *et al.*, 2016). Combining Landsat data with real-time analysis, the Global Forest Watch (<http://www.globalforestwatch.org/>) now offers interactive maps of forest fires, mining, logging, and deforestation (Showstack, 2014).

Another application of remote sensing technology has been to monitor changes in the spatial and temporal distribution of precipitation. For example, a recent study tracked air masses above the Amazon forest using multiple rainfall satellite products, including Hysplit and TRMM (Tropical Rainfall Measuring Mission) as well as reanalysis (ERA-Interim and NCEP/NCAR) data (R. Molina et al. *In prep*; and J.C. Villegas, personal communication). They found that on average, precipitation moving inland from the ocean decreases exponentially when the air masses pass over deforested areas, but remains steady when the air masses pass over forested areas or even increases when moving towards forests—a result that confirms previous findings from climate models (Costa and Pires, 2010). Satellite monitoring via the Global Precipitation Measurement (GPM) program and the recently expired TRMM has so far provided 18 years of continuous global precipitation measurements for the tropics. Such satellites provide accurate rainfall estimates at different temporal resolutions (e.g., annual, seasonal), even over complex terrain (Manz *et al.*, 2016). Indeed, TRMM data show an increase in the duration of the dry season over the Amazon forest, as validated by a limited number of field rain gauges (Fu *et al.*, 2013)—which has implications for fire frequency and land use (Alencar *et al.*, 2006; Zeng *et al.*, 2008).

The assimilation of historical ground-based data into newer datasets, including remote sensing data, has provided the community with unique, long-term records that have been crucial for developing and testing surface–atmosphere models (Ruiz-Barradas *et al.*, 2016). For example, the use of reanalysis data was key to improving global precipitation models, which then helped refine ecohydrological models for watersheds in the Andes (Strauch *et al.*, 2017) and in Puerto Rico (Auerbach *et al.*, 2016). The large land surface models that use this reanalysis data have yielded information essential for understanding the complexity of tropical ecosystems. The Joint UK Land Environment Simulator (JULES), for example, has predicted that in the Amazon Basin, climate change will lead to increased seasonality of precipitation (Zulkafli *et al.*, 2016), prolonged droughts (Boisier *et al.*, 2015), and larger floods. Recently, water isotope data has been collected remotely. The Tropospheric Emission Spectrometer (TES) aboard the Aura satellite, launched in 2004, measures the ratio of heavy water (HDO) to H₂O in the water vapor of the atmosphere. The availability of these remotely sensed isotopic data opens new opportunities to investigate ecohydrological processes at larger scales. For instance, the combination of remotely sensed isotopic data with precipitation datasets and modeled

atmospheric circulation has provided insights regarding the partitioning of land surface ET into its different components (Good *et al.*, 2015).

Another important source of environmental sensing data is the eddy flux tower, which continuously measures intermediate-scale hydrometeorological and carbon fluxes. As a result of global carbon-monitoring initiatives in the 1990s, many networks containing these towers were created that today hold more than a quarter century of stored data, contributing significantly to our understanding of global carbon cycles and detection of global environmental changes (Baldocchi *et al.*, 2001). New instruments can also easily be added as technology evolves—for example, high-resolution laser disdrometers paired with time-lapse imagers (Padrón *et al.*, 2015) are an effective way to monitor fog coverage at high spatio-temporal resolutions.

At present, the majority of the global networks that include flux towers are located in subtropical and temperate regions. In addition, despite the large volume of data generated by flux towers, methods for using them to investigate different soil–plant–atmosphere interactions are still needed (Oliveira *et al.*, 2014b; Chun *et al.*, 2014). In the tropics, additional flux monitoring networks will be needed, as well as improved modeling methods, if we are to gain an understanding of the ecohydrological processes that play key roles in global water and carbon cycles. Flux towers are long-term installations that require financial support and technical maintenance—resources not always available in tropical countries—but these installations are vital because eddy flux towers are among the few instruments collecting the intermediate-scale data necessary for understanding ecohydrology across scales.

Finally, at a smaller scale, the advent of sap flow sensors has provided insights into the role of vegetation in hydrologic fluxes. For example, the heat-based method of measuring sap flow developed in the 1980s has proved to be a cost-effective option for monitoring whole-plant water use (Swanson, 1994; Smith and Allen, 1996, Köstner *et al.*, 1998) and stem water storage (Feild and Holbrook, 2000; Goldstein *et al.*, 1998). Further, such heat-ratio sap flow sensors enabled the measurement of low and bi-directional flow (Burgess *et al.*, 2001), upward and downward hydraulic redistribution (Oliveira *et al.*, 2005), and reverse sap flow, all of which led to a recent redefinition of the soil–plant–atmosphere continuum (Eller *et al.*, 2013; Goldsmith, 2013). However, efforts to upscale sap flow measurements to stand-scale transpiration estimates are confounded by the species diversity and structural complexity of most tropical ecosystems; instrumentation capable of sampling multiple species is required, including specialized, small-

diameter, non-invasive sap flow sensors for monitoring the herbaceous understory (Clearwater *et al.*, 2009). At the stand scale, water balance and dynamics—such as the partitioning of ET—are best evaluated through integration of all three kinds of data: eddy flux, sap flow, and stable isotopes of water vapor (Williams *et al.*, 2004).

4.3 Mathematical and Process-Based Models

Mathematical and process-based approaches can reconcile scale differences among various data products used to detect and forecast environmental change (Keitt, 2000; Phillips and Jerolmack, 2016). Continuous wavelet analysis, for example, is a mathematical approach that employs a multiscalar technique to decompose aperiodic, non-stationary, and noisy data into frequency components, helping to shed light on processes that might be in play at different spatio-temporal scales. Wavelet methods have also been used to pre-process data that is then fed into data-drive hydrologic models (Nourani *et al.*, 2014). The continuous wavelet is a powerful and suitable method for analyzing ecological and hydrological data (Labat, 2005; Cazelles *et al.*, 2008). For example, Vargas *et al.* (2010) used continuous wavelet coherency analysis to show how soil temperature, soil moisture, and photosynthetically active radiation influence the production of soil CO₂ at different temporal scales. Given the advances in and increasingly wide use of automated data-collection equipment (data loggers, automatic samplers, *in situ* stable-isotope samplers) that provide continuous data at higher temporal and spatial resolutions, the application of multiscalar techniques such as continuous wavelet analysis will be invaluable for investigating ecohydrological processes in the tropics.

Process-based models have been used in hydrology (Beven, 2011) and ecology (Landsberg and Sands, 2010) to simulate complex natural processes and to further probe the linkages among different kinds of data across scales. Unlike traditional models, which analyze empirical data via correlations, process-based models simulate detailed physical, chemical, and/or biological processes to elucidate underlying mechanisms (Adams *et al.*, 2013). As simplified representations of ecohydrological mechanisms at various successional scales, process-based models incorporate internal and external variables linked by functional relationships (i.e., processes) (Friend *et al.*, 1997; Mäkelä *et al.*, 2000; Schröder and Seppelt, 2006).

In hydrology, process-based models focus on water and energy balances. In ecology, they focus on the spatial distribution of species and the evolution of interactions between species (DeAngelis and Mooij, 2005; Elith and Leathwick, 2009). When used in ecohydrological studies, these models are parameterized with exogenous and endogenous variables. Exogenous variables relate to regional and coarse-scale processes outside the plant, and endogenous variables relate to fine-scale processes within the plant. Thus, field measurements of water, carbon, and nutrients are often used as exogenous variables (Oliveira *et al.*, 2014b); and plant water storage, sap flow, cell expansion, and radial stem growth are often used as endogenous variables (Bonan *et al.*, 2012; Steppe *et al.*, 2005).

One advantage of process-based models is that they are intrinsically scale-independent (Korzukhin and Ter-Mikaelian, 1996) and can be incorporated into larger, ecosystem-scale models to improve predictive power (McDowell *et al.*, 2013). As an example, Steppe *et al.* (2010) developed a process-based model using data from thermal dissipation, heat pulse velocity, and heat field deformation sensors to obtain high-quality sap flux data for specific tree species. These data were later incorporated into a larger-scale model of whole-plant hydraulics (Steppe *et al.*, 2015), enabling plant water usage and storage to be quantified as measurements of physiological functions (i.e., endogenous variables) under different environmental conditions (i.e., exogenous variables). Finally, new field and laboratory measurements are being used to develop downscaling and upscaling models that link endogenous to exogenous variables, for elucidating how different plant species affect and are affected by local soils and nutrient cycles (Steppe *et al.*, 2005; Bonan *et al.*, 2012; Oliveira *et al.*, 2015; Adams *et al.*, 2009).

Still, process-based models have some disadvantages compared with empirical models. They not only require more data and higher computational power, but also their parameterization yields outputs with greater uncertainty (Adams *et al.*, 2013). In addition, it has proved difficult to develop process-based models to address certain specific research gaps, because of the difficulty of characterizing ecohydrological processes. One specific research gap that has not yet been addressed by process-based models is that of upscaling transpiration. Despite the fact that detailed models for leaf-scale transpiration have been proposed for decades (Ball *et al.*, 1987), in the tropics many ecosystem-scale transpiration methods yielding simpler estimates (Thornthwaite, 1948) are still in use—partly owing to the greater complexity and large number of variables involved in representing leaf-scale mechanisms. Models such as the Community

Land Model V5.0 (CLM V5.0), which is specifically designed to elucidate how changes in vegetation could affect climate, represent forest canopies essentially as a “big leaf”—without considering ecosystem demography, physiological differences, or competition among species. One significant result is that Amazonian transpiration is underestimated, further biasing land–atmosphere dynamics in the coupled models (Fisher, 2013). The consequent discrepancies between the output of large-scale models and field and laboratory data substantially increase the uncertainty and narrow the applicability of such models (Fisher, 2013). Similarly, process-based models have not yet resolved issues related to fog water inputs. Conventional rain gauges are not suitable for fog, and even specialized fog gauges give varying results, depending on the type (Frumau *et al.*, 2010; Holwerda *et al.*, 2010)—partly because they do not realistically represent the natural canopy structure (DeLay and Giambelluca, 2010). Thus, a process-based wet canopy water balance method was designed to take into account gauge–canopy differences and to improve the gross and net precipitation comparisons from earlier studies (Giambelluca and Gerold, 2011). Still, results are weakly correlated (Giambelluca *et al.*, 2011) and findings from both stable isotopes tracing and specialized hydrological models sometimes disagree with field-based estimates (Giambelluca and Gerold, 2011).

At present, our knowledge of the physical mechanisms important to the scaling of ecosystem processes remains incomplete. In most cases, effects of scale are estimated via modeling techniques that often do not capture the specific dynamics of the processes and mechanisms involved. Achieving an accurate picture of land–atmosphere interactions in the tropics will require a species-level representation of vegetation diversity (Fisher, 2013), as demonstrated in small-scale models (Villegas *et al.*, 2014). In addition, the relative scarcity of data and limited availability of mechanistic hypotheses remain hurdles to overcome, but the growing availability of laboratory data is bridging this gap (McDowell *et al.*, 2011).

4.4 Socio-ecohydrology and Social Media

Lastly, we highlight the contribution of socio-ecohydrology and social media to the development of ecohydrologic solutions for transformative changes. In hydrology, the branch known as socio-hydrology has emerged to generate information and direct environmental decisions based on the complex interactions between people and the environment (Gober and Wheeler, 2015; Sivapalan and Blöschl, 2015; Troy *et al.*, 2015). Similarly, socio-ecohydrology has emerged in response to

the urgent need to develop ecohydrological theories and hypotheses relating to soil–vegetation–climate–human interactions (Kerkhoff *et al.*, 2004; Troy *et al.*, 2015). Socio-ecohydrology seeks to understand and quantify exogenous and endogenous variables related to human responses and cultural dimensions for ecohydrological studies (Adger *et al.*, 2012; Bakker, 2012; Sivapalan and Blöschl, 2015; Loucks, 2015). These variables are useful for environmental monitoring, modeling, and decision-making. Research efforts have also focused on ecohydrological factors within urban systems (Pataki *et al.*, 2011) and within the context of environmental ethics and climate change (Falkenmark and Folke, 2002). In the field, ecohydrologists have begun to adopt approaches developed by social scientists. For example, participatory methods can be used to analyze social–ecological system dynamics and identify solutions (Walker *et al.*, 2002; Kok, 2009; Gober *et al.*, 2011; Bakker, 2012). Importantly, gender issues and environmental justice, rarely mentioned in ecohydrological research, are considered at the heart of many socio–ecohydrological issues (Falkenmark and Folke, 2002).

With the rise of technology, the use of social media is growing in the scientific community. Twitter, for instance, has become a platform for scientists to communicate new scientific findings, advertise job openings (Bombaci *et al.*, 2016), and create professional networks. One such application, introduced by Steppe *et al.* (2016), is the TreeWatch network, whereby data from trees equipped with dendrometers and sap flow sensors are transmitted from four locations in Germany and Belgium to a cloud server that posts the data online at one-minute intervals. The average shrinking/expansion of the trunk and the sap flow rate are also tweeted automatically. These “tweeting trees” have drawn a lot of attention from both the media (Russew, 2016) and the general public, as they have been “humanized.” People around the world can now follow the “heartbeats” of the trees and thereby better understand what drought looks and feels like for a tree. Such technologies are giving us a new form of interactive science—scientists communicating directly with the public—that also serves to promote the interest of young students and researchers.

5. Summary and Syntheses

To close, we propose a research agenda that we feel can best advance ecohydrology in the tropics. As early-career ecohydrologists, we advocate a research agenda that (1) encompasses a diversity of landscapes, and (2) connects researchers across the tropics. As discussed in sections 1

and 2, a wide diversity of tropical biomes and ecosystems are being rapidly transformed by changes in land use/land cover and climate. First, then, we suggest that direct experimentation across a gradient of land uses, plant community types, and hydroclimates is needed to understand how land use changes might propagate through ecohydrological processes and associated biogeochemical cycling. Specifically, this research needs to target (a) understudied tropical ecosystems, such as secondary forests and plantations, where transformative changes may affect streamflow and sediment transport; (b) tropical dry and deciduous forests, which are characterized by vegetation uniquely adapted to precipitation seasonality; (c) tropical montane grasslands such as the Páramos, where land use and climate interactions are not well documented; and (d) tropical montane forests, which may be especially vulnerable to climate change. We believe that research covering the entire spectrum of tropical ecosystems will help us better understand how changes in plant communities and hydrological processes affect water fluxes and nutrient losses at ecosystem and catchment scales, and how these processes may affect the ecosystem services people depend on (Figure 4).

Second, ecohydrology research in the tropics is disproportionately low compared with other regions, and often does not include local researchers—which we view as an opportunity for collaboration and exchange. One way in which scientists can collaborate and exchange ideas is by taking advantage of the increasing global connectivity and access to open source data and software (Figure 4). The growing availability of “big data”—ranging from high-temporal-frequency data gathered via eddy flux methods to remote sensing and climate reanalysis data—means that environmental patterns and processes will play an increasingly important role in the effort to make use of data-intensive analysis techniques. Likewise, open source software offers an accessible means for developing and sharing rigorous and robust statistical tools. Examples of *such software* include R, Python, and cloud-based geospatial platforms such as Google Earth Engine. Thus, the young ecohydrologist would do well to develop skills that combine a sound theoretical basis in ecohydrology with statistical thinking (Hoerl *et al.*, 2014; Joppa *et al.*, 2013). Synthesizing big data to generate new working hypotheses will be key to advancing our understanding of ecosystem function, predicting changes, and informing managers and policymakers (LaDeau *et al.*, 2017; Peters *et al.*, 2014). Big data will also be important for understanding large-scale environmental phenomena (Levy *et al.*, 2014), such as those resulting from transformative change. As early-career ecohydrologists, we must move from research at the

finer scales typical of ecology and the catchment scales typical of hydrology, to research aimed at larger regional, continental, and even global scales. At the same time, we must know how to extract physical and ecological meaning from the patterns discovered through the analysis of large datasets. This means that research at the smaller scales should be implemented in a way that complements larger-scale analysis. Moreover, we must ensure that our own data is transparent, reproducible, and shareable (Hampton *et al.*, 2013). Even social media, as previously discussed, represent a platform wherein data becomes not only transparent and accessible but also more easily communicated to policy-makers and a wider audience. As young scientists, we feel that this approach—one that takes advantage of existing big data and open source software—will enhance collaboration most innovatively and allow us to answer questions of broader impact.

Our proposed agenda is reinforced by the example of tropical montane cloud forests. As mentioned earlier, tropical climate change research has been dominated by studies of the Amazon Basin and of intact lowland wet forests; yet tropical montane ecosystems offer particularly valuable insights because they are ecologically and hydrologically sensitive to climate change (Messerli *et al.*, 2004). For instance, there is a high probability that climate change will decrease cloud immersion and increase vapor pressure deficits (by causing cloud bases to rise) and/or will increase atmospheric subsidence, which could impact the ecohydrology of these fog-dependent ecosystems (Oliveira *et al.*, 2014a; Hu and Riveros-Iregui, 2016). It may be possible to predict how hydrological and biogeochemical processes might change in these ecosystems (Neill *et al.*, 2006) by developing models based on field and remote sensing techniques that quantify chemical and structural plant traits (Townsend *et al.*, 2008), in combination with climate change projections. At a regional to global scale, efforts of this kind can be facilitated through collaborative research networks such as CloudNet (<http://cloudnet.agsci.colostate.edu>), which are useful for connecting researchers, standardizing measurements, and aggregating data for large-scale meta-analysis.

In summary, we contend that transformative change—whether land use/land cover changes or climatic changes—which affects ecological and hydrological processes at different spatio-temporal scales, should serve as a compass for emerging ecohydrologists. We further contend that a tropical ecohydrology agenda for the coming decades should be based on an approach that encompasses the full spectrum of tropical ecosystems and should be carried out by

researchers representing multiple affiliations and disciplines, complemented by large and open datasets. By building networks and research coalitions, we can enhance our capacity in often under-resourced tropical regions and advance understanding in both locally meaningful and scientifically rigorous ways.

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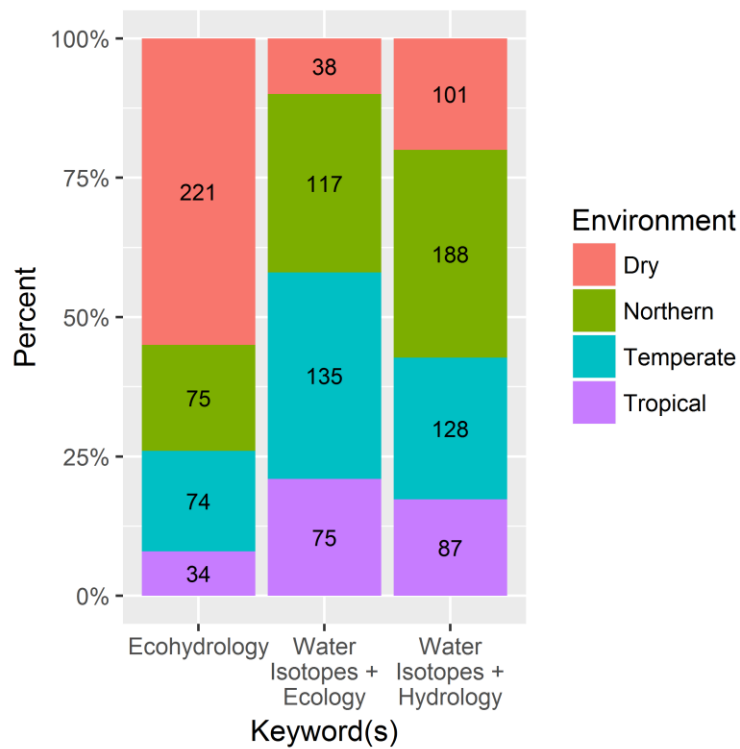


Figure 1. Numbers of studies published since 1945 for different environments (defined on the basis of climate conditions; the Dry category includes arid and semiarid environments, and the Temperate category includes Mediterranean, subtropical, and highland environments [cf. Kottek *et al.*, 2006]). The x-axis shows the keywords used in the literature search (Web of Science, date of search January 16, 2017).

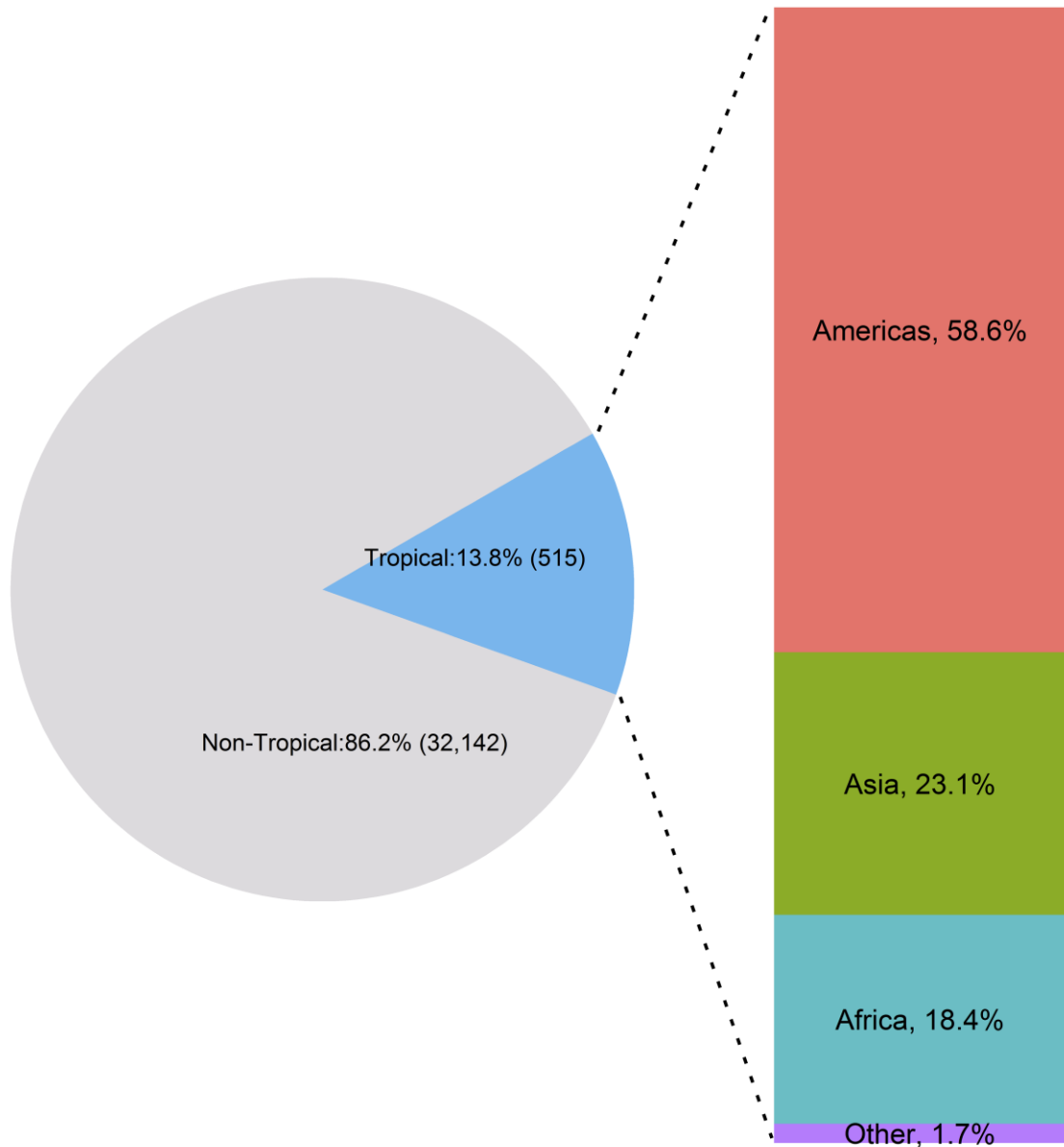


Figure 2. Ecological and hydrological studies published since 1997 by researchers affiliated with organizations from tropical vs. non-tropical regions (from Web of Science—data obtained August 26, 2016, based on keywords *plant*, *water*, and *soil*). The bar chart shows the distribution of the 515 studies published by researchers affiliated with organizations based in tropical

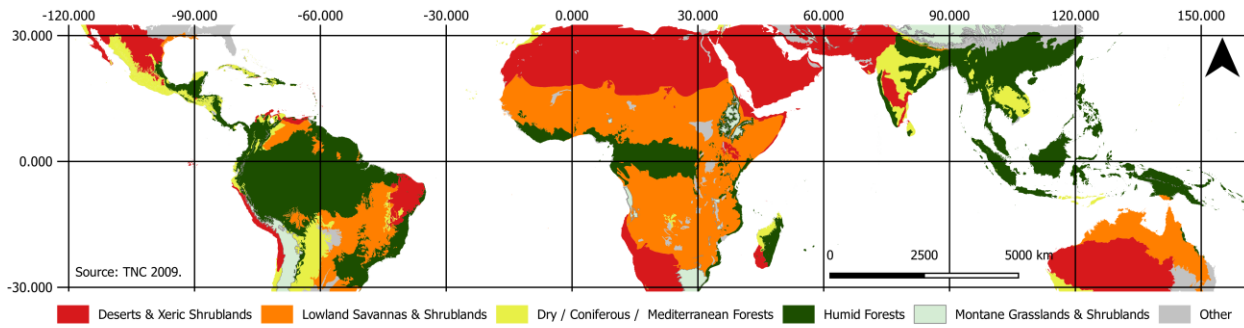


Figure 3. Tropical biomes are distributed roughly between 23°28’N and 23°28’S. “Other” includes temperate and wetland biome types, not discussed in the text. Modified from TNC, 2009.

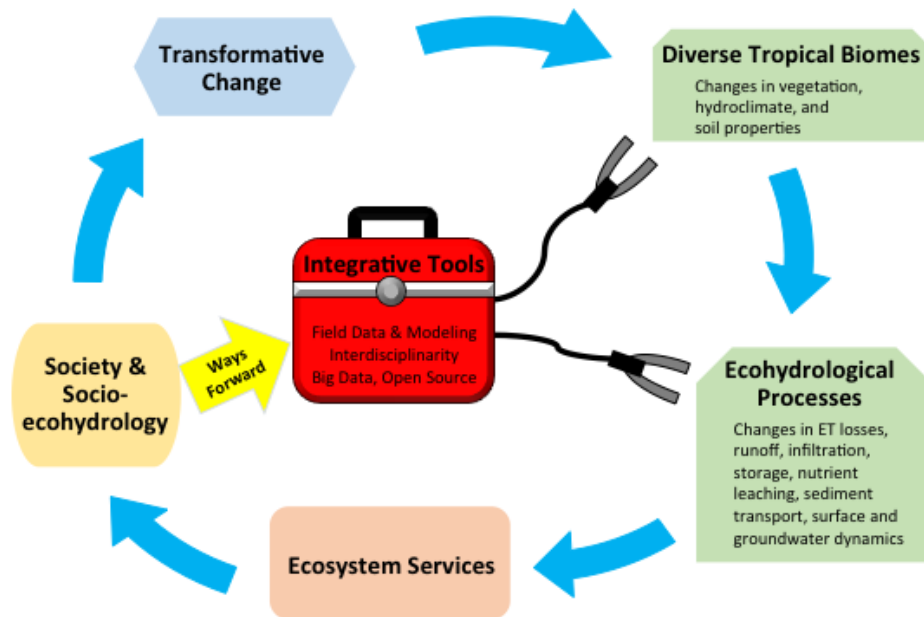


Figure 4. Conceptualization of how society functions as both the driver of transformative change and also the source of solutions.