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DRIVERS OF STREAM DRYING AND NETWORK CONNECTIVITY ACROSS SPATIAL SCALES

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DRIVERS OF STREAM DRYING AND NETWORK CONNECTIVITY
ACROSS SPATIAL SCALES

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BY THE COMMITTEE CONSISTING OF

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ABSTRACT

Nonperennial streams are widespread and abundant around the globe. Although these streams are societally and ecologically important, they are understudied relative to those that flow continuously. Because of this, we lack fundamental knowledge of nonperennial streams, such as when and where they dry and the consequences of those drying patterns. Drying patterns largely determine stream network connectivity in nonperennial systems. Stream drying and network connectivity patterns are driven by processes that act at global, regional, and local spatial scales. The goal of this dissertation is to explore the patterns and drivers of stream drying and connectivity. Chapter One explores the impact of global climate change on network connectivity in the Blue River, Oklahoma. The findings from this research suggest that stream drying is likely to increase in the future. This research also identified a threshold around which a small change in stream drying leads to a large change in connectivity. Chapter Two investigates how the influence of stream drying on network connectivity varies in relation to network-scale properties. This work found that the rate of connectivity loss is faster for larger stream networks and when drying occurs in mainstem reaches. As stream drying is expected to become more extensive due to changes in climate, this research underscores the need for managers to be vigilant about fragmentation when managing at large spatial scales and when managing systems where drying occurs in mainstem reaches. Chapter Three investigates how streamflow and connectivity are influenced by cross-scale interactions between global-scale climate change and regional-scale aridity. This analysis suggests that changes in connectivity due to climate change vary predictably in relation to aridity. Stream networks in arid regions will have more high connectivity days in the future while stream networks in wetter regions will experience increases in the number of low connectivity days in the future. The ability to predict future changes in network connectivity allows for better anticipation of and improved ability to manage for the consequences of climate change. Overall, this dissertation demonstrates how complex patterns of stream drying and connectivity vary predictably in relation to network scale, regional scale, and global scale processes.

INTRODUCTION

Nonperennial streams are societally and ecologically important

Nonperennial streams, or streams that stop flowing at some point in time and space (Busch et al. 2020), are widespread and abundant (Datry et al. 2014). Recent estimates suggest that more than half of streams worldwide are nonperennial, existing in all continents, ecoregions, and climate types (Messager et al., 2021). Nonperennial streams, like all rivers and streams, provide important ecosystem services. These services include provisioning (i.e. freshwater, food), regulating (i.e. climate regulation, water purification), supporting (i.e. nutrient cycling), and cultural (i.e. recreation) services. The ecosystem services provided by nonperennial streams differ from those provided by perennial streams in two key ways. First, in many cases, nonperennial streams are located in the headwaters of stream networks. Due to the unidirectionality of streamflow, this means that nonperennial streams have a major impact on the entirety of the stream network (Datry et al. 2023). The services provided by these nonperennial headwaters impact downstream reaches. For example, rewetting events in headwaters can send pulses of nutrients downstream, affecting downstream water quality and ecosystem functioning (Hladyz et al. 2011, Leigh et al. 2010). Second, ecosystem services are likely enhanced when nonperennial and perennial reaches intersect, due to the resulting diversity and heterogeneity of environmental conditions (Koundouri et al. 2017). For example, certain species of fish thrive when they have access to both nonperennial and perennial streams (Wigington et al. 2006).

Despite their prevalence and importance, nonperennial streams are understudied. Historically, nonperennial streams have been overlooked by researchers and, therefore, are not integrated into stream ecosystem theory (Allen et al. 2020). The limited research on nonperennial streams can be attributed to practical challenges associated with studying streams that may not flow reliably, the bias of gauge networks toward large and perennial rivers (Zimmer et al. 2020), and the omission of nonperennial streams from common conceptual models of river ecosystems (Datry et al. 2014, Allen et al. 2020). As a result, we have a limited understanding of the structure and function of nonperennial streams. Information such as current patterns of stream drying and the impacts of drying on important ecosystem attributes, including habitat availability and connectivity, is largely lacking (Datry et al. 2017).

Connectivity is dynamic and consequential in nonperennial stream networks

Hydrological connectivity is defined as the "water-mediated transfer of matter, energy, or organisms within and/or between elements of the hydrologic cycle" (Pringle 2001). Hydrologic connections are integral to physical, chemical, and biological processes. An extensive body of literature is dedicated to connectivity in perennial streams, especially human alteration of connectivity and its consequences. The construction of barriers, such as dams or culverts, prevents or alters the movement of organisms, nutrients, and sediments through the stream network. Impacts of barriers vary based on permeability, permanence, location, and abundance of those barriers (Fuller et al. 2015).

Effects of fragmentation on ecological populations and communities can alter biodiversity. At the population level, fragmentation has been associated with reduced gene flow (Junge et al. 2014), decreased population size (Bender et al. 1998, Wiegand et al. 2005), and increased extinction risk (Campbell Grant 2011). Fragmentation may also inhibit re-colonization and prevent populations from recovering after a disturbance event (Magoulick and Kobza 2003). At the community level, fragmentation has been shown to reduce species richness (Perkin and Gido 2012) and contribute to spatial shifts in fish communities (Perkin et al. 2015a). Similar patterns have been documented in freshwater mussel assemblages (Hamstead et al. 2019) and other macroinvertebrate communities (Liu et al. 2018). Alternatively, fragmentation can fundamentally alter river reaches and create new habitats, such as through the creation of reservoirs upstream of dams. This process can increase habitat heterogeneity, which itself can lead to increased biodiversity (Fuller et al. 2015).

Connectivity in nonperennial streams is dynamic. In nonperennial stream networks, dry stream reaches act as barriers. Connectivity is therefore driven by patterns of when and where streams flow. As a result, connectivity in nonperennial stream networks tends to be more variable than in perennial streams (Boulton et al. 2017). Temporal and spatial patterns of drying have important consequences. Variations in flow and connectivity have a strong impact on water quality and physico-chemistry (Gómez et al. 2017). Flow, connectivity, and physico-chemistry influence biota and ecological processes within these systems. When stream segments dry, habitat is also lost or fragmented (Perkin et al. 2015b, Crabot et al. 2020). As a result, the biodiversity of nonperennial stream ecosystems tends to be spatially and temporally variable (Stubbington et al. 2017).

Connectivity is driven by processes that act at multiple spatial scales

Streamflow regime is closely linked to global climate, especially precipitation and temperature. As the global climate changes, flow regimes around the world will also change. In the continental United States, changes in flow intermittency are already occurring due to global-scale climate change. General trends indicate increased duration of drying in nonperennial streams in the past several decades (Zipper et al. 2021a). Changes in stream drying patterns are likely to continue under future climates (Chiu et al. 2017). How flow regimes change as a result of climate change will vary based on interactions of global climate with regional and local factors.

Important regional factors that influence flow regimes include topology, geology, and land cover (Costigan et al. 2016). Watershed shape can impact flow permanence, with steeper slopes more likely to have intermittent flows. Slope can influence relationships between stream water and groundwater. Reaches that drive groundwater to the river tend to have more permanent flows, whereas those that lose water to the aquifer are more likely to dry (Mayer and Naman 2011). More permeable soils contribute to faster movement of water, which can contribute to more rapid wetting and drying cycles (Shanafield et al. 2021). Alternatively, permeability can be associated with increased storage and consequently increased flow permanence. Land cover is related to vegetation cover, which affects evapotranspiration rates. Streams in biomes like deserts, grasslands, and tundras are more likely to be intermittent (Poff 1996, Dodds 1997). Impervious surfaces associated with urban land uses reduce infiltration, and ultimately reduce groundwater recharge. This can contribute to increasing intermittence and more rapid wetting and drying cycles. More localized factors, such as the location and management of dams and human water use, also exert a strong influence on flow regimes (Smakhtin 2001). As a result, shifts in drying vary at regional (Beaufort et al. 2018, Allen et al. 2019), continental (Zipper et al. 2021b), and global scales (Sauquet et al. 2021).

Dissertation overview

The goal of this research is to improve understanding of the patterns and drivers of stream drying and connectivity in nonperennial stream networks. This research combines analyses that consider drivers of connectivity that act across spatial scales. In Chapter One, I ask how stream drying and connectivity patterns will change in the Blue River, Oklahoma under multiple future climate scenarios. In Chapter Two, I investigate how stream network properties influence network connectivity. In Chapter Three, I analyze how interactions between regional-scale aridity and global-scale climate change influence changes in stream network connectivity. Finally, I provide a synthesis and discussion of findings from Chapters One, Two, and Three.

Chapter One was carried out with co-authors Shang Gao, Darin Kopp, Yang Hong, Daniel Allen, and Thomas Neeson. Chapters Two and Three were conducted with co-authors Shang Gao, Daniel Allen, and Thomas Neeson.

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CHAPTER ONE

SMALL INCREASES IN STREAM DRYING CAN DRAMATICALLY REDUCE ECOSYSTEM CONNECTIVITY

Keywords:

connectivity, fragmentation, hydrology, intermittent river, nonperennial stream, stream drying

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ABSTRACT

Habitat fragmentation drives biodiversity loss in rivers around the world. Although the effects of anthropogenic barriers on river connectivity are well known, there has been little research on the ways in which stream drying may alter connections among habitats and resources. Given that stream drying is increasing in many regions, there is a pressing need to understand the effects of drying on habitat fragmentation. Here, we quantify spatiotemporal drying patterns under current and future climate scenarios in the Upper Blue River Basin, Oklahoma. We used a hydrologic model to simulate daily streamflow for nine climate scenarios. For each scenario, we calculated metrics of streamflow temporal continuity (dry days, dry periods, and dry period duration) and spatial connectivity (wetted length, number of dry stream fragments, length of dry stream fragments, and dendritic connectivity index) from simulated daily streamflow. We found that stream drying is likely to increase in all future climate scenarios and that increases in stream drying reduce connectivity. However, the effects of stream drying on connectivity were highly nonlinear. Specifically, we observed a threshold around which a small increase in stream drying led to a rapid drop in connectivity. We also found that the greatest increases in stream drying were not associated with the highest emissions scenarios, underscoring the complex linkages among climate, water availability, and connectivity. Given that connectivity is essential to ecosystem structure and function, we discuss water management strategies informed by impacts of stream drying.

INTRODUCTION

Drying has an important, but understudied, role in stream ecosystems. Recent estimates suggest that more than half of streams worldwide are nonperennial (i.e., they stop flowing at some point in time and space; Busch et al., 2020; Datry et al., 2014; Messager et al., 2021). Nonperennial streams exist in all continents, ecoregions, and climate types (Messager et al., 2021). Despite their prevalence, nonperennial streams have historically received less attention from researchers. The relative lack of research on nonperennial streams can be attributed to practical challenges associated with studying streams that may not flow reliably, the bias of gauge networks toward large and perennial rivers (Zimmer et al. 2020), and the omission of nonperennial streams from common conceptual models of river ecosystems (Datry et al. 2014; Allen et al. 2020). The paucity of research on nonperennial streams has led to a poor understanding of their structure and function and, therefore, the biological communities that rely on them.

Widespread changes in stream drying patterns are already being observed. Flow regimes, and specifically stream drying, are closely linked to precipitation and temperature. As a result, shifts in drying vary geographically at regional (Beaufort et al. 2018; Allen et al. 2019), continental (Zipper et al. 2021), and global scales (Sauquet et al. 2021). For example, decreased drying has been identified in the Northern Plains region of the United States (Sauquet et al. 2021), while increased drying has been widespread in the southern continental United States (Zipper et al. 2021) and throughout Australia (Sauquet et al. 2021). Changes in stream drying patterns are likely to continue under future climates (Chiu et al. 2017).

Temporal and spatial patterns of drying have important consequences. Increases in stream drying are associated with reductions in biodiversity of macroinvertebrates (Bogan et al. 2013; Leigh and Datry 2017), fish (Perkin et al. 2015a), and algae (Tornés and Ruhí 2013). The decreases in biodiversity that result from drying have been attributed to loss of habitat (Bogan et al. 2013), loss of food resources (Arias-Real et al. 2021), interruptions in the reproductive cycle (Perkin et al. 2015b), and elimination of disturbance sensitive taxa (Tornés and Ruhí 2013; Stubbington et al. 2017). Further, the spatial arrangement of wet and dry river reaches can have important consequences for the hydrological connectivity of streams and rivers, otherwise referred to as riverine connectivity (Freeman et al. 2007) or ecological connectivity (Allan et al. 2021). Longitudinal hydrological connectivity (connectivity in the upstream-downstream dimension; here-after ‘connectivity’; Ward 1989) impacts geomorphology, hydrology, water chemistry, and ecology (Boulton et al. 2017).

Despite increased research on nonperennial streams (Datry et al. 2011) and an extensive body of literature dedicated to connectivity, little research has been conducted examining the impacts of changes in stream drying patterns on connectivity. Human alteration of connectivity and its consequences are well documented. The construction of barriers, such as dams or culverts, prevents or alters the movement of organisms, nutrients, and sediments through the stream network. Impacts of barriers vary based on permeability, permanence, location, and abundance (Fuller et al. 2015). Habitat fragmentation in streams is associated with decreased biodiversity (Liermann et al. 2012), decreased population size (Perkin et al. 2015b), decreased population connectivity (Junge et al. 2014), and reduced dispersal ability (Perkin et al. 2013). In nonperennial stream networks, dry stream reaches act as barriers. Although some degree of fragmentation is natural in nonperennial stream systems, increased fragmentation resulting from increased drying is expected to have widespread consequences. However, little research is dedicated to understanding these consequences. Jaeger et al. (2014) showed that reduced connectivity resulting from increased stream drying will threaten movement and reproduction abilities of fishes in a naturally nonperennial watershed located in the southwest United States. More research is needed to examine how consequences of reduced connectivity in nonperennial stream networks vary geographically and among taxa. Understanding patterns of stream drying, how they may change, and associated impacts on connectivity is critical for effective ecosystem management (Allen et al. 2019).

Here, we investigated how changes in spatiotemporal patterns of stream drying may impact connectivity under future climate scenarios in the Upper Blue River Basin of Oklahoma. We used a hydrologic model to predict changes in stream drying under nine climate scenarios. Using several metrics to quantify stream drying, we compared streamflow continuity and connectivity in current and future climate scenarios.

METHODS

Study location

The Upper Blue River Basin is located in southern Oklahoma, USA (Figure 1-1). The region is characterized by temperature and precipitation extremes, resulting in periods of drought and flood (Dodds et al. 2004). The average temperature is 16.9°C, with an average of 73 days per year above 32.2°C. Average annual rainfall is 1080 mm, with monthly rainfall ranging 55 mm in January to 141 mm in May (Oklahoma Climatological Survey n.d.). Land cover in the basin is predominantly grassland and pasture/hay, with deciduous forest bordering the stream network (Dewitz 2019). The basin is hilly, with elevation ranging from 180 to 409 m above sea level (Figure S1-1; Gesch et al. 2018). The drainage area of the Upper Blue River Basin is 483 km^2. Perennial reaches of the river are sustained by the Arbuckle-Simpson aquifer. Portions of the basin are nonperennial, with temporal and spatial distribution of these reaches dependent on groundwater level and meteorology (Fabian 2008). The probability of water occurrence is greatest in the main stems with drying tending to occur in the headwaters (Figures S1-2 and S1-3; Gao et al. 2021). Central Oklahoma is expected to experience increased temperatures and decreased precipitation due to climate change (Zhang and Nearing 2005) which will make the basin increasingly vulnerable to drought (The Choctaw and Chickasaw Nations et al. 2017; Bertrand and McPherson 2018) and may potentially alter stream drying patterns.

The Upper Blue River Basin is a good model system for studying the effects of stream drying on connectivity because it is unregulated. As a result, changes in streamflow and drying are due solely to changes in water availability rather than water storage and release decisions by reservoir managers. Human consumption of water from the Arbuckle-Simpson aquifer is primarily used for municipal and industrial purposes. Recent periods of drought have depleted surface water resources in the region. High water demand for residential and agricultural water usage has led to water emergencies and unprecedented measures to maintain water availability, including the establishment of connections to other surface and groundwater sources (The Choctaw and Chickasaw Nations et al. 2017).

Hydrologic modeling

We used the Couple Routing and Excess Storage (CREST) model to simulate current and future streamflow. CREST is a distributed hydrologic model that simulates surface and subsurface flow (Wang et al. 2011). The model setup and parameterization for the Upper Blue River Basin were previously established in Gao et al. (2021), where extensive calibration and validation work was conducted using stream gauges, satellite imagery, and in situ water status loggers. Calibration and validation focused on capturing the low flow conditions and stream intermittency in numerous small headwater streams. As a result, this model has been shown to be capable of estimating daily water occurrence at various stream orders in the study area.

Outputs were simulated at a 10 m grid spatial resolution at a daily timestep. Using 10 m elevation grids, we delineated 2510 stream reaches on a confluence-to-confluence basis. Reaches had a mean length of 456.7 m (SD = 352.1 m). Streamflow grids were spatially averaged over each reach to calculate mean daily flow. We then converted the daily streamflow to binary wet/dry status using 0 m^3/day as the threshold. We modeled streamflow for the years 2010-2088. We considered output from 2010 to 2029 to represent current streamflow and output from 2060 to 2079 to represent future streamflow for our analyses.

Climate models

We used statistically downscaled climate projections of daily temperature and precipitation as hydrologic model forcing data (Bertrand and McPherson 2019). Nine downscaled climate scenarios are available, which are the result of all combinations of three general circulation models (GCMs; CCSM4, MIROC5, and MPI_ESM_LR) and three representative concentration pathways (RCPs; 2.6, 4.5, and 8.5 W/m^2). Using three GCMs allowed us to represent a range of uncertainty. For example, MIROC5 tends to predict warmer temperatures and moderate precipitation, MPI_ESM_LR tends to predict cooler temperatures and wet summers, and CCSM4 tends to predict moderate temperatures, wet winters, and dry summers (Bertrand and McPherson 2019). Together, these three GCMs captured a range of potential climate futures. The RCPs are scenarios of anthropogenic greenhouse gas emissions and changes in land cover. RCP 2.6 represents a scenario where the concentration of greenhouse gases reaches 490 ppm by the year 2100, RCP 4.5 stabilizes around 650 ppm by 2100, while RCP 8.5 represents a scenario where greenhouse gas concentration exceeds 1370 ppm by 2100 (Moss et al. 2010).

We used downscaled temperature and precipitation data from each of the above nine climate scenarios to force the hydrologic model, resulting in nine hydrologic models. To produce the forcing input for the CREST model, the daily maximum and minimum temperature grids in the nine GCMs were converted to potential evapotranspiration (PET) using the scheme in Oudin et al. (2005). We then resampled the 0.125° precipitation and PET grids at 10 m resolution using bilinear interpolation. We analyzed each of the nine hydrologic models for patterns of spatial and temporal drying.

Streamflow temporal continuity

To understand the temporal continuity of streamflow within each reach, we used three metrics. Following Jaeger et al. (2014), we calculated the annual number of dry days, annual number of dry periods, and duration of dry periods for each stream reach. These metrics are useful for quantifying habitat loss for aquatic organisms, especially those with limited dispersal abilities (Matthews and Marsh-Matthews 2003; Vaughn et al. 2015). For each metric, we looked at the difference between the current (2010-2029) and future (2060-2079) study periods for each of the nine climate scenarios.

Streamflow spatial connectivity

To calculate the extent of stream drying across the river network, we calculated the percent of the network that was wet, the number of dry fragments, and the average length of dry fragments. Fragments were defined as consecutive reaches of the stream that had the same wet or dry status. These metrics are useful for understanding patterns of connectivity through space, which can have an important influence on ecosystem structure and function. For example, connectivity has been shown to impact macroinvertebrate and fish diversity (Datry et al. 2007; Beesley and Prince 2010).

To calculate how stream drying might change connectivity among wet reaches, we used a modified version of the dendritic connectivity index (DCI). The DCI was originally developed to measure the impact of point barriers (e.g., road culverts and dams) on fish passability (Cote et al. 2009). We used a modified version of the original formulation in which we consider dry stream reaches to be barriers. For all stream reaches *i* and *j*, DCI was calculated as:

$$DCI = \sum_{i=1}^{n} \sum_{j=1}^{n} c_{ij} \frac{l_i}{L} \frac{l_j}{L} * 100$$

where c_{ij} is a Boolean variable that takes the value 1 if reach *i* is connected to reach *j*, or 0 if not. Two reaches were considered connected if there was a path between them made entirely of wet reaches. The lengths of stream reaches *i* and *j* are identified as l_i and l_j, with L representing the total length of the drainage network. We calculated these metrics at a daily timestep for current and future time periods in each of the nine climate scenarios.

Finally, we examined DCI in relation to daily streamflow at the outlet of the watershed to understand how water quantity is related to fragmentation. We used t-tests to compare daily streamflow of the current and future time periods for each of the hydrologic models. We fit smoothing splines to model the relationship between DCI and streamflow using the cobs package (Ng and Maechler 2007, 2020) in R (v4.1.1; R Core Team 2021).

RESULTS

We found that the number of dry days is projected to increase in most future climate scenarios (Figure 1-2, S1-4). For eight of the nine climate scenarios, models showed an increase in the average number of dry days for the future period when values for all reaches within the watershed are averaged. However, changes in stream drying were highly variable across space, and the change in the average annual number of dry days for individual reaches ranged from -19 days (MPI_ESM_LR and RCP 2.6) to 46 days (MPI_ESM_LR and RCP 8.5). Overall, larger increases in the number of dry days were associated with more extreme RCPs for GCMs MIROC5 and MPI_ESM_LR.

We also found that while the number of dry periods varied among climate scenarios (Figures 1-3 and S1-5), dry periods were projected to become longer in most future climate scenarios (Figures 1-4, 1-5, and S1-6). Less clear relationships existed between RCPs and both the average annual number of dry periods and the average duration of dry periods (Figures 1-3 and 1-4). Change in the average number of dry periods for an individual reach ranged from -2.45 periods (MIROC5 and RCP 4.5) to 2.65 periods (MPI_ESM_LR and RCP 2.6). Change in the average duration of dry periods for an individual reach ranged from -32.67 days (CCSM4 and RCP 8.5) to 60 days (CCSM4 and RCP 2.6). Four climate scenarios showed an increase in the average number of dry periods (Figures 1-3 and 1-5). Seven climate scenarios showed an average increase in the duration of dry periods (Figures 1-4 and 1-5). Two climate scenarios exhibited an increase in both the number of dry periods and the duration of dry periods. No climate scenarios had a decrease in both the number of dry periods and the duration of dry periods.

These changes in stream drying drove increases in habitat fragmentation in the Upper Blue River watershed in future climate scenarios (Figures 1-6, S1-7 – S1-15). Increases in the number of dry fragments and the average length of dry fragments were associated with decreases in connectivity metrics. Percent wetted length and DCI were correlated ($r = 0.99$, $p < 0.05$; Figure S1-16). Increases in stream drying and associated decreases in connectivity were especially evident during summer months.

In all climate scenarios, small declines in daily streamflow could lead to large decreases in watershed connectivity. Modeled relationships between daily streamflow and connectivity for the study periods indicated the presence of a streamflow threshold around which small decreases in daily streamflow were associated with a dramatic decrease in connectivity (Figure 1-7). Away from this threshold, low streamflow values were consistently associated with low DCI values and high streamflow values were consistently associated with high DCI values. Additionally, daily streamflow values were lower in the future period than the current period in seven of the nine climate scenarios ($p < 0.05$; Figures 1-7, S1-17 – S1-24).

DISCUSSION

Future stream drying patterns

Our analysis of streamflow continuity under nine future climate scenarios shows a trend of increased drying in the Upper Blue River Basin (Figures 1-2 and 1-5). Specifically, our findings tend to indicate prolonged dry periods in the future, observed in seven of the nine climate scenarios (Figure 1-4). Additionally, we found that the Upper Blue River Basin is projected to be more fragmented in future climate scenarios, especially during the summer months (Figure 1-6).

There were clear trends in changes in drying patterns among the GCMs. All three hydrologic models driven by the MPI_ESM_LR (lower temperatures and wetter summers) temperature and precipitation data projected a decrease in the annual number of dry periods (Figure 1-3). The three hydrologic models driven by MIROC5 (warmer temperatures and moderate precipitation) projected an increase in the number of dry periods. Hydrologic models driven by CCSM4 (moderate temperatures, wet winters, and dry summers) represented more moderate scenarios, with change in annual number of dry days projected to be near zero. The mean number of dry days of models driven by CCSM4 decreased for RCPs 2.6 and 4.5 and increased for RCP 8.5. Similarly, we also observed patterns between the projected change in length of dry periods and GCMs (Figure 1-4). All hydrologic models driven by CCSM4 and MPI_ESM_LR data projected an increase in the duration of dry periods. Hydrologic models driven MIROC5 projected an increase in the duration of dry periods for RCP 2.6 and decreases in length of dry periods for RCPs 4.5 and 8.5. Changes in drying predominately occurred in the headwaters (Figures 1-2 – 1-4).

Patterns in connectivity were also evident among the GCMs. The CCSM4 GCM is characterized by dry summers. This tendency was evident in the connectivity metrics for the hydrologic models. Hydrologic models driven by CCSM4 climate data tended to have larger differences in connectivity metrics between current and future time periods, where future time periods were less connected (Figures 1-6, S1-7, and S1-8). Models driven by MPI_ESM_LR data showed similar patterns of decreased connectivity, especially for the more extreme RCPs (Figures S1-12 – S1-14). Models that were driven by MIROC5 data followed a similar pattern during early summer months. However, during the late summer months, connectivity tended to be higher during the future time period (Figures S1-9 – S1-11). Across models, there was a tendency for longer dry fragments during the future scenario (Figure S1-15).

Modeled differences in drying patterns between current and future climate scenarios were driven solely by changes in precipitation and temperature. Changes in precipitation affect watershed inputs (i.e., water entering the watershed) while changes in temperature directly affect evapotranspiration and thus watershed output. All else held constant, increased evapotranspiration will result in decreased streamflow. Evapotranspiration has the potential to change due to factors that are not explicitly included in our hydrologic model. For example, land use change may alter vegetation composition and thus transpiration. Additionally, water use efficiency of plants has been shown to improve with increased atmospheric CO_2 concentrations for individuals (Farquhar 1997), which has been associated with increased foliage in water limited regions (Donohue et al. 2013). The relationship between CO_2 concentrations and evapotranspiration is not fully understood at the landscape scale. Despite the uncertainty associated with these factors, evapotranspiration in drylands is generally expected to increase with climate change (Huang et al. 2017).

Streamflow in nonperennial streams is largely driven by precipitation. Surface flow can occur when the rate of rainfall exceeds the rate of infiltration into the soil (when the soil is unsaturated) or when the soil becomes saturated (Shanafield et al. 2021). Thus, antecedent soil moisture conditions as well as interactions between the surface and subsurface can influence stream drying patterns. Climate change may alter soil conditions, and soil conditions may in turn alter surface-subsurface interactions, ultimately influencing stream drying patterns.

In addition to surface-subsurface interactions, there are also important relationships between streamflow and the Arbuckle-Simpson aquifer that occur in the Upper Blue River Basin. Groundwater was not explicitly included in our hydrologic model. However, groundwater interactions likely play an important role in determining stream drying patterns. Groundwater outflow, called baseflow, contributes to streamflow. Increasingly dry conditions resulting from climate change and human extraction of groundwater have the potential to reduce groundwater levels. Groundwater demand in this region is largely driven by irrigation (Oklahoma Water Resources Board 2020). Demand for groundwater increases during periods of low precipitation to sustain crops. Additionally, during a recent drought in the Upper Blue River Basin, at least one municipality was forced to drill a well to maintain sufficient supply (The Choctaw and Chickasaw Nations et al. 2017). Increased demand for groundwater could reduce groundwater contributions to streamflow, thereby altering patterns of stream drying.

We observed that connectivity can decrease drastically with only small changes in daily streamflow. The slope of the modeled relationship between streamflow and DCI indicates the presence of a threshold in the Upper Blue River Basin between daily streamflow values of 10^5 and 10^6 m^3/day. The watershed tended to be well connected when the daily streamflow was above this threshold and more poorly connected when the daily streamflow was below the threshold. In some future scenarios, the threshold shifted so that higher daily streamflow values are required to maintain equivalent watershed connectivity. Simultaneously, daily streamflow values were, on average, lower in the future period than in the current period. The drying that takes place in the modeled future scenarios resulted in daily streamflow values that were more frequently below the threshold, which resulted in a system that was more fragmented more often. While we observed this general trend, we also observed variability in DCI values at the same or similar streamflow values.

Stream drying thresholds have been observed in other watersheds. For example, Ward et al. (2018) documented threshold behavior exhibited by network expansion and contraction in a watershed in the Pacific Northwest, USA. In this watershed, during high streamflow conditions, the wetted length and connectivity are nearly constant. When streamflow drops below a threshold, the wetted length and connectivity are more variable, expanding and contracting in response to precipitation. Threshold behavior in mountainous watersheds has been attributed to interactions between geology and precipitation, and is thus sensitive to climate change (Prancevic and Kirchner 2019; Ward et al. 2020). Understanding controls on the connectivity threshold in the Upper Blue River Basin, a dryland watershed, has critical management implications (see *Implications for ecology and management*).

While drying patterns differed among the nine scenarios, drying increased by some metric in every scenario. The nine hydrologic models here represent a range of potential future scenarios. This indicates that increases in spatial and temporal drying will likely occur in the Upper Blue River Basin as a result of climate change. How changes in drying patterns manifest, whether via more frequent dry periods, longer dry periods, or a more fragmented watershed, has ecological and management consequences.

Implications for ecology and management

A projected increase in the duration of dry periods can affect stream ecosystems in many ways. It has been hypothesized that prolonged dry periods can lead to the development of hydrophobic soils, contributing to increased surface flow during precipitation events (Dahm and Molles 1992; Molles Jr. et al. 1992). By this logic, increased dry periods in the Upper Blue River Basin could contribute to a flashier flow regime with more dynamic physicochemical processes. Rapid rewetting after long periods of zero flow has been associated with high rates of metabolism which quickly results in hypoxic events (Hladyz et al. 2011; Whitworth et al. 2012).

Prolonged drying can directly affect the ecological composition of streams. Many organisms have strategies of resistance and resilience to stream drying, but longer dry periods may be detrimental (Perkin et al. 2015; Vaughn 1997). Bacteria community composition in a nonperennial stream has been shown to vary temporally based on physical and chemical processes, with richness and diversity declining during drying phases (Rees et al. 2006; Portillo et al. 2012; Febria et al. 2012; Timoner et al. 2014; Freixa et al. 2016). Longer drying phases can eliminate sensitive algae species, reducing immediate and long-term biodiversity, as there are fewer species able to recolonize when flow returns (Tornés and Ruhí 2013). The same is true for aquatic macrophytes (Brock and Casanova 1997). For aquatic invertebrate communities, prolonged dry periods can cause diversity to decline as specialist taxa dominate (Datry et al. 2014). Some invertebrates stabilize substrate and prevent erosion, an ecosystem service that may be lost if species are eradicated due to increased drying (Johnson et al. 2009, Vaughn 2018). Prolonged drying can also act as a bottle neck, decreasing genetic diversity (Zickovich and Bohonak 2007). In fishes, prolonged dry periods may temporarily reduce diversity. However, populations that are adapted to frequent droughts may recover relatively quickly following rewetting events (Matthews and Marsh-Matthews 2003).

In climate scenarios where dry periods decreased in length, we observed an increase in the number of dry periods (Figure 1-5). An increase in the number of dry periods indicates more frequent switching between wet and dry status. The effect of the drying and rewetting cycle in nonperennial streams on physicochemical processes is highly variable, which contributes to variability in these processes even throughout reaches of the same watershed (Gómez et al. 2017). As a result, water quality can be highly variable, both spatially and temporally. For example, a rewetting event can transport high concentrations of detritus and nutrients downstream causing rapid changes in water quality (Datry et al. 2014). Flow pulses may then provide nutrients and resources, stimulating primary production and consumers (Corti and Datry 2012; Rosado et al. 2015). An increase in the number of transitions between flow status may alter diversity of invertebrate communities (Bêche et al. 2006). More frequent drying is also consistently associated with reductions in food chain length, typically due to the loss of top predators (Closs and Lake 1994; Sabo et al. 2010; Woodward et al; 2012, McHugh et al. 2015).

Our results indicated that that Upper Blue River Basin will become more fragmented in the future. The increase in fragmentation was especially pronounced in the summer months (June–August). Stream network fragmentation can have especially large impacts on species that require the presence of water for dispersal. For example, dry stream reaches act as barriers to fish movement. Perkin and Gido (2012) showed that reduced species richness of Great Plains fish communities may result from fragmented stream networks. Fragmentation can contribute to spatial shifts in fish communities (Perkin et al. 2015a) and local extirpations throughout the Great Plains (Perkin and Gido 2011). Because fish ecology is driven by source-sink dynamics in nonperennial streams and fragmentation prevents recolonization, increased drying can inhibit the ability of fish communities to recover following disturbance events (Magoulick and Kobza 2003). Timing of drying events can also have implications for ecosystem recovery (Heim et al.

2016). In fragmented systems, fish may no longer be able to migrate to cooler waters during summer months (Schaefer 2001). If drying occurs during spawning periods, spawning habitat may be lost or inaccessible, which may have potential long-term effects on ecosystem structure (Detenbeck et al. 1992). Most riverine fish disperse moderate distances (on the order of 10 km), though some species and individuals can move much further, exceeding 1000 km (Comte and Olden 2018). Individuals that disperse long distances can have a disproportionate impact on populations, as they may be more likely to contribute to reestablishment following disturbances and the maintenance of genetic connectivity (Trakhtenbrot et al. 2005). The Upper Blue River Basin drains an area of approximately 400 km^2. Thus, given the degree of increased fragmentation modeled for the Upper Blue River Basin under future climate scenarios, even species that routinely disperse only short distances may be affected.

Species with minimal dispersal abilities are likely to also be affected by increased fragmentation. Although freshwater mussels themselves are largely sedentary, they rely on host fish for reproduction and dispersal. The Blue River was historically known for its rich mussel assemblages, though they have now been extirpated from much of the river (Vaughn 1997). This decline is likely linked to factors including habitat degradation, flow regime alteration, heat stress, and restricted movement of host fish (Vaughn et al. 2015). Mussel abundance can be directly affected by stream drying (Gough et al. 2012), with secondary stressors, such as high water temperatures and high oxygen demand, also having detrimental impacts (Haag and Warren Jr. 2008).

Our analysis of projected stream drying resulting from future climate scenarios indicates the importance of water management decisions on watershed integrity. Importantly, we observed that small decreases in daily streamflow can drastically reduce connectivity. This suggests that even small alterations of hydrologic regimes can have significant ecological consequences. Water management strategies that aim to incentivize reductions in water usage (Zamani Sabzi et al., 2019) or set targets for environmental flows (Wineland et al. 2021a; Sandoval-Solis et al. 2022) should carefully consider the potential for nonlinear impacts of stream drying. In our study, stream drying is associated solely with climatic changes, and water managers should seek to identify water sustainability strategies that are robust to future climate uncertainty (Wineland et al. 2021b; Fovargue et al. 2021; Farzaneh et al. 2021). Independent of climate, humans can exacerbate drying further via consumptive water use and land use change (Bond et al. 2008; Jung and Kim 2017), raising the potential for hotspots of declining water availability due to groundwater pumping (Perkin et al. 2017) or other societal uses (Guo et al. 2019; Zamani Sabzi et al. 2019a). As decisions are made about watershed management, it is important to be aware that small changes can have big impacts.

Conclusion

In our analysis of the Upper Blue River Basin, drying increased, by some metric, in all climate scenarios. The climate models selected to drive the hydrologic models represent a wide range of temperature and precipitation variability. Of the nine hydrologic models, the RCPs associated with lower carbon emissions were not clearly associated with smaller increases in stream drying, highlighting the complex challenges associated with predicting the impacts of climate change on connectivity. Further, we have shown that relatively small increases in drying can be associated with a significant loss of connectivity. Given that small hydrological alterations can have major cascading effects in nonperennial streams, our work underscores the need for careful consideration of the impacts of water management strategies on connectivity.

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FIGURES

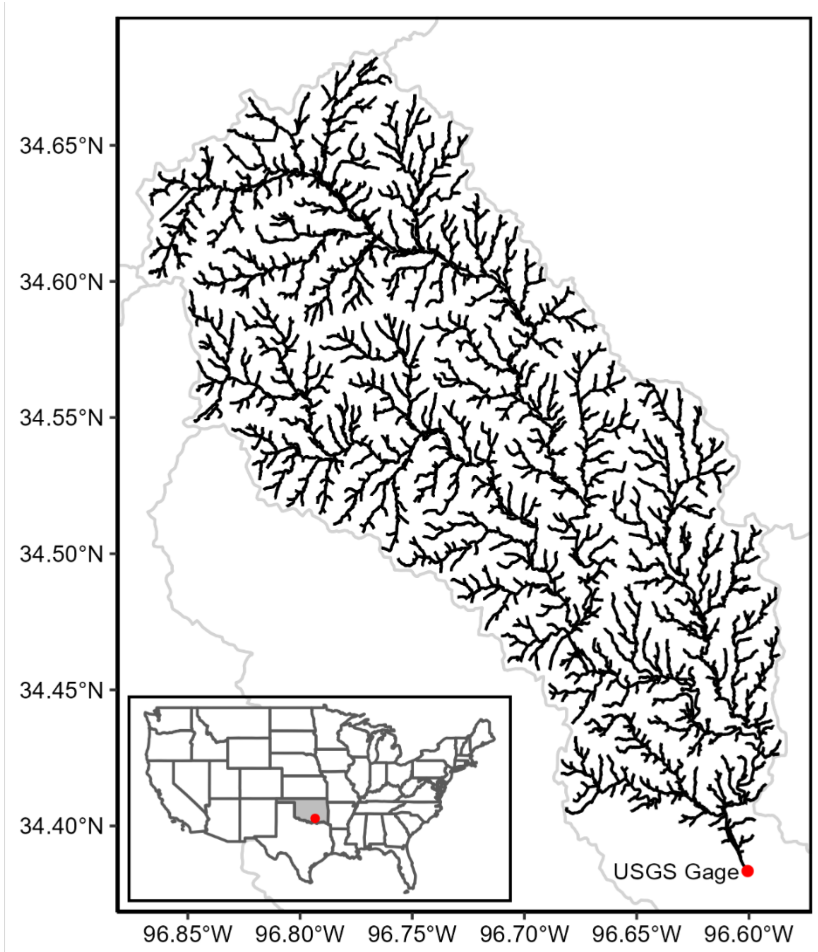

Figure 1-1. The study region of the Upper Blue River Basin in Oklahoma, USA.

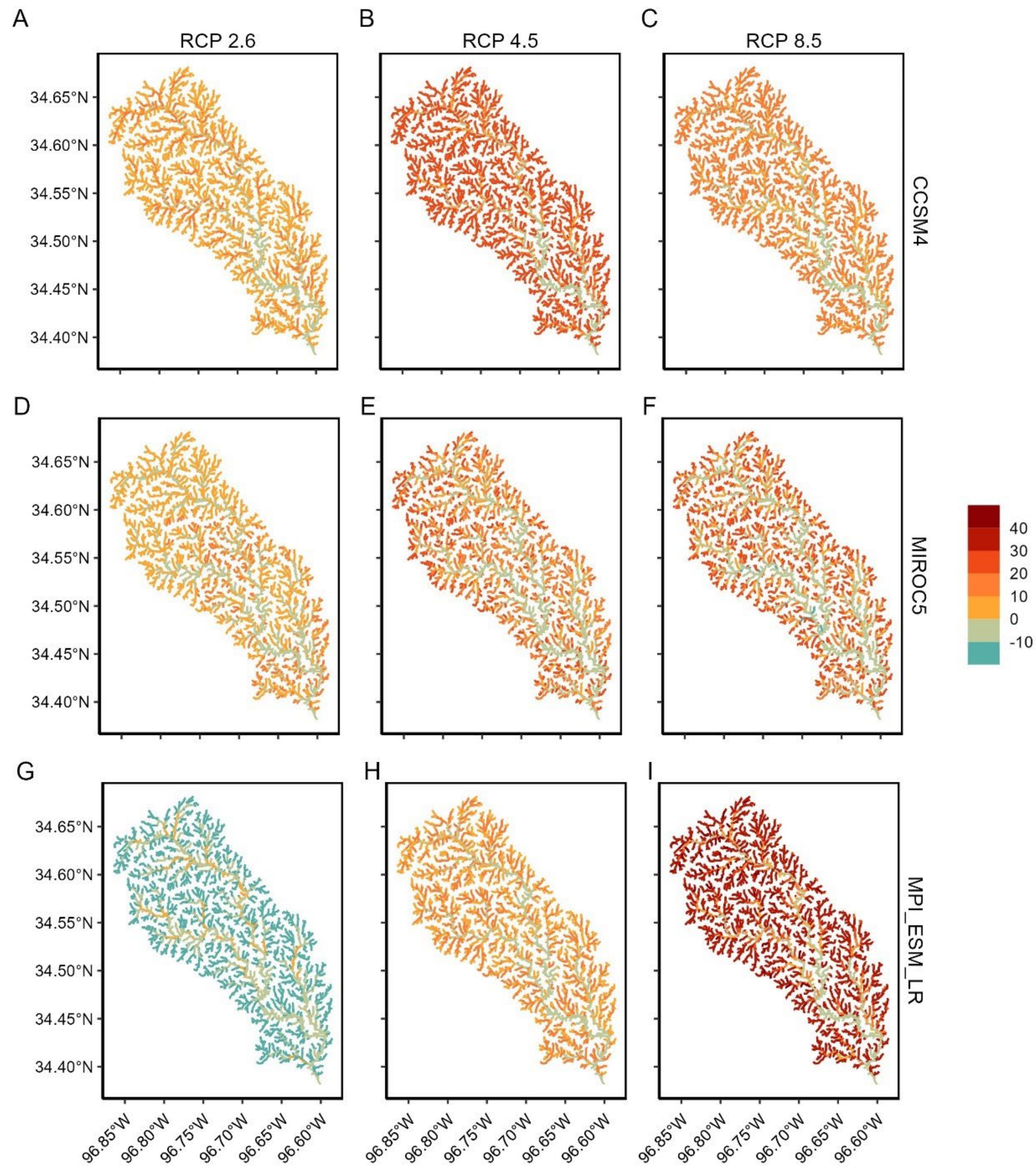

Figure 1-2. Change in the average annual number of dry days from the current (2010-2029) to future (2060-2079) study period for the nine modeled climate scenarios. Values are calculated for each of 2510 stream reaches.

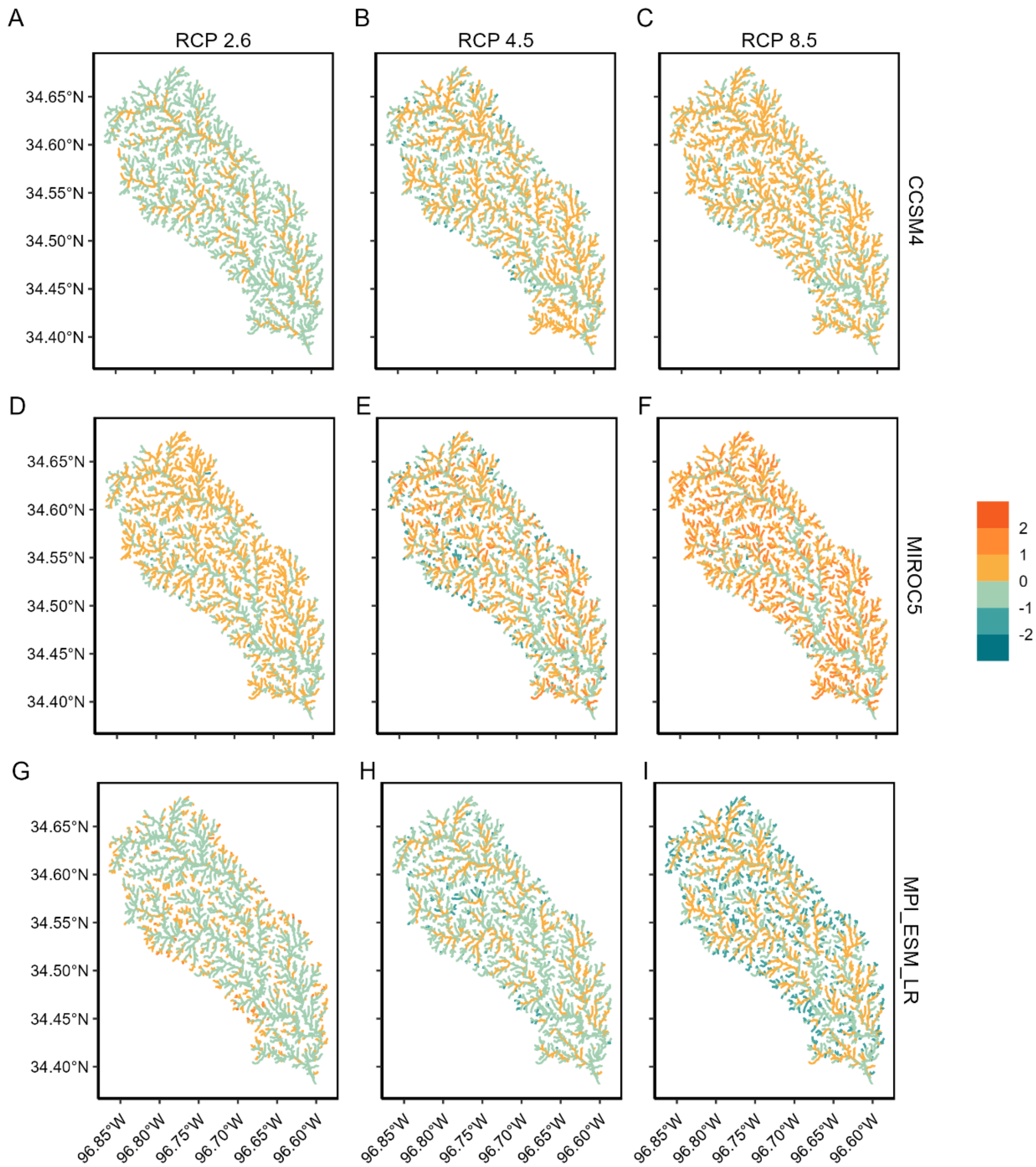

Figure 1-3. Change in the average annual number of dry periods from the current (2010-2029) to future (2060-2079) study period for the nine modeled climate scenarios. Values are calculated for each of 2510 stream reaches.

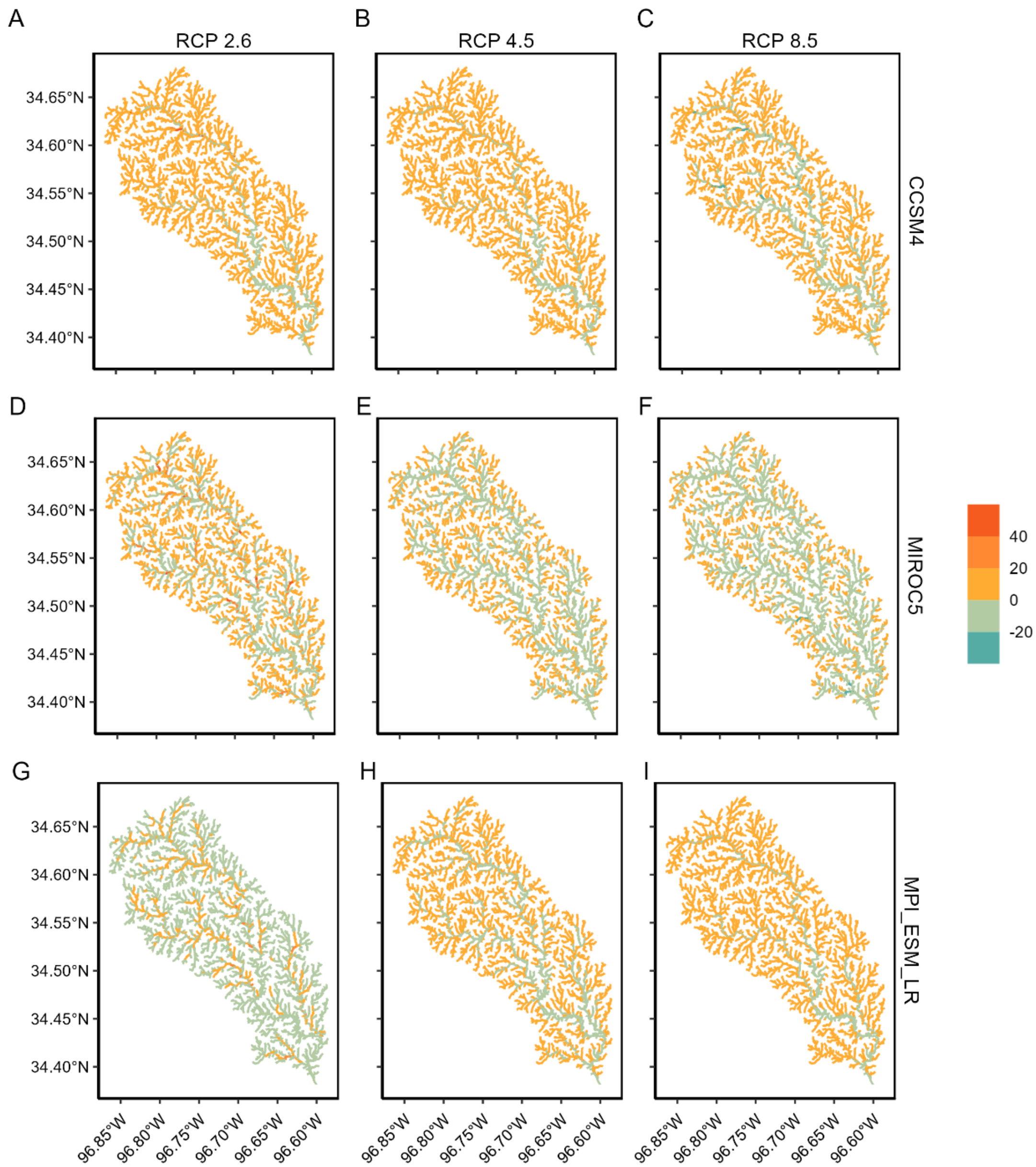

Figure 1-4. Change in the average duration of dry periods from the current (2010-2029) to future (2060-2079) study period for the nine modeled climate scenarios. Duration is measured in number of days. Values are calculated for each of 2510 stream reaches.

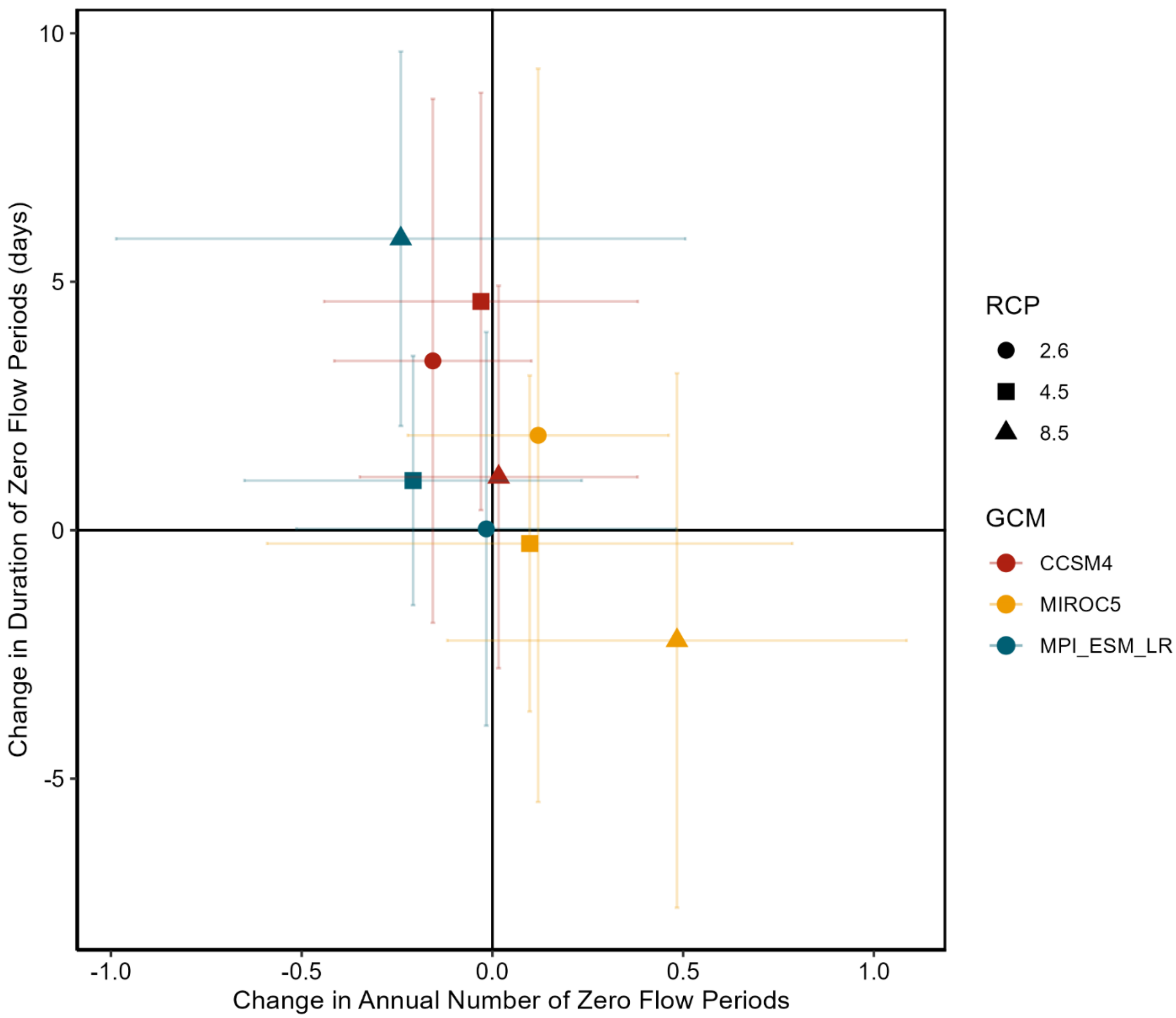

Figure 1-5. Mean and standard deviations of the change in annual number of dry periods and the change in duration of dry periods. Values are calculated as the differences between current (2010-2029) and future (2060-2079) study periods for the nine climate scenarios. Points represent the mean of the 2510 stream reach values shown in Figures 1-3 and 1-4.

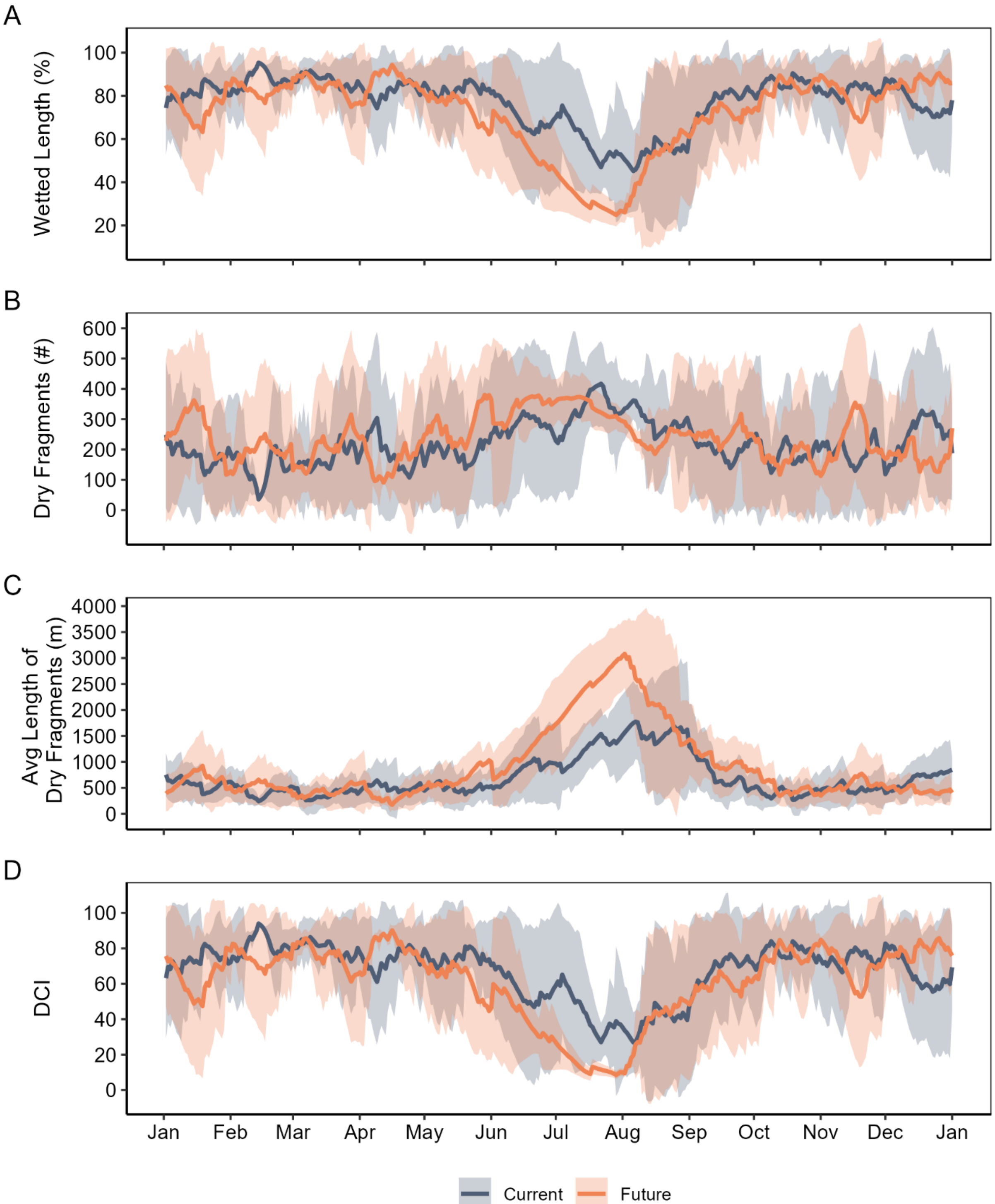

Figure 1-6. Daily percent wetted length (A), number of dry fragments (B), average length of dry fragments (C), and dendritic connectivity index (DCI; D) for current (2010-2029) and future (2060-2079) periods from hydrologic model driven by CCSM4 GCM for RCP 4.5. Plots show mean (line) and IQR (shaded).

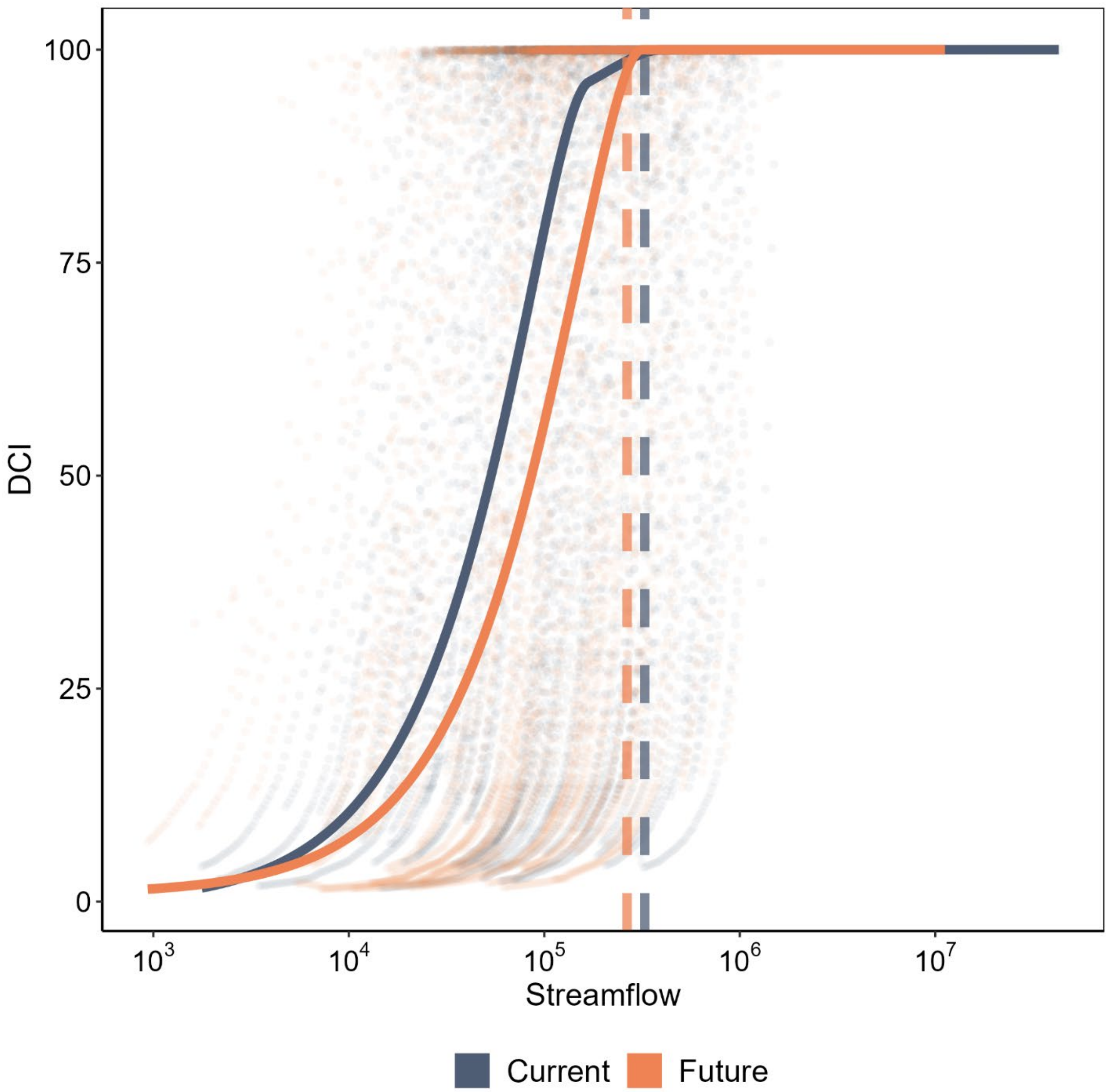

Figure 1-7. Relationship between watershed daily streamflow (m^3/day) and dendritic connectivity index (DCI) for the hydrologic model driven by CCSM4 GCM for RCP 4.5 for current and future study periods. Points represent days and solid lines represent relationship modeled using smoothing splines. Dashed lines represent mean daily streamflow for current and future study periods.

CHAPTER TWO

IMPACTS OF STREAM DRYING DEPEND ON STREAM NETWORK SIZE AND LOCATION OF DRYING

Keywords:

connectivity, ephemeral stream, fragmentation, intermittent river, nonperennial stream, structural property

ABSTRACT

Stream drying is increasing globally, with widespread impacts on stream ecosystems. Here, we investigated how the impacts of drying on stream ecosystem connectivity might depend on stream network size and the location of drying within the stream network. Using eleven stream networks from across the United States, we simulated drying scenarios in which we varied the location and spatial extent of drying. We found that the rate of connectivity loss varied with stream network size, such that larger stream networks lost connectivity more rapidly than smaller stream networks. We also found that the rate of connectivity loss varied with the location of drying. When drying occurred in the mainstem, even small amounts of drying resulted in rapid losses in ecosystem connectivity. When drying occurred in headwater reaches, small amounts of drying had little impact on connectivity. Beyond a certain threshold, however, connectivity declined rapidly with further increases in drying. Given trends in stream drying worldwide, our findings underscore the need for managers to be particularly vigilant about fragmentation when managing at large spatial scales and when stream drying occurs in mainstem reaches.

INTRODUCTION

Stream drying occurs in more than half the world's streams (Messager et al. 2021) and flow intermittency is increasing in many places. Drying duration and extent are increasing in naturally nonperennial streams, while many formerly perennial streams are now becoming intermittent (Larned et al. 2010, Zipper et al. 2021). These changes are due to human impacts on climate, land use (Zipper et al. 2021), and consumption (Datry et al. 2014). The timing and location of stream drying within a stream network can alter habitat fragmentation and connectivity, a key structural property of that network.

Structural properties of stream networks (e.g., network connectivity) can exert strong control on spatial patterns of biodiversity. Stream network properties such as size, complexity, centrality, and drainage density can influence the flow regime (Pallard et al. 2009, Godsey and Kirchner 2014), habitat heterogeneity (Benda et al. 2004), primary production (Istvánovics et al. 2014), movement of organisms (Brown and Swan 2010), and ecosystem services (Helton et al. 2018, Karki et al. 2021). Each of these have direct and indirect impacts on biodiversity patterns (Poff 1997, Compin and Céréghino 2007, Chaput-Bardy et al. 2009, Dias et al. 2013, St. Pierre and Kovalenko 2014, Bernhardt et al. 2018, He et al. 2020). Alteration of these structural properties by stream drying or other disturbances can therefore have strong effects on biodiversity and ecosystem services (Neeson et al. 2011, Perkin et al. 2013).

In nonperennial stream networks, connectivity is an especially consequential structural property. The absence of connectivity (i.e., fragmentation) prevents the movement of matter, energy, and organisms (Boulton et al. 2017). Communities in nonperennial stream networks are frequently subjected to connectivity loss due to drying in stream reaches, which can lead to threats to population persistence (Jaeger et al. 2014), shifts in species richness (Matthews and Robison 1998), and changes in community composition (Perkin and Gido 2012). Structural properties of stream networks can also interact, having ecological consequences. For example, stream network topology mediates how ecological communities respond to connectivity loss. Metacommunity modeling studies have shown that the response of local species richness to connectivity loss depends on whole network topology and the location of connectivity loss (Lee et al. 2022) and that loss of connectivity decreases community recovery following disturbance events (Jacquet et al. 2022).

In nonperennial streams, connectivity is dependent on when and where flow occurs. Flow occurrence reflects external forcings and internal processes (Shanafield et al. 2021). Important external forcings are climate (Poff et al. 1997, Malish et al. 2023), geology (Mayer and Naman 2011), vegetation (Schreiner-McGraw et al. 2020), and human impacts (Smakhtin 2001). Internal processes that can affect connectivity include streamflow generation, stream water loss, and spatio-temporal variability in flow (Shanafield et al. 2021). The variability of where and when flow occurs in nonperennial streams results in networks that differ in spatio-temporal patterns of connectivity. As a result, the spatial location of drying varies widely among watersheds. In some watersheds, drying occurs primarily in the headwaters (e.g. Sagehen Creek, CA, USA; Godsey and Kirchner 2014) and downstream flow is sustained by groundwater inputs (Lake 2003). In other basins, drying occurs in the mainstem. This often is found where headwaters are associated with permanent sources (Jaeger and Olden 2012), where downstream infiltration losses exceed inflows (Datry 2012), or where water loss is driven by human overconsumption throughout the watershed (e.g., the Colorado River and the Rio Grande River, USA).

Here, we investigated how the impacts of stream drying on ecosystem connectivity might depend on stream network size and the location of drying within the network. To do this, we used eleven stream networks of varying size from across the continental United States, and simulated drying scenarios in which we varied the location and spatial extent of drying. We hypothesized that rate of stream network connectivity loss is driven by 1) stream network size and 2) drying location. We expected connectivity to decline more rapidly in smaller stream networks than in larger stream networks because in smaller networks, an individual dry reach makes up a larger proportion of the total stream network. We expected connectivity to decline more rapidly when drying occurs in the mainstem than in the headwaters because mainstem reaches tend to be more centrally located within the watershed. Given wide variation in the observed extent and location of drying among basins, our aim was to better understand when and where stream drying may have the greatest impacts on ecosystem connectivity.

METHODS

Stream networks

Eleven nonperennial stream networks were selected for this study (Figures 2-1 and S2-1). These networks were chosen because they experience stream drying and are minimally impacted by urbanization and dams. We derived the stream networks from 10 m elevation grids using a threshold of drainage accumulation above 0.1 km^2, with reaches delineated on a confluence-to-confluence basis. Because in our models drying occurs at the reach scale, we hypothesized that the number of reaches in the network would be the most relevant measure of network size (e.g., rather than drainage area) for the purposes of our study. The stream networks range in size from 43 to 2510 reaches (Table 2-1).

Drying simulations

We quantified the effects of drying in the stream networks using three simulation experiments (Figure 2-2). In a first experiment, to quantify how the rate of connectivity loss varies with stream network size, we used a Monte Carlo approach to simulate spatially random drying in the stream networks. At the start of each simulation, all stream reaches were classified as wet. We then randomly selected one reach and changed its status to dry. We repeated this process until no wet reaches remained. Network connectivity was calculated at each step. For each stream network, we carried out a total of 99 random drying simulations and reported the mean and variance in network connectivity across these 99 simulations.

To quantify how the rate of connectivity loss varies with the location of drying, we performed two further experiments in which we simulated mainstem-first drying (experiment 2) and headwater-first drying (experiment 3) in the stream network (Figure 2-2). Both the mainstem-first and headwater-first drying scenarios were deterministic. In these two experiments, the order of drying was determined by the Strahler stream order of the reaches and reach length (Figure S2-2). Mainstem-first simulations selected reaches of the highest stream order to dry first. When multiple reaches were of the same stream order, the longest reach of that stream order was selected for drying. Headwater-first simulations represent the opposite of mainstem-first simulations, by selecting reaches of the lowest stream order to dry first and selecting the shortest reach when there were multiple reaches of the same stream order. Reaches were dried one at a time until no wet reaches remained. Network connectivity was calculated at each step. There were n steps in each simulation, where n is the number of stream reaches in a stream network. Because the location-based simulations were deterministic, each simulation was carried out once per stream network.

Reach contributions to connectivity

To aid our interpretation of the drying simulations, we carried out an experiment to determine the contributions of individuals reaches to network connectivity (experiment 4). For each stream network, we iteratively dried each individual stream reach. At each iteration, we calculated network connectivity. This experiment provides information on the magnitude of the decrease in connectivity associated with drying in each individual stream reach.

Connectivity

To measure stream network connectivity, we used a modified version of the dendritic connectivity index (DCI). The DCI was originally developed to measure the impact of point barriers on fish passability (Cote et al. 2009) and is widely used to quantify ecosystem connectivity in river networks (Perkin et al. 2013, Edge et al. 2017, Flecker et al. 2022). In the modified version of the DCI, we consider dry stream reaches to act as physical barriers that block connectivity (Malish et al. 2023). For all stream reaches i and j, DCI was calculated as follows:

$$DCI = \sum_{i=1}^{n}\sum_{j=1}^{n} c_{ij}\frac{l_i}{L}\frac{l_j}{L} * 100$$

where c_{ij} is a Boolean variable that takes the value 1 if reach i is connected to reach j, or 0 if not. Two reaches were considered connected if there was a path between them made entirely of wet reaches. The lengths of stream reaches i and j are identified as l_i and l_j, with L representing the total length of the drainage network. DCI can take values ranging from 100 (in the case of a fully connected network with no dry reaches) to 0.

RESULTS

From the random drying simulation experiment, we found that mean declines in ecosystem connectivity from stream drying were strongly related to river network size, such that the largest networks experienced the greatest losses in connectivity (Figure 2-3). When 5% of the reaches in the network were dry, for example, the mean DCI value for the largest watershed was nine times greater than the mean DCI value for the smallest watershed (Figure 2-3B). Across all watersheds there was a strong negative correlation between DCI and stream network size at this stage of drying (Figure 2-3C; $r = -0.84$, $p = 0.001$). When 15% of the reaches in the network were dry, DCI in the largest watershed was 29 times greater than in the smallest watershed, and a strong negative correlation between DCI and stream network size remained (Figure 2-3C; $r = -0.71$, $p = 0.015$).

While mean declines in connectivity were related to network size, we also found that variability of connectivity loss differed among stream network sizes. Across 99 simulations in which stream drying was spatially random, the range of resulting DCI values for the smallest network was often an order of magnitude larger than the range of DCI values for the largest network (Figure 2-4A). When 5% of the reaches in the network were dry, the range of DCI values for the smallest watershed (DCI between 35.4 and 98.2) was four times greater than the range of DCI values for the largest watershed (DCI between 3.4 and 19.2; Figure 2-4B). Across all watersheds there was a strong negative correlation between variability in DCI and stream network size (Figure 2-4C; $r = -0.88$, $p < 0.001$). When 15% of the reaches in the network were dry, the range of DCI values for the smallest watershed (DCI between 18.1 and 77.6) was 49 times greater than the range of DCI values for the largest watershed (DCI between 0.9 and 2.1; Figure 2-4C), and a strong negative correlation between range of DCI values and stream network size remained ($r = -0.77$, $p = 0.006$).

Comparing the results of headwater-first and mainstem-first drying simulations, we found that the rate of connectivity loss varied with the location of drying, but this effect was modulated by network size for mainstem-first drying (Figure 2-5). Connectivity declined relatively slowly when drying was concentrated in the headwaters (Figure 2-5A), and more rapidly when drying was concentrated in mainstem reaches (Figure 2-5B). In the headwater-first simulations, there was no clear relationship between rate of connectivity loss and stream network size. In the mainstem-first simulations, larger stream networks tended to lose connectivity at a more rapid rate than smaller stream networks (Figure 2-5C). When 5% of the reaches in the network were dry, for example, DCI values were two times greater for headwater-first drying than mainstem-first drying in the smallest watershed, and 19 times greater in the largest watershed. When 15% of reaches were dry, DCI values for headwater-first drying were nine times greater than mainstem-first drying for the smallest watershed, and 118 times greater in the largest watershed.

The impact of individual stream reaches on connectivity loss varied with network size (Figure 2-6). In smaller stream networks, a greater proportion of reaches were moderately impactful or highly impactful on connectivity loss. Moderate impact reaches resulted in DCI values between 80 and 95 when dried, while high impact reaches resulted in DCI values less than 80 when dried. The minimum DCI resulting from the drying of a single stream reach ranged from 48.23 in the smallest stream network to 51.15 in the largest stream network. The maximum DCI resulting from the drying of a single stream reach ranged from 99.4 in the smallest stream network to 100.0 in the largest stream network.

DISCUSSION

Here we demonstrate how, in nonperennial streams, connectivity is influenced by the spatial patterning of wet and dry reaches – an important structural property of the stream network itself. This adds to established knowledge that stream network connectivity is influenced by processes and forcings that take place across multiple spatial scales (Jencso et al. 2009, Fullerton et al. 2010). Our simulation-based experiments reveal that rate of connectivity loss is driven by interactions between stream network size and the location of stream drying within the stream network. Given increases in stream drying globally, our results underscore the need for managers to be vigilant about increased stream drying in networks where it is likely to have the greatest impacts on fragmentation.

Connectivity and network size

We first hypothesized that rate of connectivity loss is driven by stream network size. We expected that connectivity would decline more rapidly in smaller stream networks than in larger stream networks, but found the opposite. Our simulations illustrate how larger stream networks tend to be less connected than smaller stream networks at equivalent stages of drying (Figures 2-3 and 2-5). While the drying simulation experiments showed that larger stream networks tend to lose connectivity more rapidly than smaller stream networks, the drying experiment examining impacts of individual stream reaches showed that the drying of a single stream reach is likely to reduce connectivity much more in smaller stream networks than in larger stream networks (Figure 2-6). We attributed the findings of the experiment examining impacts of individual stream reaches to the fact that in smaller stream networks, a single stream reach is likely to be a larger proportion of total stream length in the network. Our measurement of connectivity is weighted so that longer stream reaches have a greater impact on connectivity. As a result, drying of longer stream reaches has a larger impact on connectivity loss than the drying of a smaller but equivalently located stream reach. With this information, we attributed the rapid connectivity loss in larger stream networks to greater potential for fragmentation compared to smaller stream networks. To reach equivalent stages of drying, there will be more dry stream reaches in a larger stream network than in a smaller stream network. Increased dry stream reaches, especially when those dry reaches are not contiguous, are likely to be associated with a more fragmented stream network. While drying in a single reach in a larger stream network may have a minimal impact on connectivity (Figure 2-6), in the larger networks, progressive drying and fragmentation leads to disproportionate declines in connectivity.

The random drying simulations showed that variability in the rate of connectivity loss also varied with stream network size. Smaller stream networks had more variability in the rate of connectivity loss than larger stream networks (Figure 2-4). We again attributed this to the fact that there is likely to be more fragmentation in larger stream networks, resulting in consistent, rapid losses of connectivity. When multiple reaches dry randomly, the dry reaches are less likely to be adjacent in larger stream networks. As a result, larger stream networks are likely to be more fragmented more consistently, resulting in less variability in the rate of connectivity loss. While it is possible for random drying simulations to result in high fragmentation in smaller stream networks, there is a greater probability for dry reaches to be adjacent in smaller stream networks than in larger stream networks. This leads to the observed greater variability in the rate of connectivity loss in smaller stream networks.

The relationship we have found between connectivity and network size points to the importance of considering scale when conducting research on stream network connectivity. One goal of landscape ecology is to identify scales that best characterize relationships between spatial heterogeneity and the processes or response variables of interest (Turner and Gardner 2015). When attempting to connect network patterns to an ecological process, it’s important to consider the scale, or more specifically the spatial extent, at which the ecological process works (Heino et al. 2015). For example, when conducting a study examining the impacts of connectivity loss on a population with low dispersal ability, a spatial extent should be chosen that is relevant to that population (Alp et al. 2012). In some cases, this could mean carrying out simulations over multiple spatial extents in order to determine which best explains observed patterns.

Connectivity and location of drying

We hypothesized that the rate of connectivity loss is driven by the location of drying, with greater losses in connectivity associated with mainstem-first drying than headwater-first drying. Our study supported this hypothesis. Where drying occurs within a stream network greatly influenced the effect of drying on network connectivity (Figure 2-4). Above we explained the important relationship between fragmentation and connectivity. The findings of our location-based drying experiments show how impactful the role of fragmentation can be. No fragmentation occurred during the headwater first drying scenario, meaning that all wet reaches were always neighboring one another. In this scenario, disproportionately high connectivity was maintained until approximately 30 percent of reaches were dried. After this point, connectivity was rapidly lost. Conversely, when mainstem reaches dried first, a scenario with relatively high fragmentation, connectivity was immediately lost rapidly. Connectivity values were halved before 10 percent of reaches were dried in the stream networks.

The point at which connectivity was rapidly lost for the headwater first drying experiments is indicative of a threshold (Groffman et al. 2006). Similar thresholds have been observed in actual stream networks (Ward et al. 2018, Malish et al. 2023) and in other connectivity loss simulations (Lee et al. 2022). With roots in percolation theory (Stauffer and Aharony 2018), significant research effort has established that in terrestrial landscapes a critical threshold exists where small changes in habitat type result in sudden changes in landscape properties. The hierarchical stream network structure differs from the typical grid-based landscape structure in many landscape ecology studies. Despite this difference, a threshold was still identified. It is noteworthy that a threshold was identified in the headwater first drying simulations, but not the mainstem first or random drying simulations. Where drying occurs can have vastly different impacts on connectivity and biodiversity (Crabot et al. 2020, Lee et al. 2022).

Classification of spatial patterns of drying have been used to better understand ecological effects (Lake 2003, Datry et al. 2016, Sánchez-Montoya et al. 2018). When headwaters dry, refugia for aquatic organisms exist downstream. Drying of the headwaters is consistent with a pattern of network expansion and contraction. In cases of network expansion and contraction, fragmentation is minimal. When mainstem drying occurs, the headwaters serve as refugia for biota (Cooling and Boulton 1993). As a result of drying in the mainstem, the network becomes fragmented, resulting in highly variable communities (Erman and Erman 1995) and reduced gene flow (Schanke et al. 2017). While both fragmentation and contraction result in reduced habitat, the effects on connectivity are different. Our findings help to demonstrate why ecological consequences of drying vary according to spatial patterns of drying.

Management implications

As stream drying increases globally (Sauquet et al. 2021, Zipper et al. 2021), management concerns about associated habitat loss and connectivity loss will become more prevalent. Our findings demonstrate that managers should not only be concerned with the extent of drying, but also the location of drying. Due to variations in hydrology, geology, and human impacts, drying can occur in different parts of the stream network (Boulton et al. 2017). For example, mainstem drying is common in watersheds where headwaters are located in mountain ranges or mesic uplands and then flow into more arid areas, or where streams flow over highly permeable geologic formations (Meyer and Meyer 2000, Jaeger and Olden 2012). Headwater drying is common where downstream reaches are sustained by groundwater inputs (Lake 2003). Spatial patterns of drying control the degree of fragmentation that is associated with stream drying. Drying in the headwaters creates patterns of network contraction and expansion through time. Patterns of network contraction and expansion mean that wet reaches of the network are generally connected to one another, and therefore fragmentation is not a major concern. Instead, habitat loss should be the major concern for watershed managers. Mainstem drying, in contrast, can result in high degrees of fragmentation and connectivity loss. As a result, consequences of fragmentation should be the primary concern in these systems.

Additionally, when managing for specific taxa, managers must carefully consider the spatial scales that are most relevant. Populations that are characterized by high dispersal abilities should be managed from the perspective of a larger spatial scale. At larger spatial scales, addressing the effects of fragmentation is likely to be a primary concern. In contrast, populations characterized by low dispersal abilities may be best managed at a smaller spatial scale. At smaller scales, populations are more likely to be affected by habitat loss and management actions to create or restore habitats is likely to be high priority. Differentiating between fragmentation and habitat loss as consequences of stream drying, as well as identifying the scenarios where each is likely to be of primary concern, is key for managing nonperennial streams.

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TABLES

Table 2-1. Stream networks included in the study.

Stream Network	State	Reaches (*n*)
Shane Creek	Kansas	43
Teakettle Creek	California	44
East Turkey Creek	Arizona	239
Deer Creek	California	415
Cave Creek	Arizona	703
South Sandy Creek	Alabama	797
Chalone Creek	California	1310
Passage Creek	Virginia	1428
McDowell Creek	Kansas	1462
Sycamore Creek	Arizona	2247
Blue River	Oklahoma	2510

FIGURES

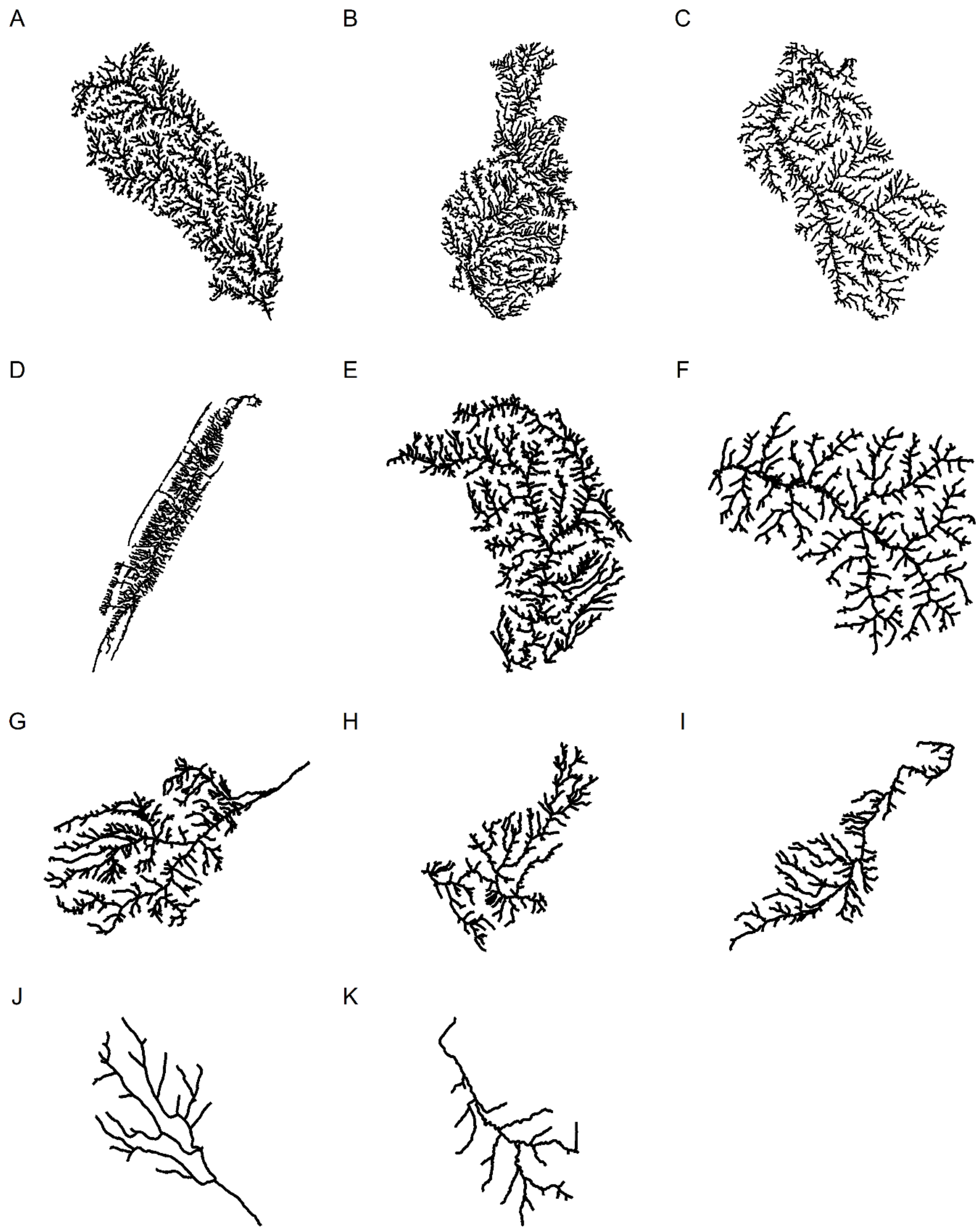

Figure 2-1. Maps of stream networks included in the study, ordered from largest to smallest. (A) Blue River, OK; (B) Sycamore Creek, AZ; (C) McDowell Creek, KS; (D) Passage Creek, VA; (E) Chalone Creek, CA; (F) South Sandy Creek, AL; (G) Cave Creek, AZ; (H) Deer Creek, CA; (I) East Turkey Creek, AZ; (J) Teakettle Creek, CA; (K) Shane Creek, KS.

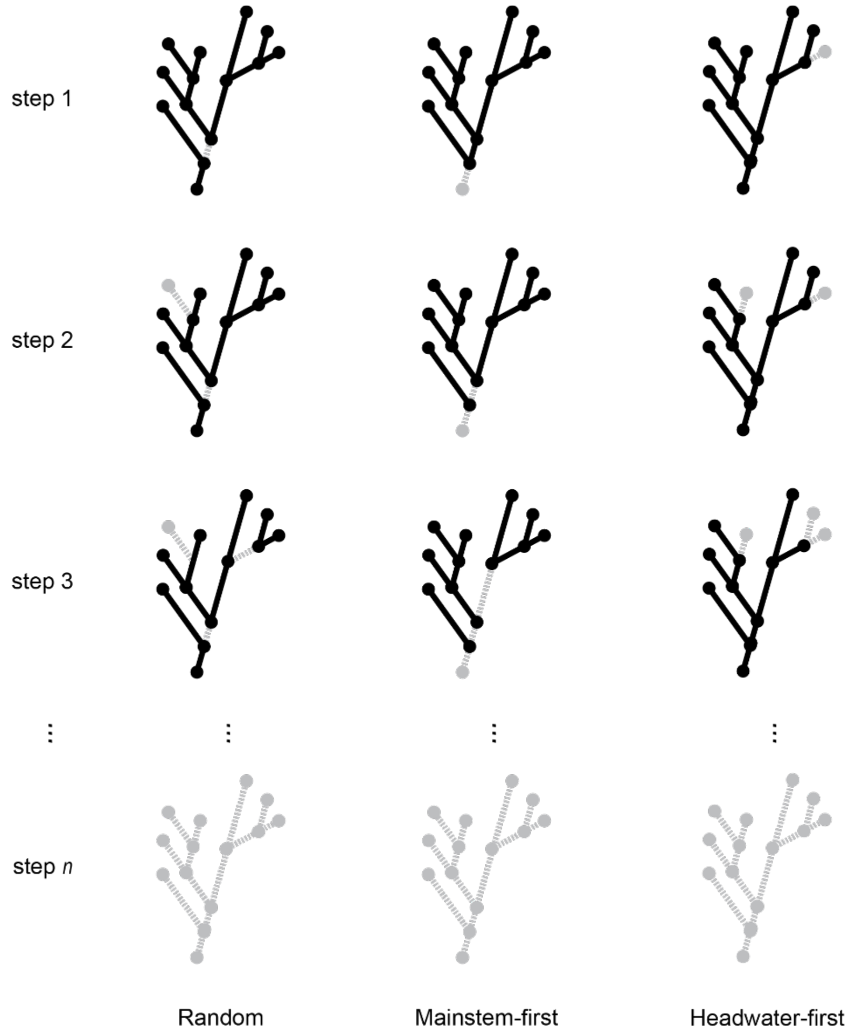

Figure 2-2. Conceptual figure of random, mainstem-first, and headwater-first drying simulations in a stream network. Wet stream reaches are represented by solid black lines and dry stream reaches are represented by dashed gray lines. Reaches were selected randomly at each step during the random drying simulations. Mainstem-first simulations dried reaches of the highest stream order first and selected the longest stream reach when there were multiple reaches of the same stream order. Headwater-first simulations dried reaches of the lowest stream order first and selected the shortest stream reach when there were multiple reaches of the same stream order. For all simulations, reaches were dried one at a time until there were no more wet reaches in the network. There were *n* steps in each simulation, where *n* is the number of stream reaches in a stream network. Connectivity was calculated at each step.

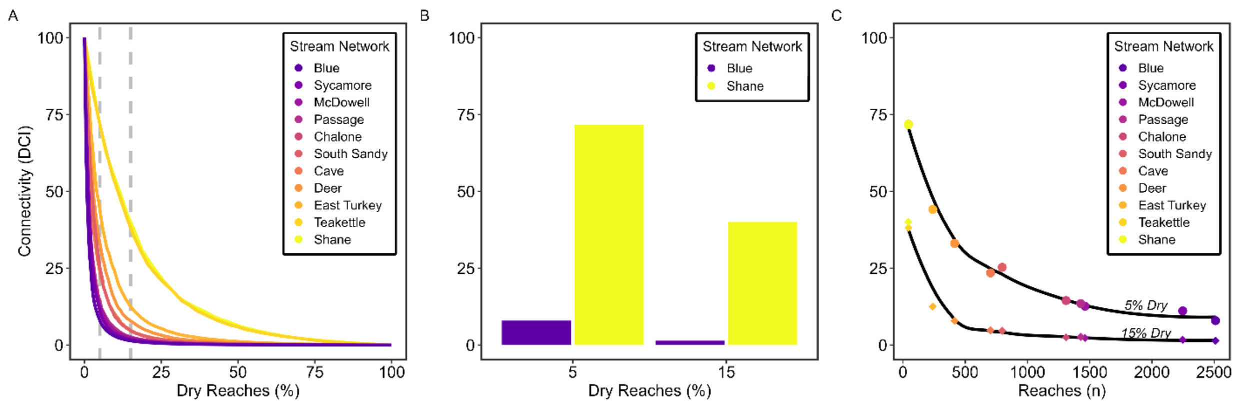

Figure 2-3. Connectivity loss associated with stream drying varied with stream network size. (A) Results of random drying simulations. Lines show mean values of random drying simulations (*n* = 99) for the eleven stream networks. Dashed gray lines indicate percent dry reaches represented in panels B and C. (B) Differences in connectivity between the largest (Blue River) and smallest (Shane Creek) stream networks at 5% and 15% reaches dry. (C) Relationship between stream network size and connectivity at 5% and 15% reaches dry. Circles represent 5% drying and diamonds represent 15% drying. Lines are locally weighted regressions fit to data points. In all panels, colors indicate the size of the stream network with darker colors representing larger stream networks.

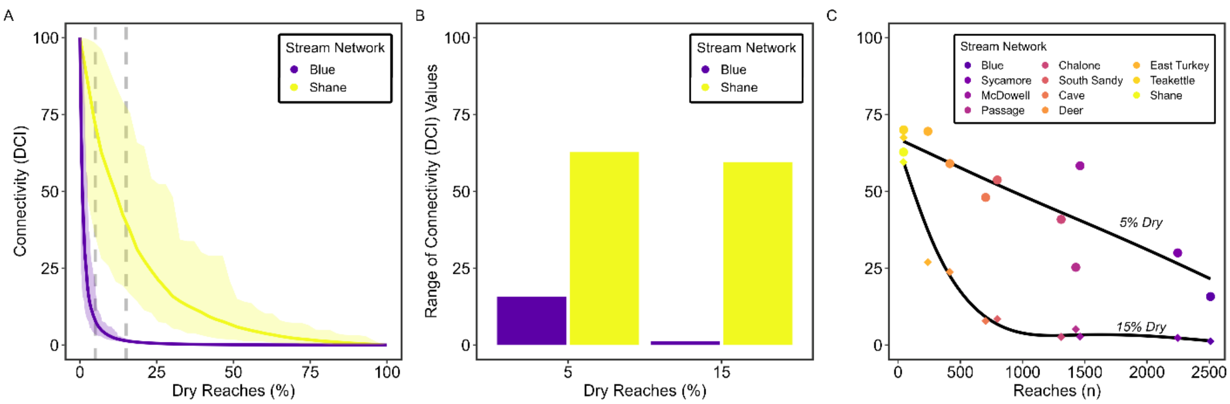

Figure 2-4. Variability of connectivity loss associated with stream drying varied with stream network size. (A) Lines show mean values of random drying simulations (n = 99) for the largest (Blue River) and smallest (Shane Creek) stream networks. Shaded regions show the area between the maximum and minimum connectivity values of random drying simulations for each stream network. Dashed gray lines indicate percent dry reaches represented in panels B and C. (B) Differences in range of connectivity between the largest and smallest stream networks at 5% and 15% reaches dry. (C) Relationship between stream network size and range of connectivity at 5% and 15% reaches dry. Circles represent 5% drying and diamonds represent 15% drying. Lines are locally weighted regressions fit to data points. In all panels, colors indicate the size of the stream network with darker colors representing larger stream networks.

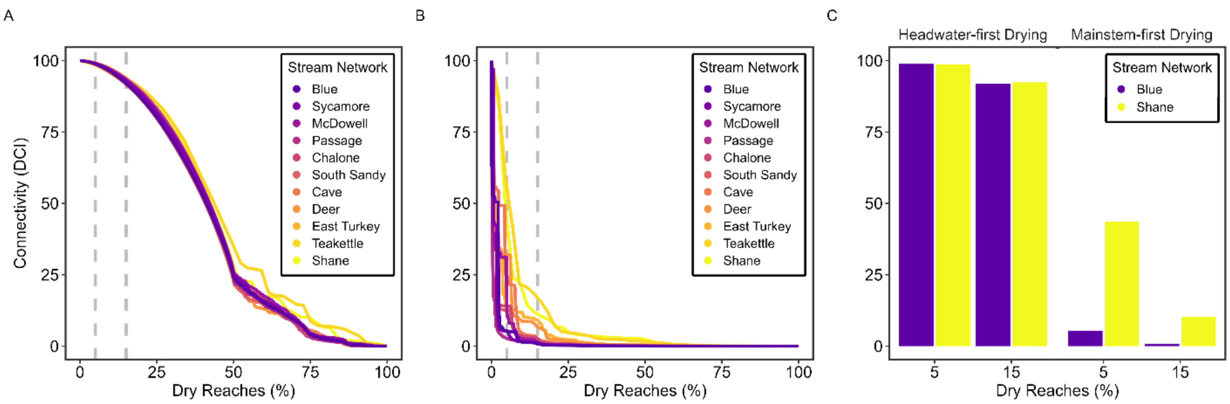

Figure 2-5. Connectivity loss varies with drying location. (A) Connectivity loss associated with headwater-first drying experiments. Dashed gray lines indicate percent dry reaches represented in panel C. (B) Connectivity loss associated with mainstem-first drying experiments. Dashed gray lines indicate percent dry reaches represented in panel C. (C) Differences in connectivity loss between the largest and smallest stream networks at 5% and 15% reaches dry for headwater-first and mainstem first drying experiments. In all plots, colors indicate the size of the stream network with darker colors representing larger stream networks.

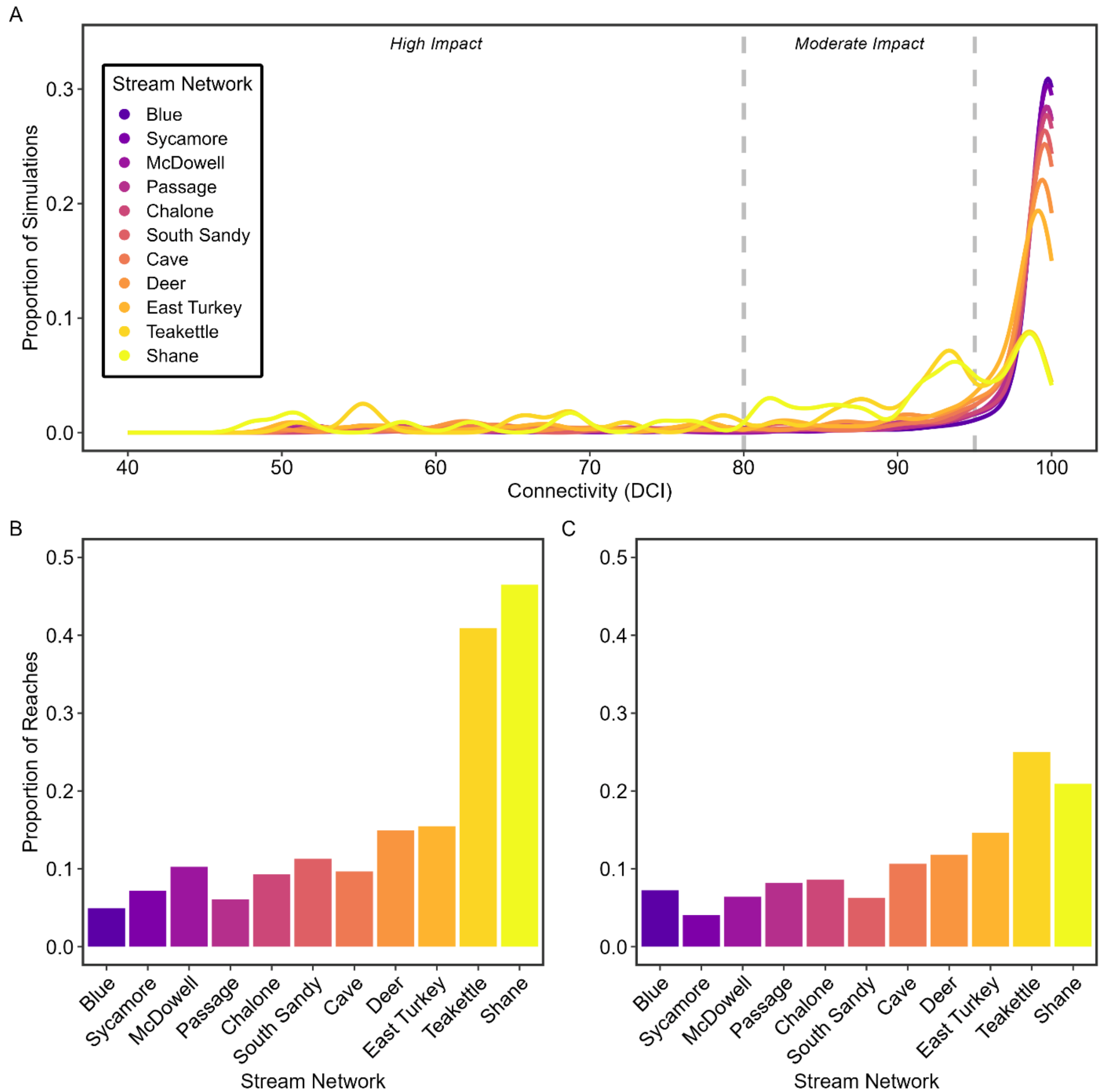

Figure 2-6. (A) Distribution of connectivity values resulting from the experiment where each stream reach within a network was iteratively dried. Gray dashed lines delineate moderate impact and high impact reaches. Moderate impact reaches resulted in connectivity values between 80 and 95 when dried, while high impact reaches resulted in values less than 80 when dried. (B) Proportion of reaches in each stream network found to have a moderate impact and (C) high impact. In all plots, colors represent the size of the stream network with darker colors representing larger stream networks.

CHAPTER THREE

DRY GETS WETTER, WET GETS DRIER: COUNTERINTUITIVE CHANGES IN STREAM DRYING DRIVEN BY CROSS-SCALE INTERACTIONS BETWEEN REGIONAL AND GLOBAL HYDROLOGIC PROCESSES

Keywords:

aridity, connectivity, climate, cross-scale interactions, fragmentation, intermittent river

ABSTRACT

Nonperennial streams are globally widespread and increasingly common. In many river basins, the spatial and temporal patterning of stream drying emerges from cross-scale interactions among local, regional and global hydrologic processes. Here, we evaluated how changes in streamflow and river network connectivity might be influenced by interactions between global-scale climate change and regional aridity. We modeled streamflow in stream networks across the continental United States for current and future climate scenarios to investigate how drivers of connectivity across spatial scales interact. We found that while nine of eleven stream networks had increased flow in the future, only four stream networks showed increased network connectivity. A prominent narrative states that, in general, wet regions will get wetter while dry regions will get drier due to climate change. By extension, it is often assumed that stream networks in wet regions will become more connected, those in dry regions will become less connected. Our results indicated the opposite. Changes in the number of days annually that the stream networks were very highly or very poorly connected varied with aridity. However, more arid networks tended to have more high connectivity days in the future while more mesic networks tended to have more low connectivity days in the future. Our findings overall highlight how cross-scale interactions between climate change and aridity drove predictable changes in network connectivity. The ability to predict future changes in connectivity improves our ability to anticipate the consequences of climate change and manage ecosystems in a changing world.

INTRODUCTION

Nonperennial streams (i.e., those that cease to flow at some point in time and space) are widespread and abundant. These streams occur on all continents and all ecoregions, together composing more than half of the world's streams (Busch et al. 2020, Messager et al. 2021). Where and when streams dry has important consequences for humans and ecosystems. Streams sustain agricultural and domestic water supply and provide a wide range of ecosystem services (Koundouri et al. 2017). Streamflow is also essential for ecological function. In particular, ecological connectivity, or the ability for organisms, nutrients, and matter to move throughout a network, is determined by the timing and magnitude of flow throughout the river network (Shanafield et al. 2021).

Spatial and temporal patterns of stream intermittency are the result of interactions among a suite of local, regional, and global hydrologic processes (Costigan et al. 2016). In the continental United States, changes in flow intermittency are already occurring due to global-scale climate change. General trends indicate increased duration of drying in nonperennial streams during the past several decades (Zipper et al. 2021). At the regional scale, aridity is recognized as a strong predictor of stream intermittency, explaining flow permanence and timing (Jaeger et al. 2019, Hammond et al. 2021). At more local scales, geology, geomorphology, and human impacts, such as water withdrawal, can be important drivers of stream drying (Palmer et al. 2008, Perkin et al. 2015a, Hammond et al. 2021). Spatial and temporal patterns of flow intermittency interact to drive patterns of network connectivity (Jaeger et al. 2014, Malish et al. 2023).

Given that patterns of stream drying emerge from cross-scale interactions among local, regional, and global processes, conceptual frameworks from macrosystems ecology may be useful for understanding drivers of network connectivity. Riverine macrosystems are defined as hierarchical dynamic networks, influenced by strong directional connectivity that integrates processes across multiple scales and broad distances through time (McCluney et al. 2014). Macrosystems have cross-scale interactions that determine ecological properties, like connectivity. Cross-scale interactions occur when processes at one scale interact with processes at another scale, sometimes having non-linear responses (Heffernan et al. 2014, Soranno et al. 2014). Understanding relationships that exist across spatial scales is necessary to predict likely outcomes and determine management strategies to address complex environmental problems (Miller et al. 2004, Soranno et al. 2014).

One such complex environmental problem is predicting how stream drying patterns might change in the future. Climatological studies often find a “rich get richer” pattern in global moisture trends, in which wet locations are projected to become more wet in the future, and dry locations are projected to become drier (Held and Soden 2006, Chou et al. 2009, Durack et al. 2012). However, other studies have found that this pattern is inconsistent, particularly over land (Greve et al. 2014, Feng and Zhang 2015). In the case of stream drying, hydrologic processes unrelated to global climate (e.g., local geology, land use, and human water consumption) may, in some places, further counteract global “rich get richer” trends in moisture. Thus, a key research challenge is to understand how cross-scale interactions among global climate and local hydrology might drive spatiotemporal patterns of stream drying across a river network.

The purpose of this study was to investigate how drivers of network connectivity that act at multiple spatial scales interact in nonperennial stream networks. Specifically, we asked: (1) How do changes in climate impact streamflow and network connectivity?, and (2) Do changes in streamflow and network connectivity vary predictably with watershed aridity and match the “rich get richer” paradigm? We answered these questions using a hydrological modeling approach in which we simulate daily streamflow in stream networks that span the continental United States under current and future climate simulations. We used these models to explore changes in watershed daily discharge and connectivity, as well as the relationship between the two. We also used linear models to explore changes in the number of very high and very low connectivity days during each climate simulation in relation to watershed aridity. The ability to reliably predict future connectivity is important for the management of ecologically and societally important stream networks in a changing climate.

METHODS

Study watersheds

We focused on eleven stream networks from the southern half of the continental United States (Figure 3-1). Distinct spatial patterns of changes in stream intermittency in the US have been identified, with the southern US experiencing widespread increases in stream drying (Zipper et al. 2021). Stream drying occurs in each of the watersheds to varying degrees. The study networks were selected to span the continental aridity gradient across the southern US while being minimally impacted by anthropogenic influences such as dams and urbanization. Watershed aridity, defined here as mean annual precipitation divided by mean annual reference ET, ranged from 2349 for Sycamore Creek, AZ to 9737 for South Sandy Creek, AL (Trabucco and Zomer 2019).

Hydrologic modeling

We used the Couple Routing and Excess Storage (CREST) model for hydrologic modeling. CREST is a distributed hydrologic model that simulates surface and subsurface flow (Wang et al. 2011). Calibration and validation focused on capturing the low flow condition and stream intermittency in numerous small headwater streams using data collected by in situ loggers (Chapin et al. 2014) and USGS stream gages. As a result, we have shown this model to be capable of estimating daily water occurrence at various stream orders in the study watersheds in prior studies (Gao et al. 2021, Malish et al. 2023).

Model outputs were simulated at a 10 m grid spatial resolution at a daily timestep. Using 10 m elevation grids, we delineated stream reaches on a confluence-to-confluence basis. Streamflow grids were spatially averaged over each reach to calculate mean daily flow. We then converted the daily streamflow to a binary wet or dry status.

Hydrologic models were created for current and future climate simulations. Models were forced with climate data resulting from two 13-year Weather Research and Forecasting model simulations which used 4-km grid spacing over CONUS (Liu et al. 2017). The spatial extent of the simulations allows for comparisons of the study watersheds. The current climate simulation runs from October 1, 2001 to September 30, 2012 and is forced with ERA-Interim reanalysis data (Dee et al. 2011), which combined modeled data and observational data to provide a complete and consistent climate dataset. The future climate simulation spans the same time period and is forced with the ERA-Interim reanalysis data plus a climate perturbation, which represents 'pseudo global warming'. The climate perturbation is the 95-year CMIP5 multi-model ensemble mean change signal under the RCP8.5 emission scenario, corresponding to an approximately 3-6 °C warming signal. The use of ensembles reduce biases introduced by individual models. The use of these climate models allows for direct comparisons of the current and future climate simulations that are not influenced by natural climate variations (Liu et al. 2017).

Measuring discharge and connectivity

To understand the impacts of climate change, we measured watershed discharge and connectivity. Watershed discharge was quantified as streamflow at the outlet of the watershed. To measure connectivity, we used a modified version of the dendritic connectivity index (DCI). The DCI was originally developed to measure the impact of point barriers (e.g., road culverts and dams) on fish passability (Cote et al. 2009). We used a modified version of the original formulation in which we considered dry stream reaches to be barriers. For all stream reaches i and j, DCI was calculated as:

$$DCI = \sum_{i=1}^{n}\sum_{j=1}^{n} c_{ij}\frac{l_i}{L}\frac{l_j}{L} * 100$$

where c_{ij} is a Boolean variable that takes the value 1 if reach i is connected to reach j, or 0 if not. Two reaches were considered connected if there was a path between the two made entirely of wet reaches. The lengths of stream reaches i and j are identified as l_i and l_j, with L representing the total length of the drainage network. DCI ranges from 0-100 where 0 represents a completely dry stream network and 100 represents a completely wet, and therefore completely connected, stream network. We calculated discharge and DCI at a daily timestep for both climate simulations in the 11 study watersheds (Malish et al. 2023).

Analysis

We visualized effects of climate on discharge and connectivity using exceedance probability curves and histograms. We also examined the relationship between discharge and connectivity, which tends to be sigmoidal (Malish et al. 2023). For each river network, there exists a low discharge threshold below which the river network is maximally fragmented and DCI is always 0. Similarly, for each river network there exists a high discharge threshold above which the river network is maximally connected and DCI is always 100. How rapidly networks transition from states of high connectivity to states of low connectivity is an indicator of the stability of connectivity in the network (Malish et al. 2023).

To quantify the stability of connectivity, we used piecewise linear regression to model the relationship between log transformed daily discharge and DCI. Using this method, we identified two breakpoints (i.e., the low and high discharge thresholds) in the relationship between discharge and connectivity in each river network. The two break points resulted in three line segments: a horizontal line of best fit below the low discharge threshold, a line with positive slope between the two thresholds, and a horizontal line above the high discharge threshold. We fit models for every stream network and each climate simulation. For each model, the first and third regression lines were constrained with zero slope and y-intercepts equal to the minimum or maximum DCI value, respectively. These constraints reflect the data showing that above and below certain discharge values, connectivity does not change. With these constraints, we used the slope of the second line as a measure of how changes in discharge influence changes in connectivity. Models were fit using the R package 'optimx' (Nash and Varadhan 2011). We then used linear regressions to model the relationships between aridity and slope for each climate simulation, as well as between aridity and change in slope from the current to future climate simulation.

Finally, we were interested in frequency distributions of daily DCI values in relation to climate simulation and aridity. We focused on high connectivity days (DCI > 80, DCI > 95) and low connectivity days (DCI < 5, DCI < 20), because extremes in connectivity are ecologically important. Low connectivity days represent high amounts of drying and fragmentation. High connectivity days provide potential opportunities for recovery following low connectivity days. We calculated the percent change in the number of high and low connectivity days per year and examined those changes in relation to aridity using linear models.

All analyses were completed in R (R Core Team 2023).

RESULTS

We found that climate change caused a projected increase in mean annual discharge in 9 of 11 stream networks in our study (Figure 3-2A). Increases in discharge were largely driven by increases in the frequency and magnitude of extreme high and low flow events (Figure 3-3). A clear example of this is Shane Creek, where much of the current and future climate simulation discharge exceedance probability curves are similar, but maximum discharge was greater in the future climate (Figure 3-3H). Similar patterns were observed in McDowell Creek (Figure 3-3G), Passage Creek (Figure 3-3I), and South Sandy Creek (Figure 3-3J). In Teakettle Creek, where mean discharge was projected to decrease, the future climate simulation again showed an increase in maximum discharge, but reduced flows for the majority of the simulation (Figure 3-3F).

Although most watersheds are projected to become wetter in the future when considering mean discharge, projected changes in mean river network connectivity were less consistent. Indeed, mean DCI increased in only 4 watersheds (Figure 3-2B). In East Turkey, Cave, Blue, Passage, and South Sandy watersheds, mean DCI is projected to decrease despite a projected increase in mean discharge. Changes in connectivity were largely driven by days with very high and very low connectivity (Figure 3-4). In networks where connectivity increased in the future simulation, we either observed an increased maximum DCI value such as in Sycamore Creek where the maximum DCI value increased from 63 during the current climate simulation to 85 during the future climate simulation (Figure 3-4A), or an increase in the number of very high connectivity days (i.e. McDowell Creek, Shane Creek watersheds; Figures 3-4G, 3-4H). In networks where connectivity decreased in the future simulation, we observed more low connectivity days (Cave Creek; Figure 3-4D), fewer high connectivity days (Deer Creek, Teakettle Creek; Figures 3-4E, 3-4F), or both (South Sandy Creek, Figure 3-4K).

Within each river network, the relationship between daily discharge and DCI was highly nonlinear and exhibited two thresholds (Figure 3-5A). Changes to connectivity also include a loss of stability around thresholds, where a small change in stream drying results in rapid change of connectivity. We used piecewise regression to measure how rapidly network connectivity increased as discharge increased during current and future climate simulations (Figure 3-5B). We used the slope of the regression line to measure the stability of network connectivity. The slope for current and future climate simulations was related to aridity. Slope tended to increase with aridity index, such that more arid networks had less steep slopes (current climate: $p < 0.05$, $R^2_{adj} = 0.45$; future climate: $p < 0.05$, $R^2_{adj} = 0.39$). The slope was steeper in the future climate simulation than in the current climate simulation in seven watersheds (Figure 3-5C), indicating that an equivalent change in discharge will lead to a bigger change in connectivity in the future. Slope decreased in three networks and did not change in one network. The percent change in slope from the current to the future climate simulation was not related to aridity ($p > 0.05$, $R^2_{adj} = -0.11$; Figure 3-5D).

The impacts of climate change on the ecologically important very high and very low connectivity days depended on the aridity of the watershed. Arid stream networks tended to have large, positive percent change in the number of high connectivity days, while wetter stream networks experienced small, near-zero percent change (Figures 3-6A and 3-6B; Table 3-1). There was a significant relationship between aridity and percent change in days with DCI > 95 ($p < 0.05$, $R^2_{adj} = 0.53$), but not days with DCI > 80 ($p > 0.05$, $R^2_{adj} = 0.22$). In the future climate simulation, there was a more than a 200% increase in days with DCI > 95 in the three most arid watersheds. We observed the opposite trend with low connectivity days (Figures 3-6C and 3-6D). Arid stream networks experienced small, near-zero percent change in days with low connectivity, while wetter stream networks tended to have larger percent change values. There was a significant relationship between aridity and percent change in days with DCI < 5 ($p < 0.01$, $R^2_{adj} = 0.60$), but not days with DCI < 20 ($p > 0.05$, $R^2_{adj} = 0.13$).

DISCUSSION

In our simulations, cross-scale interactions drove changes in stream network connectivity. Interactions between global scale climate change and regional scale aridity resulted in predictable patterns of connectivity change in stream networks across the continental United States. These patterns did not reflect the traditional "rich get richer" paradigm found in other studies (Chou et al. 2009, Feng and Zhang 2015). Instead, we found that the most arid networks are likely to see the largest increases in stream network connectivity, while the least arid networks are likely to see the largest decreases. Our findings highlight the spatial complexities of interacting hydrological processes that act at multiple spatial scales.

Impacts of climate change on streamflow and network connectivity

Hydrologic models of current and future climate conditions showed that mean discharge increased in the future climate simulation in 9 of 11 study networks, while it decreased in only two study networks (Figure 3-2). In our models, changes in discharge between the current and future climate simulations are driven solely by changes in precipitation and temperature (Wang et al. 2011). Our findings reflect current understanding about the impacts of climate change on precipitation and temperature. Due to climate change, there is expected to be an increase in the frequency of extreme precipitation events, meaning that precipitation is expected to occur during fewer events that are greater in magnitude (Payton et al. 2023). Because precipitation will occur during fewer events, there will be longer periods of low or no precipitation. Concurrently, rising temperatures associated with climate change are expected in all regions of the United States. Rising temperatures result in increased potential evaporation (Marvel et al. 2023). Together, change in precipitation and temperature are likely to result in more extreme high and extreme low flow events. In this study, we observed more days with extremely high streamflow and often an increase in maximum streamflow during the future climate simulation (Figure 3-3), resulting in the increase in average daily discharge we observed in many of the study networks despite concurrent increases in low and zero-flow days. More days with high streamflow and higher high flows are likely to contribute to more flooding events. Potential negative consequences of flooding events include displacement of organisms and destruction of habitats (Fisher et al. 1982), while potential positive consequences include increased upstream-downstream connectivity and increased connectivity between the stream channel and floodplain (Boulton et al. 2017).

We also observed changes in the relationship between discharge and connectivity due to climate change. In a stream network, high discharge is generally associated with high connectivity while low discharge is associated with low connectivity (Malish et al. 2023). How suddenly networks transition from states of high connectivity to low connectivity can be understood as the stability of network connectivity. We found that climate change reduced the stability of connectivity in seven of the study networks (Figure 3-5). This reduction means that equivalent decreases in discharge result in larger decreases of connectivity in the future than in the current climate simulation. Decreased stability of network connectivity thresholds suggests that stream ecosystems are likely to lose connectivity more rapidly and more often in the future. How rapidly fragmentation occurs in stream networks is known to influence biodiversity. For example, rapid fragmentation limits the ability of taxa to move elsewhere in the network to avoid no flow conditions (Vander Vorste et al. 2021). Therefore, networks that lose connectivity more slowly may be more diverse and have higher survival rates during drying events (Price et al. 2021).

In contrast to our finding of increased daily discharge in most stream networks in the future climate simulation, connectivity decreased in seven networks while it increased in only four (Figure 3-2). Climate change tended to particularly impact the number of very low and very high connectivity days (Figures 3-4 and 3-6). The observed reductions in average network connectivity despite increased average daily discharge is largely because a network cannot exceed being fully connected (where DCI = 100). Therefore, despite higher magnitude flows and more frequent high flows, increases in daily connectivity are limited. This combined with an increase in low connectivity days resulted in reductions in average connectivity in many study networks.

The number of very low and very high connectivity days is understood to be ecologically consequential. During low connectivity days, there is less habitat availability and existing habitat is often fragmented. The ability for organisms to move around to access habitats and other resources is reduced. This causes population declines, loss of genetic diversity, and local extirpations (Meyer and Meyer 2000, Matthews and Marsh-Matthews 2003, Bonada et al. 2017). In contrast, periods of high connectivity represent opportunities for ecological recovery (Dodds et al. 2004, Acuña et al. 2005). Organisms can re-colonize parts of the stream network, there is opportunity for gene flow among previously isolated populations, and population sizes can increase. Therefore, to predict changes in how often stream networks experience very high and very low connectivity is important to be able to predict ecological impacts of climate change.

Cross-scale interactions between climate change and aridity

We found that the impacts of global-scale climate change interact with regional-scale aridity to drive changes in the number of very high and very low connectivity days. Generally, the more arid a stream network, the larger the percent increase in the number of high connectivity days from the current climate simulation to the future climate simulation (Figure 3-6). The least arid stream networks tended to experience a slight percent decrease in the number of high connectivity days. In contrast, the least arid stream networks tended to experience the largest percent increases in the number of very low connectivity days, while the more arid networks tended to experience near-zero percent change. Our study included stream networks that span the southern portion of the continental United States, encompassing much of the continental US aridity gradient. Generally, aridity increases from east to west across the continental US with impacts of climate change also varying by region. The southcentral and southeastern regions of the United States are expected to experience future increases in annual precipitation, while the southwestern region is expected to experience decreases in annual precipitation (Marvel et al. 2023). These regional patterns alone don't explain our findings.

Our findings are explained by the increase in extreme precipitation events in the future climate simulation. In the arid stream networks (e.g. Sycamore Creek, East Turkey Creek, Chalone Creek, and Cave Creek), the extreme precipitation events cause systems that are generally poorly connected to be well connected more often (Asadieh and Krakauer 2017). Precipitation is an important driver of streamflow and connectivity (Costigan et al. 2016, Jaeger et al. 2019). The extremely large percent increases in the number of high connectivity day are also explained by the fact that there are very few (0-4) high connectivity days in these networks during the current climate simulation models. Therefore, even 1-2 more high connectivity days during the future climate simulation models represents large percent increases. Additionally, Sycamore Creek had zero days with DCI > 95 or 80 in the current climate simulation and is therefore not represented in Figures 3-5A or 3-5B. While the number of days with DCI > 95 did not change in the future climate simulation, the number of days with DCI > 80 annual increased to 0.3, a substantial relative increase (Table 3-1). Also in the arid stream networks, there were already many low connectivity days during the current climate simulation. Therefore, any changes, whether increases or decreases, resulted in near-zero percent change. The opposite trends occurred in the least arid networks (e.g. Passage Creek and South Sandy Creek). These systems were generally well connected, with many high connectivity days per year during the current climate simulation, so any changes in the number of high connectivity days in the future climate simulation resulted in near-zero percent change. In contrast, these systems had relatively few low connectivity days during the current climate simulation. The increases in the number of low and no precipitation days associated with the increase in extreme precipitation events in the future climate simulation resulted in more low connectivity days.

The scale at which we conducted our analysis allowed us to identify the effects of cross-scale interactions. Spatial scale is likely an important explanation for the counterintuitive nature of our findings. The studies that have identified the 'rich-get-richer' trend are generally conducted at the global scale at a coarse resolution (e.g. 25 km in Feng and Zhang 2015, 1.5° in Chou et al. 1982). We used hydrological models with 10 m resolution for each study watershed (<1000 km^2). Analysis at a finer spatial scale allowed us to identify exceptions to general, large-scale trends.

Implications for water management and sustainability

We showed that global-scale climate change induced alterations in the number of days with very high and very low connectivity in stream networks, and that these alterations varied predictably with regional-scale aridity. There is a general understanding that in nonperennial stream networks, more water is associated with a more connected system (Bonada and Resh 2013, Messager et al. 2021). By extension, it's often assumed that regions that will experience more precipitation and associated increases in streamflow in the future will therefore be more connected in the future. Combining this logic with the "rich get richer" paradigm would lead one to assume that stream networks in currently dry regions will get more dry and less connected in the future, while those in wet regions will get more wet and more connected. Our study demonstrates that this assumption is not only false, but that the opposite is true in many cases. Regions of the continental United States that are currently very arid are expected to see decreases in precipitation in the future (Marvel et al. 2023). Our study stream networks located in these networks experienced more high connectivity days in the future. Regions of the continental United States that are currently more humid are expected to see increases in precipitation. We found that stream networks in these regions are likely to experience more low connectivity days in the future.

The impact of human development may dampen the trends we identified in our unregulated stream networks. The networks selected for our study were selected because they are relatively unimpacted by anthropogenic factors such as instream structures (e.g. dams) and water withdrawal. However, this is uncharacteristic of rivers in the United States, where rivers are generally heavily regulated (Ostroff et al. 2013). Prior to human development in the continental United States, stream networks were less connected in arid basins than in humid basins due to naturally occurring drying in arid basins. Now, humid basins are the most fragmented due to the construction of dams and other structures (Spinti et al. 2023). As a result of the construction of these dams and associated reservoirs, humid basins have more potential for regulation of streamflow (Spinti et al. 2023), which itself has potential to counteract the increase in the number of low connectivity days due to the stream drying we identified in our analysis through strategic releases of waters (e.g. e-flows). Previous work has shown that in some basins, dams impact the flow regime more than climate change (Arheimer et al. 2017). This is likely true also for more developed, humid watersheds, where increased fragmentation due to drying may be less of a concern and addressing the consequences of fragmentation due to anthropogenic structures should be prioritized. Water withdrawal associated with development is also likely to increase stream drying and decrease connectivity in both arid and humid basins (Deacon et al. 2007, Bogan and Lytle 2011, Rugel et al. 2012), although impacts are likely to be smaller in humid basins with greater water availability. Impacts of human development on hydrology are heterogeneous, even within the same region (Bhaskar et al. 2020) and effective management of watersheds requires consideration of factors across spatial scales, from global climate to local infrastructure.

Conclusion

Cross-scale interactions between global climate and regional aridity drive predictable changes in stream network connectivity. These changes are antithetical to common narratives regarding the influence of climate change – that wet regions will get wetter and dry regions will get drier (Chou et al. 2009, Feng and Zhang 2015). The contrast between our findings and common narratives illustrates why site-specific information is imperative for management. As changes in stream drying (Zipper et al. 2021) and connectivity (Jaeger et al. 2014, Perkin et al. 2015b) continue, effective management of stream networks requires consideration of global, regional, and local processes that influence network scale hydrology (Costigan et al. 2017, Shanafield et al. 2021).

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TABLES

Table 3-1. Annual number of high connectivity and low connectivity days for current and future climate simulations. Stream networks are ordered from most arid to least arid.

Stream Network	Annual Days with DCI > 95		Annual Days with DCI > 80		Annual Days with DCI < 20		Annual Days with DCI < 5	
	Current	Future	Current	Future	Current	Future	Current	Future
Sycamore	0.0	0.0	0.0	0.3	350.5	342.9	315.6	306.8
East Turkey	0.4	1.4	1.4	4.1	342.1	347.2	214.5	320.2
Chalone	0.1	0.5	4.3	5.9	321.3	319.9	199.5	208.6
Cave	0.2	1.3	5.1	6.9	333.4	339.6	287.6	300.9
Deer	267.7	257.2	281.6	269.9	42.2	49.1	21.5	23.5
Teakettle	280.4	269.0	293.3	284.6	38.1	42.8	26.9	29.3
McDowell	12.9	24.6	23.8	42.6	258.7	253.3	226.5	227.2
Shane	13.6	27.1	27.7	46.3	278.8	266.5	235.5	236.0
Blue	16.7	19.9	41.9	44.4	237.9	242.5	123.4	140.8
Passage	151.6	143.5	189.4	175.0	46.5	56.1	0.0	0.5
South Sandy	91.8	78.5	121.3	106.3	121.2	130.5	27.7	38.2

FIGURES

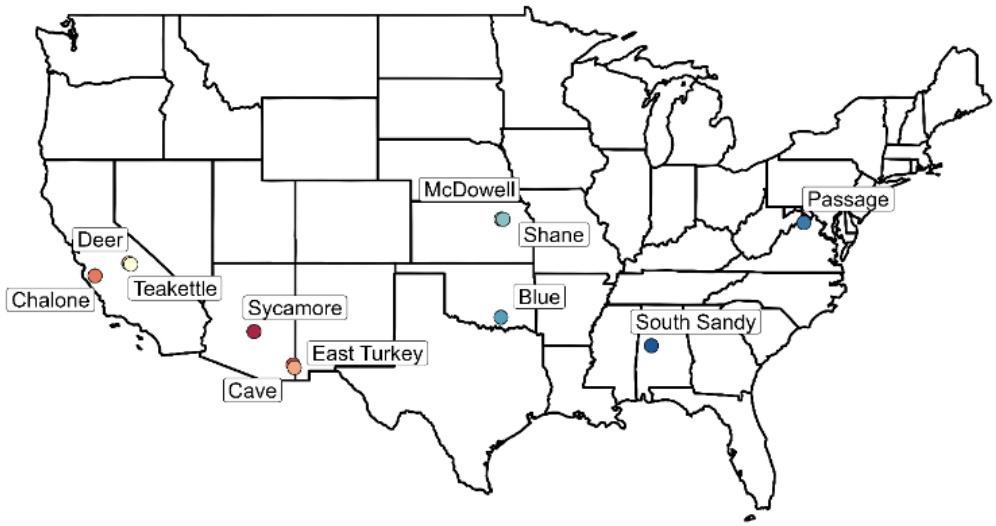

Figure 3-1. Map of stream network locations. Color represents aridity, with lighter, warmer colors indicating more arid networks and darker, cooler colors representing more humid networks.

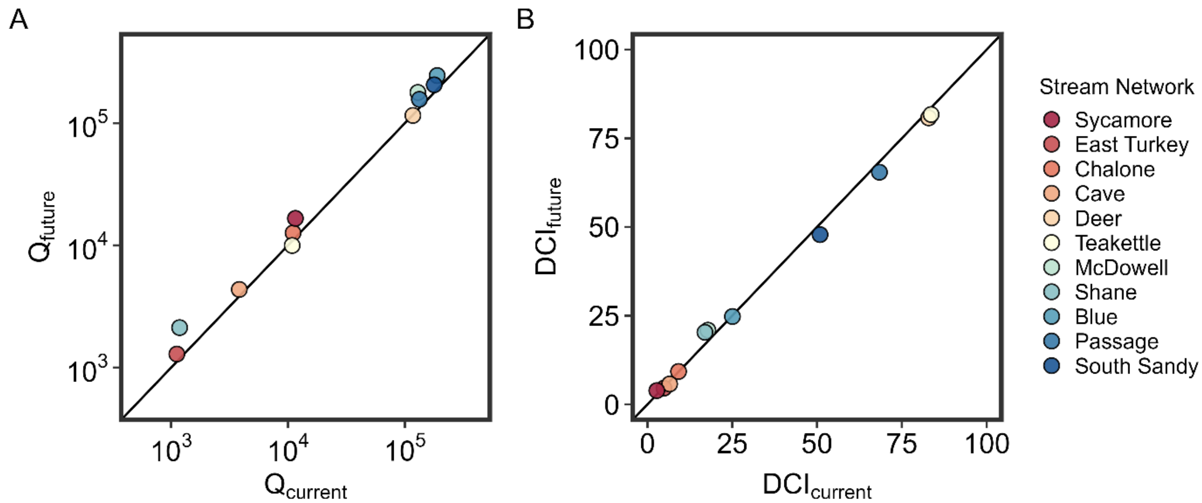

Figure 3-2. Mean daily discharge (Q, m^3/day; A) and dendritic connectivity index (DCI; B) values under current and future climate simulations. Black line indicates 1:1 relationship. When points are above the 1:1, there was an increase in daily discharge or DCI in the future. When points are below the 1:1, there was a decrease in daily discharge or DCI in the future. Color represents aridity, with lighter, warmer colors indicating more arid networks and darker, cooler colors representing more humid networks.

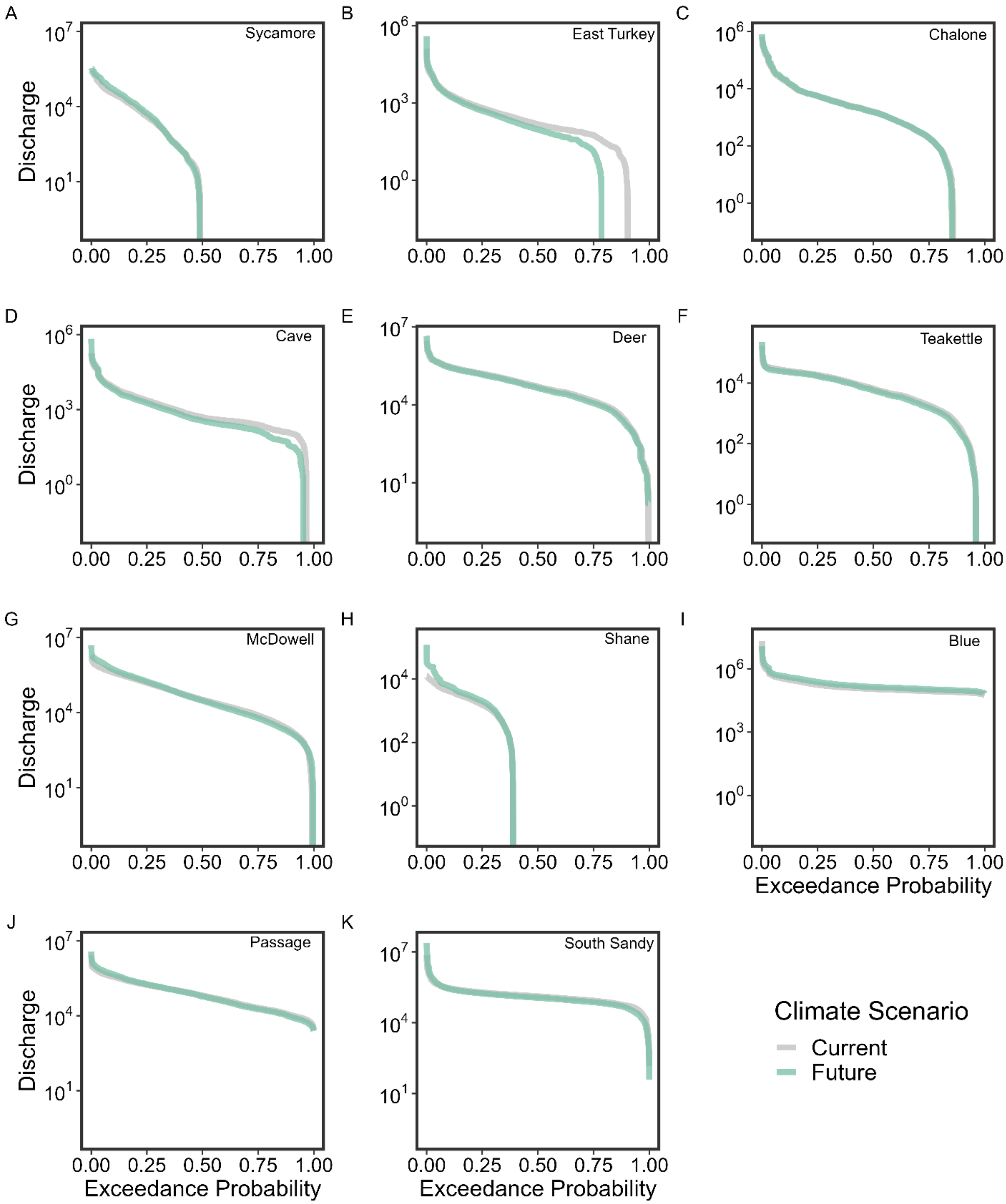

Figure 3-3. Daily discharge (m^3/day) exceedance probability curves for current and future climate simulations in A) Sycamore, B) East Turkey, C) Chalone, D) Cave, E) Deer, F) Teakettle, G) McDowell, H) Shane, I) Blue, J) Passage, K) South Sandy. Plots are arranged from the most arid to the least arid watershed.

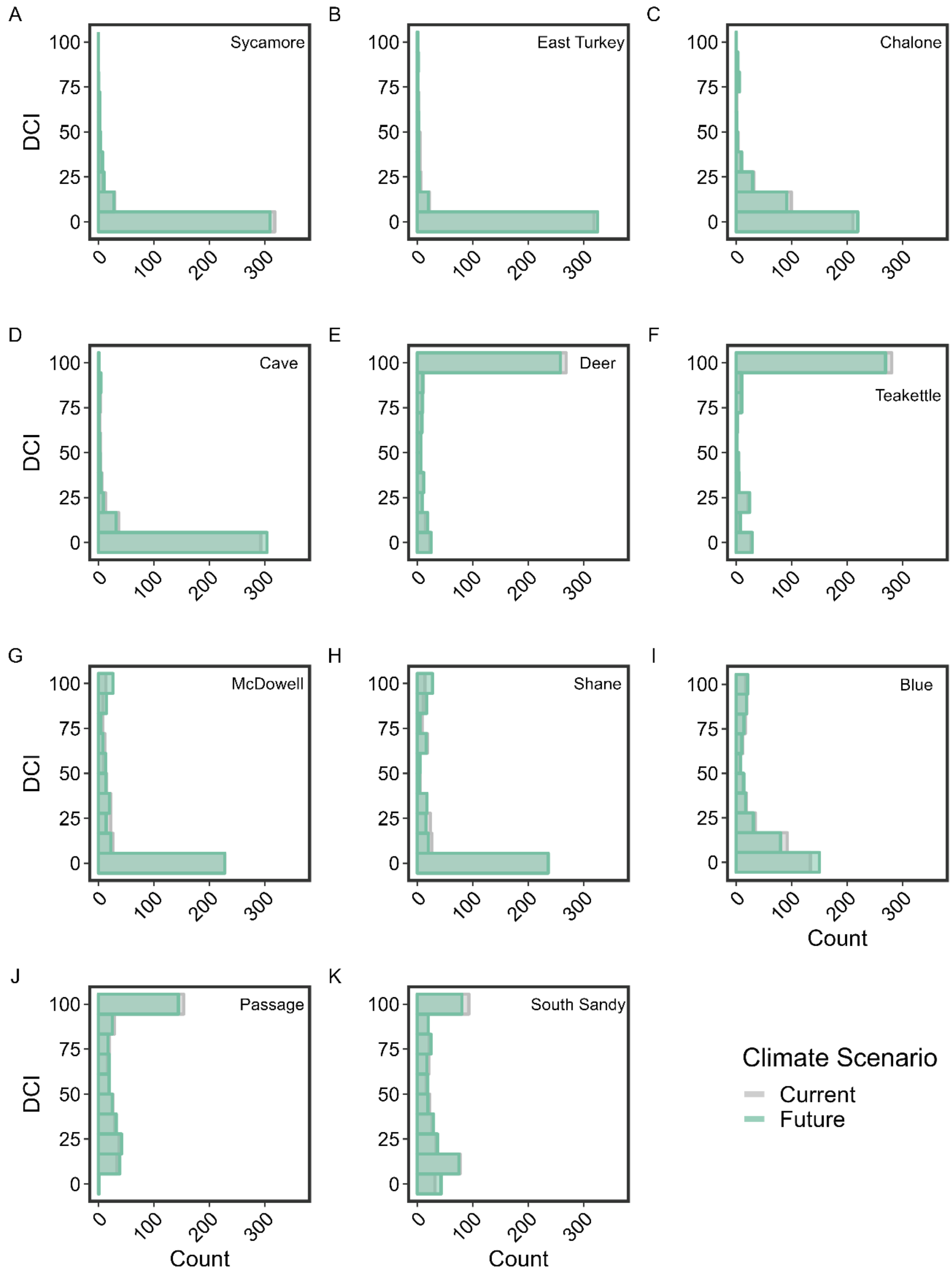

Figure 3-4. Histogram of daily DCI values for current climate (grey) and future (green) climate simulations for A) Sycamore, B) East Turkey, C) Chalone, D) Cave, E) Deer, F) Teakettle, G) McDowell, H) Shane, I) Blue, J) Passage, K) South Sandy. Plots are arranged from the most arid to the least arid watershed.

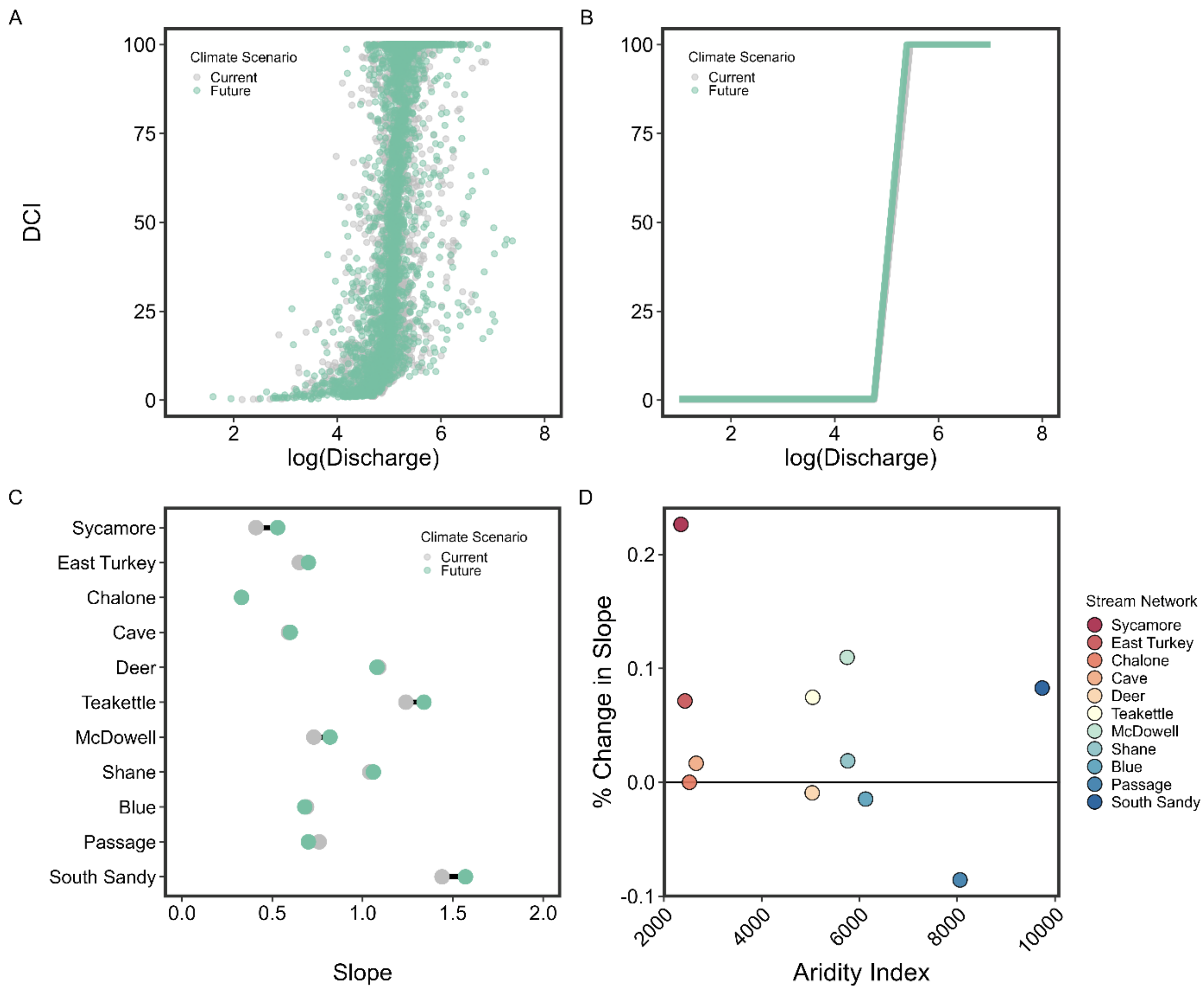

Figure 3-5. Piecewise regression between daily discharge (m^3/day) and dendritic connectivity index (DCI). A) Example of the sigmoidal relationship between log(Discharge) and DCI, here showing data for South Sandy Creek. B) Piecewise regression fit to the points shown in panel A. The first and third lines are constrained to have a slope of zero and y-intercept equal to the minimum or maximum DCI value, respectively. C) Slope of piecewise regression for current and future climate simulations. Slope refers to the slope of the second line of the piecewise regression, as shown in panel B. A steeper slop indicates more rapid transitions between connected and disconnected states. D) There is no relationship between aridity index and percent change in slope from the current to future climate simulation. In panels A-C, grey represents current climate and green represents future climate. In panel D, color represents aridity, with lighter, warmer colors indicating more arid networks and darker, cooler colors representing more humid networks.

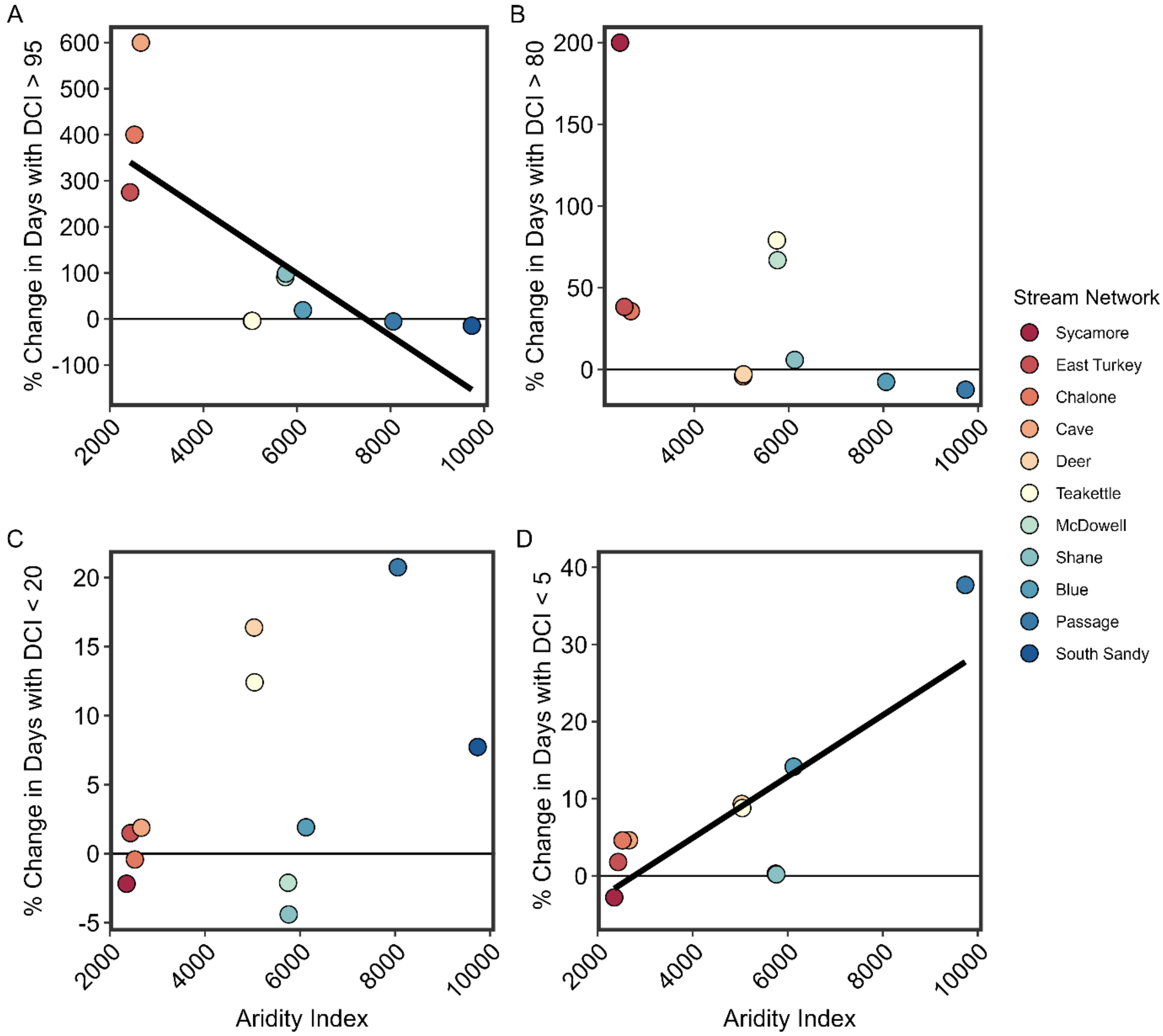

Figure 3-6. Relationship between aridity index and percent change in A) days with DCI > 95, B) days with DCI > 80, C) days with DCI < 20, and D) days with DCI < 5 from the current to the future climate simulation. Panels show linear regression where a significant relationship was identified ($p < 0.05$). Color represents aridity, with lighter, warmer colors indicating more arid networks and darker, cooler colors representing more humid networks.

SYNTHESIS AND CONCLUSIONS

Connectivity is a fundamental property of stream ecosystems (Pringle 2003, Fuller et al. 2015). Flowing water allows for the movement of organisms and resources across broad geographic scales and supports key ecosystem processes (Acuña et al. 2005, Perkin et al. 2013, Vaughn et al. 2015, Heim et al. 2016). Fragmentation in river ecosystems often decreases biodiversity due to habitat alteration, habitat loss, and limitation of organism movement (Perkin and Gido 2012, Bogan et al. 2013, Datry et al. 2014). In nonperennial stream networks, spatial and temporal connectivity patterns are largely determined by where and when stream drying occurs. Because of this, connectivity in nonperennial stream networks is dynamic (Boulton et al. 2017). Drying and connectivity patterns in nonperennial streams are driven by processes that act at multiple spatial scales (Costigan et al. 2016). How connectivity patterns change in the future will vary based on the cross-scale interactions of these processes (Hammond et al. 2021, Zipper et al. 2021). The overarching goal of this dissertation research was to improve understanding of the patterns and drivers of stream drying and connectivity in nonperennial stream networks

In Chapter One, I identified critical tipping points in stream drying. To identify these tipping points, I used a hydrological modeling approach to quantify spatiotemporal drying patterns under current and future climate scenarios in the Blue River, Oklahoma. I found that stream drying is likely to increase in all future climate scenarios and that increases in stream drying reduce connectivity. Importantly, the effects of stream drying on connectivity were highly non-linear. There is watershed daily discharge threshold around which a small increase in stream drying led to a rapid drop in connectivity. Identifying the presence of a connectivity threshold is a key insight when considering management of this watershed: water managers must carefully consider the potential impacts of even small increases in stream drying.

In Chapter Two, I explored how the impacts of stream drying on connectivity vary by stream network size and the location of drying within the stream network. I simulated drying scenarios in eleven stream networks from across the United States and varied the location and spatial extent of drying. The rate of connectivity loss varied with stream network size, such that larger stream networks lost connectivity more rapidly than smaller stream networks. The rate of connectivity loss also varied with the location of drying. When drying occurred in the mainstem, even small amounts of drying resulted in rapid losses in connectivity. When drying occurred in headwater reaches, small amounts of drying had little impact. However, beyond a certain threshold, connectivity declined rapidly with further increases in drying. These findings underscore the need for managers to be particularly vigilant about fragmentation when managing at large spatial scales and when stream drying occurs in mainstem reaches.

In Chapter Three, I built on the findings of Chapter One by expanding the geographic scope to examine the effects of future climate change on streamflow and connectivity in the eleven stream networks studied in Chapter Two. Again using a hydrological modeling approach, this work showed that cross-scale interactions of drivers of stream drying result in counterintuitive changes in connectivity. Arid stream networks tended to have more high connectivity days in the future while the number of low connectivity days did not change. In contrast, in wetter stream networks the number of high connectivity did not change and there tended to be large increases in the number of low connectivity days. These findings highlight how cross-scale interactions between global-scale climate change and regional-scale aridity drive predictable changes in stream network connectivity. The ability to predict changes in connectivity allows for the anticipation and management of the consequences of climate change.

Taken together, the research contained in this dissertation demonstrates that stream drying and connectivity patterns are complex, but vary in predictable ways. Stream drying, network connectivity, and the relationship between the two is mediated by factors and processes that act at the network scale (network size, drying location), the regional scale (aridity), and the global scale (climate change). The alteration of stream drying and connectivity will have ecological consequences. My research shows that we can anticipate changes in in stream drying and connectivity patterns, improving our ability to predict ecological consequences and manage changing ecosystems.

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SUPPLEMENTAL INFORMATION

CHAPTER ONE

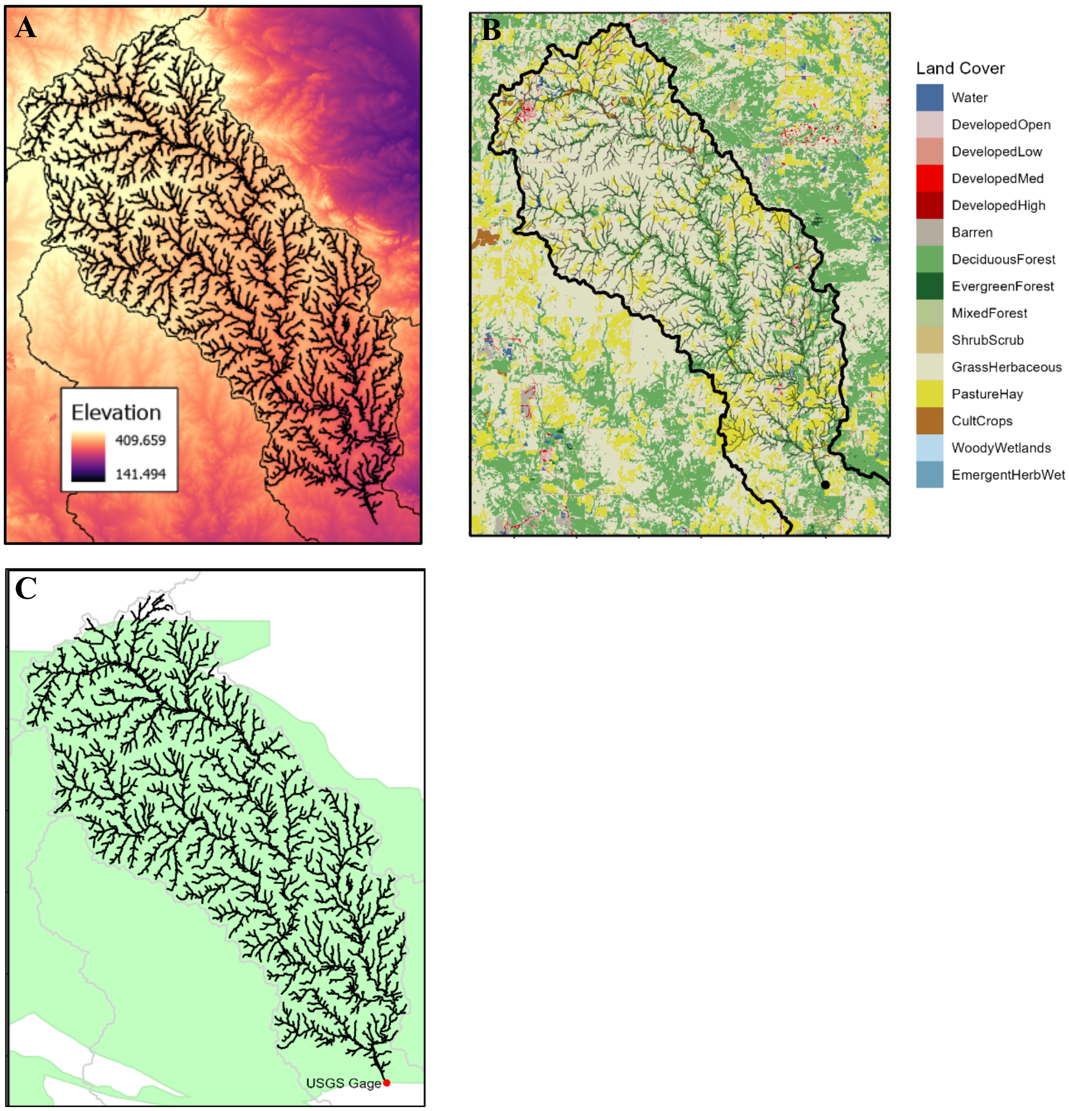

Figure S1-1. Elevation (Gesch et al. 2018; A), land cover (Dewitz 2019; B), and aquifer extent (Oklahoma Water Resources Board 2011; C) of the study area.

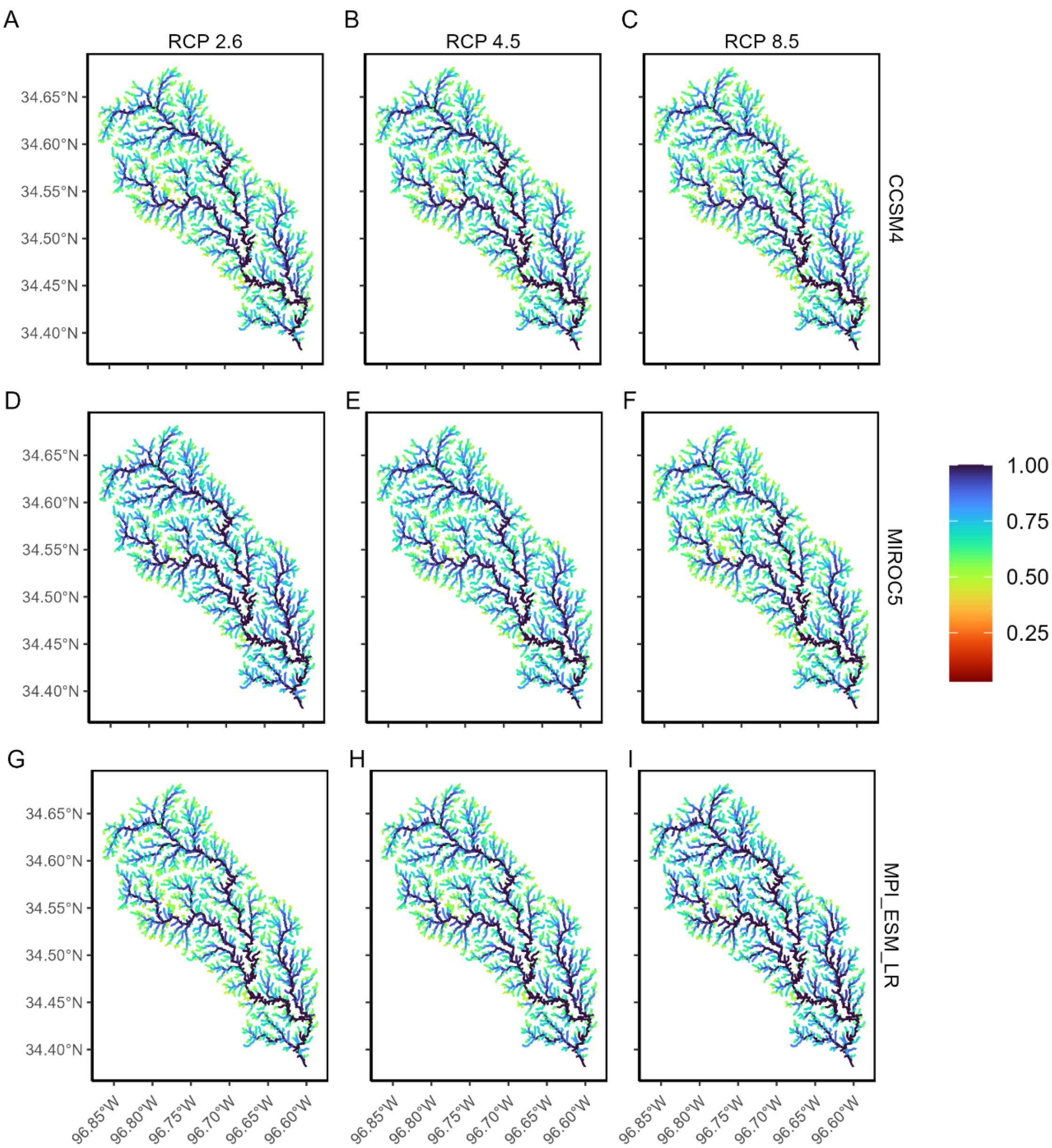

Figure S1-2. Water occurance frequency (i.e., proportion of days in which the stream reach was wet) during the current study period (2010-2029).

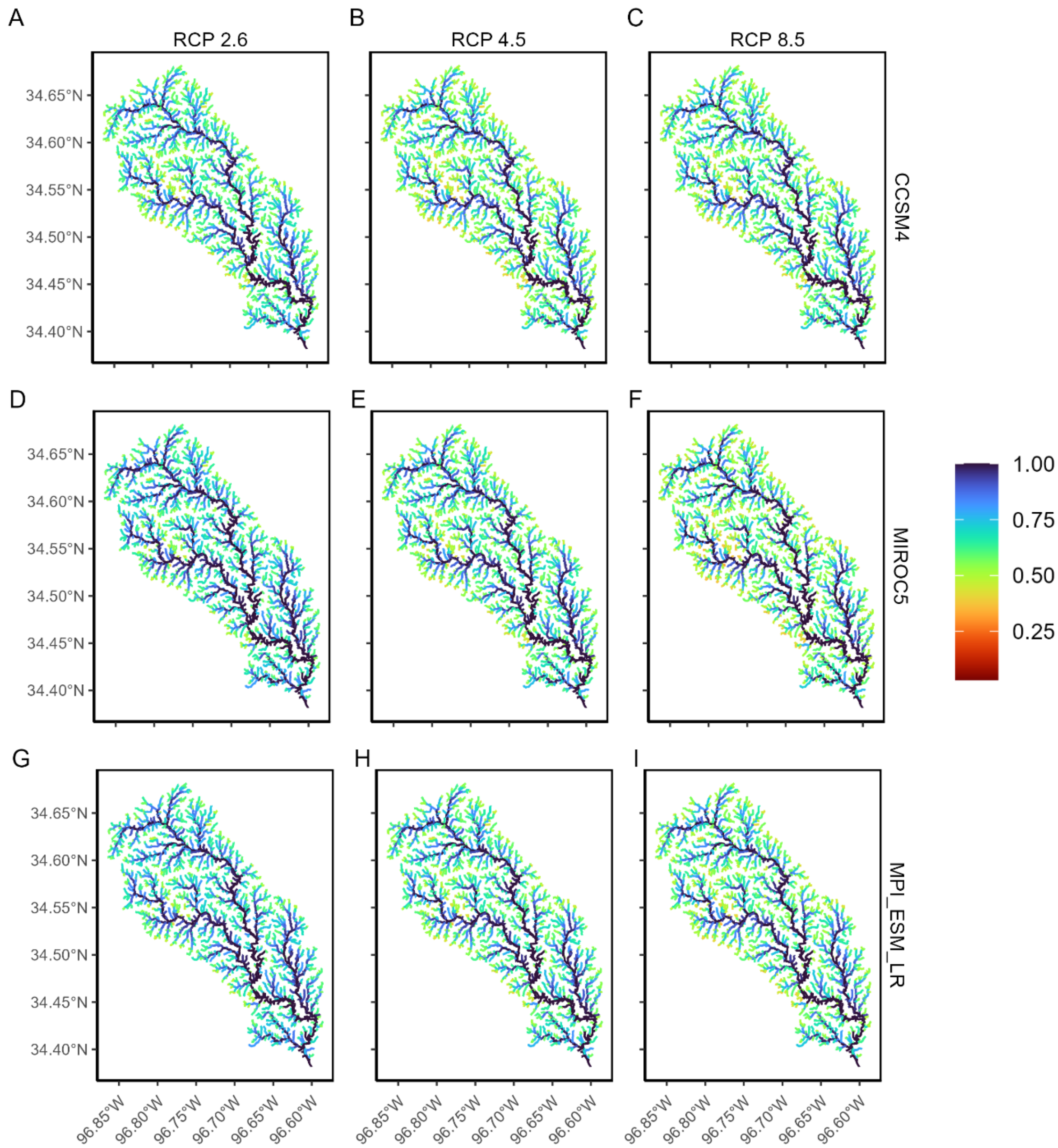

Figure S1-3. Water occurance frequency (i.e., proportion of days in which the stream reach was wet) during the future study period (2060-2079).

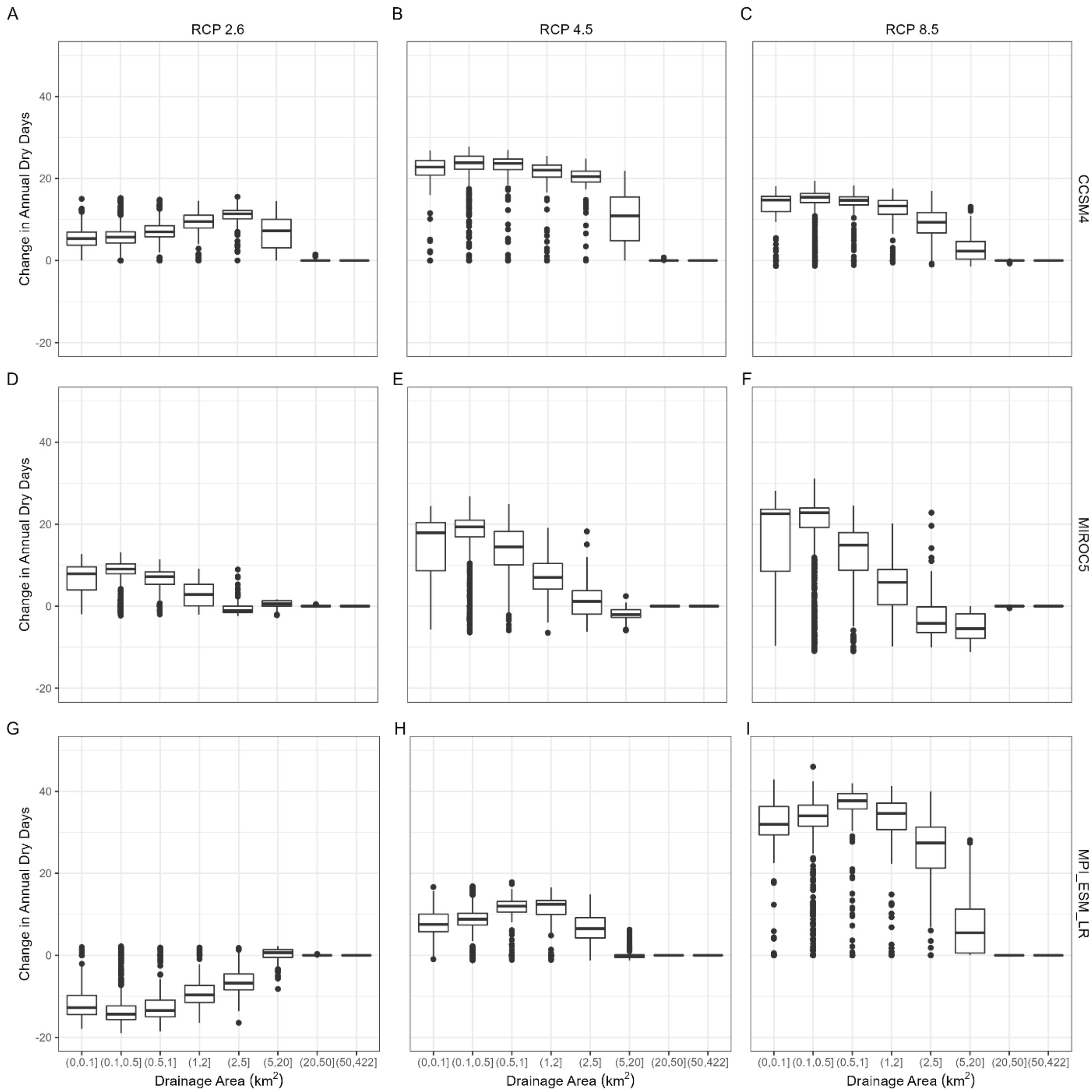

Figure S1-4. Change in annual number of dry days by drainage area across nine future climate scenarios. Climate scenarios result from all combinations of three GCMs (rows) and three RCPs (columns). Within each plot, each box-and-whisker plot shows the distribution of the change in number of dry days for all stream reaches of a given drainage area.

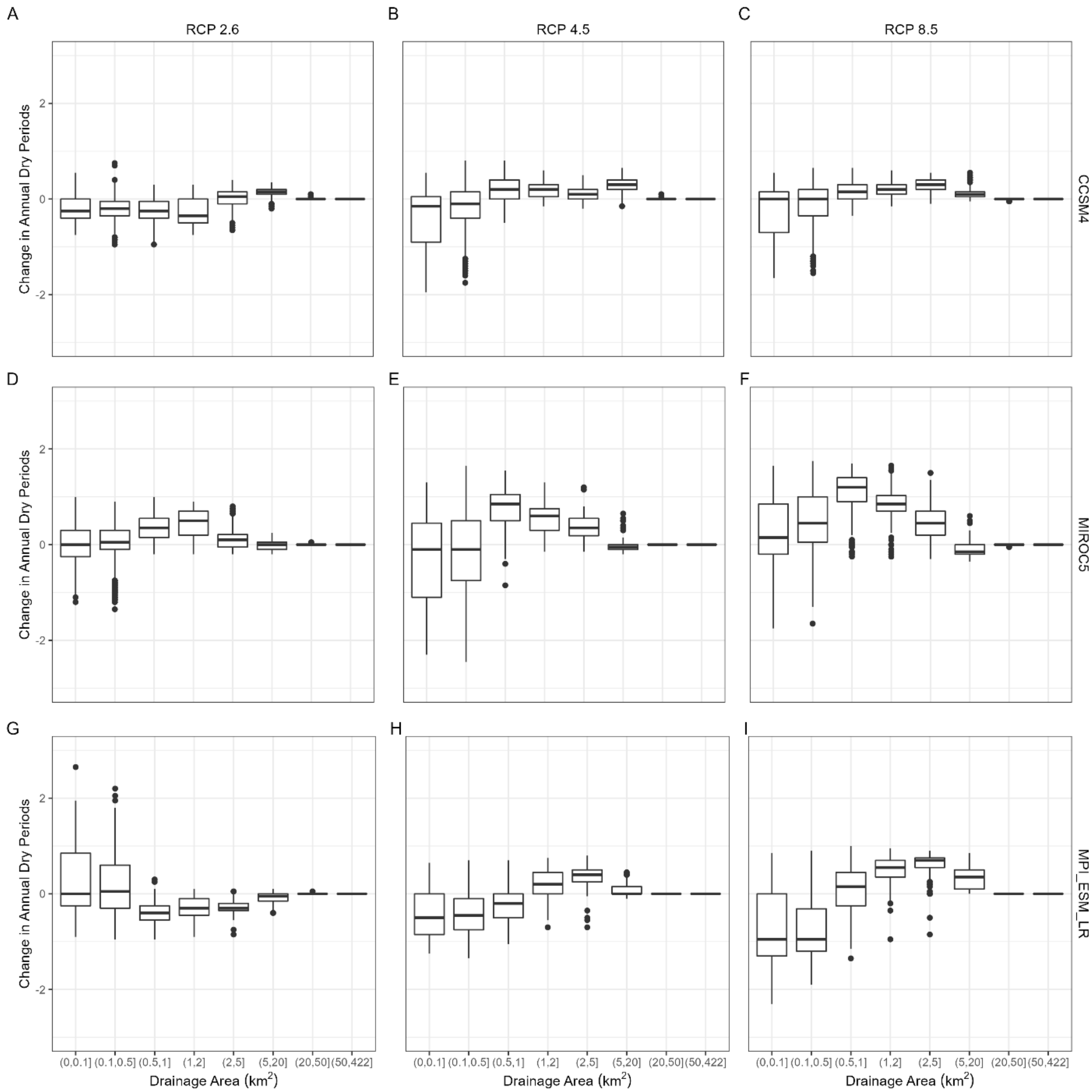

Figure S1-5. Change in annual number of dry periods by drainage area across nine future climate scenarios. Climate scenarios result from all combinations of three GCMs (rows) and three RCPs (columns). Within each plot, each box-and-whisker plot shows the distribution of the change in number of dry periods for all stream reaches of a given drainage area.

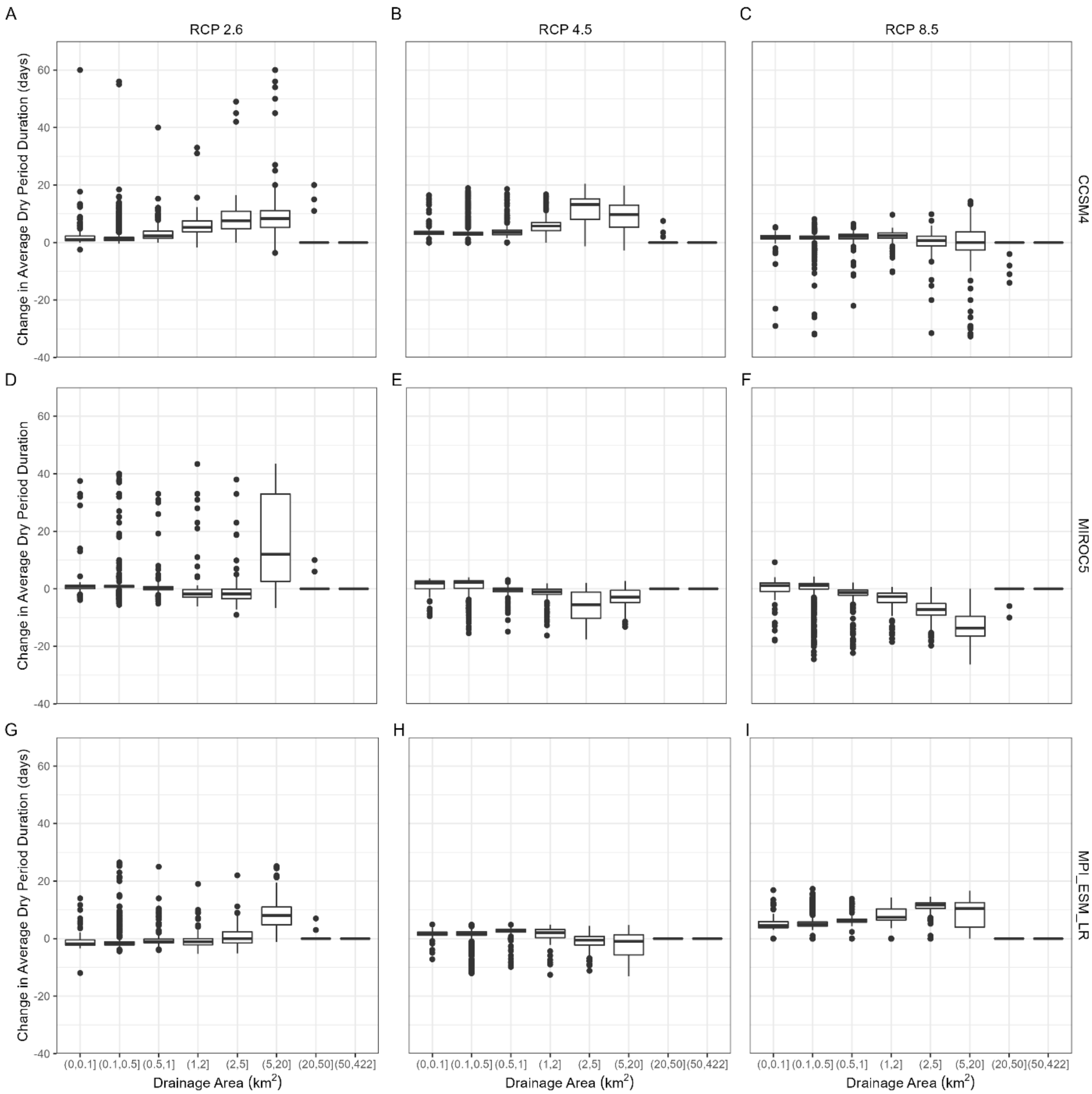

Figure S1-6. Change in average dry period duration by drainage area across nine future climate scenarios. Climate scenarios result from all combinations of three GCMs (rows) and three RCPs (columns). Within each plot, each box-and-whisker plot shows the distribution of the change in duration of dry periods for all stream reaches of a given drainage area.

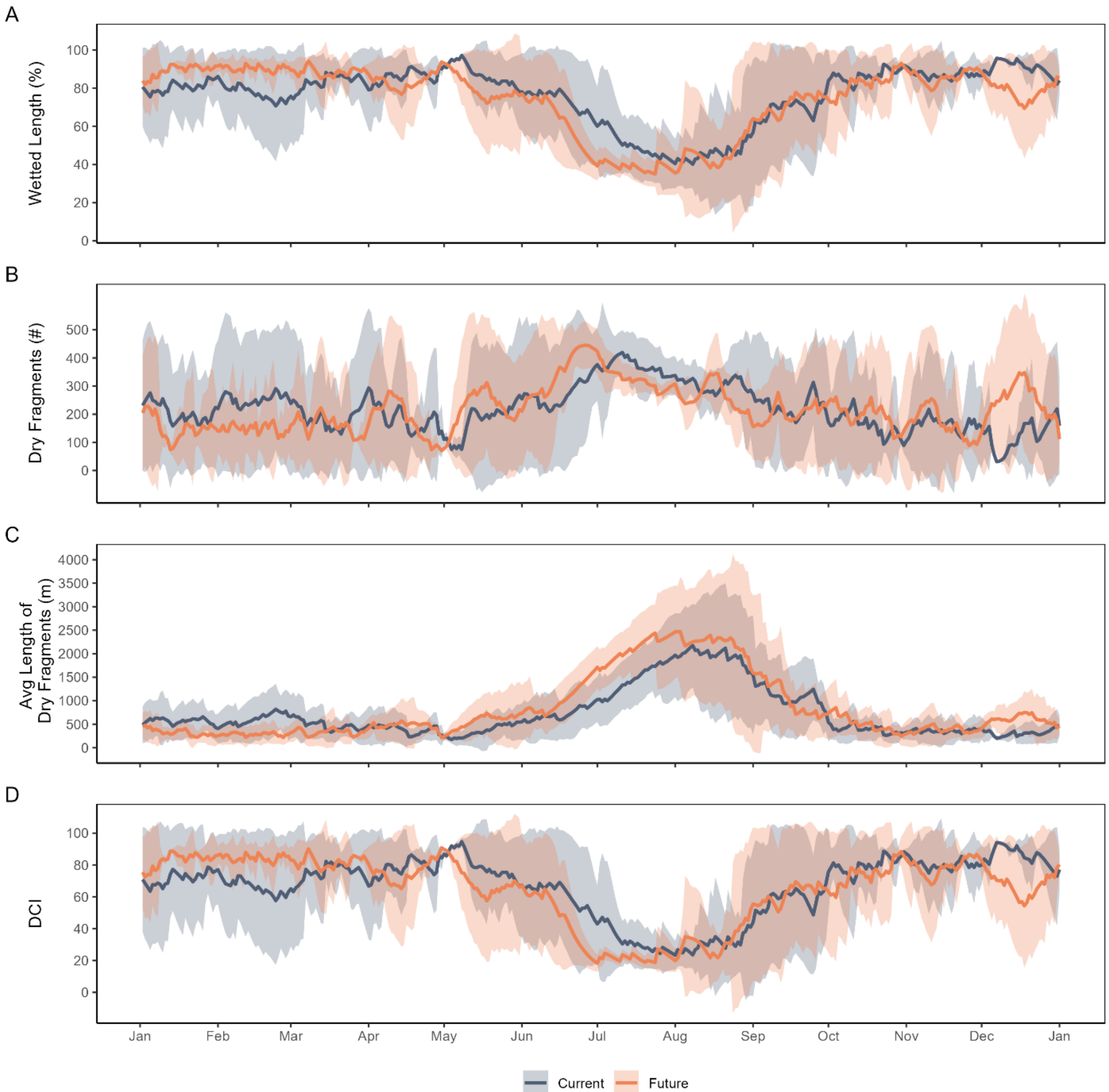

Figure S1-7. Daily percent wetted length (A), number of dry fragments (B), average length of dry fragments (C), and connectivity (D) for current (2010-2029) and future (2060-2079) periods from hydrologic model driven by CCSM4 GCM for RCP 2.6. Plots show mean (line) and IQR (shaded).

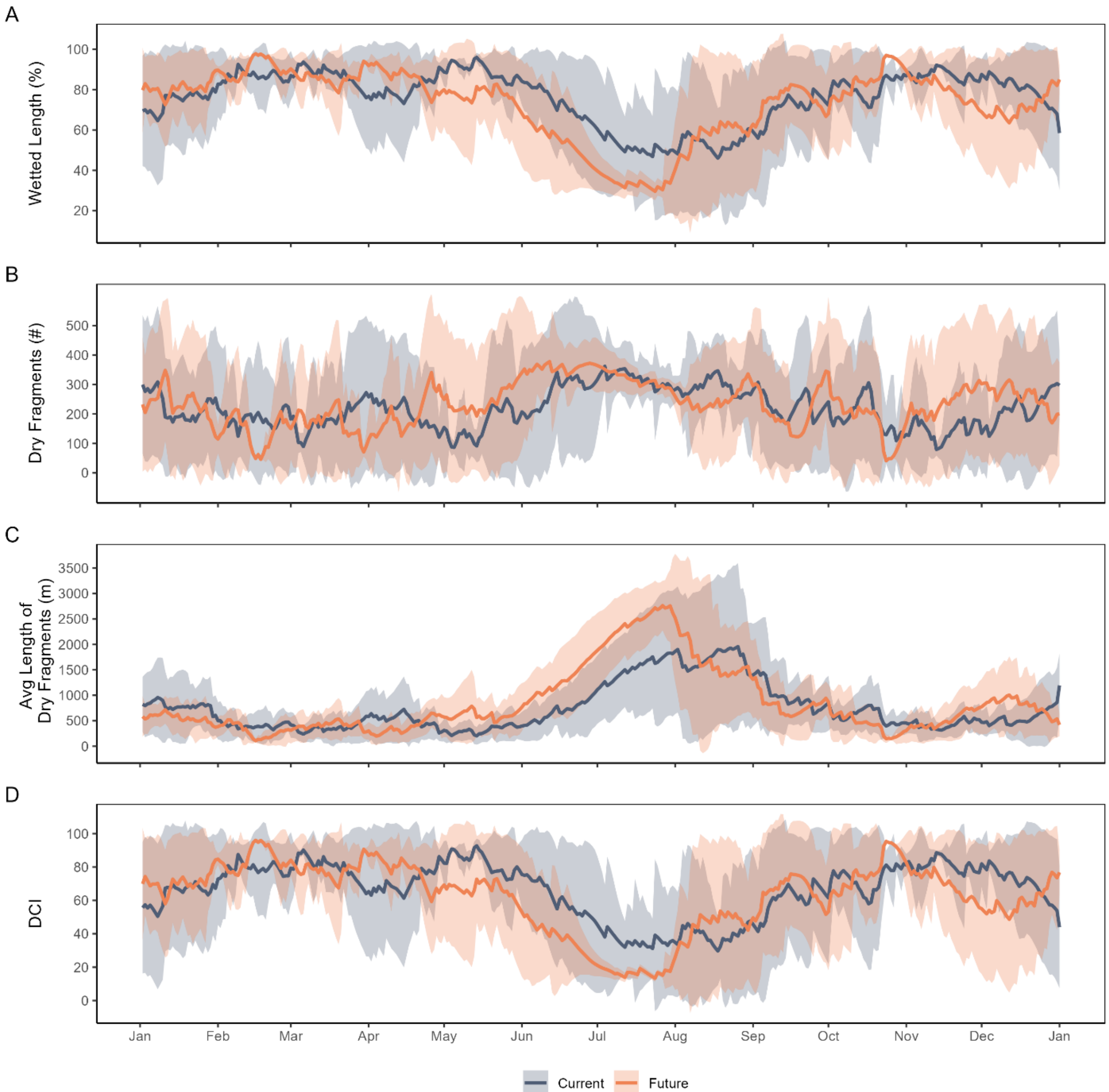

Figure S1-8. Daily percent wetted length (A), number of dry fragments (B), average length of dry fragments (C), and connectivity (D) for current (2010-2029) and future (2060-2079) periods from hydrologic model driven by CCSM4 GCM for RCP 8.5. Plots show mean (line) and IQR (shaded).

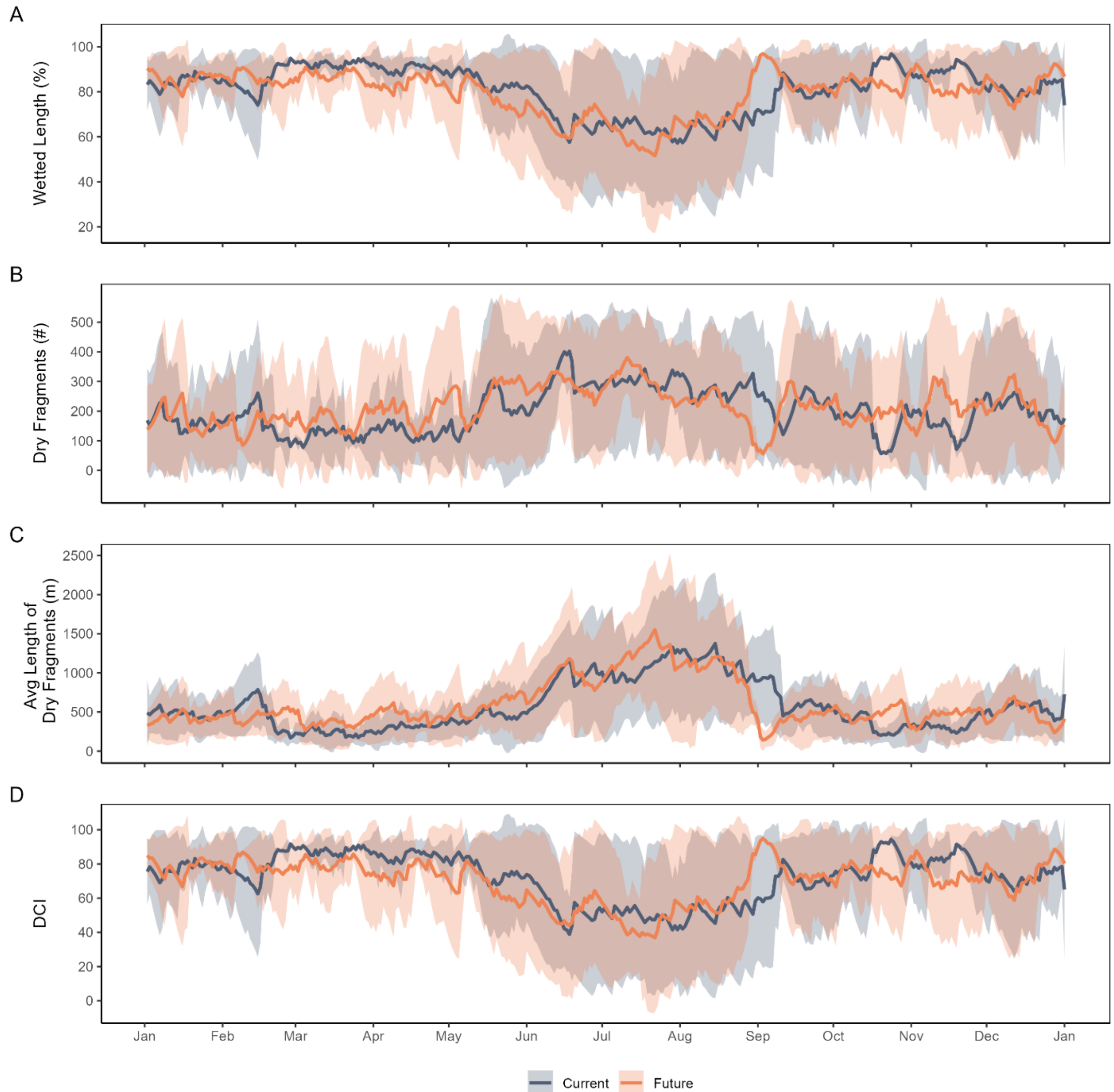

Figure S1-9. Daily percent wetted length (A), number of dry fragments (B), average length of dry fragments (C), and connectivity (D) for current (2010-2029) and future (2060-2079) periods from hydrologic model driven by MIROC5 GCM for RCP 2.6. Plots show mean (line) and IQR (shaded).

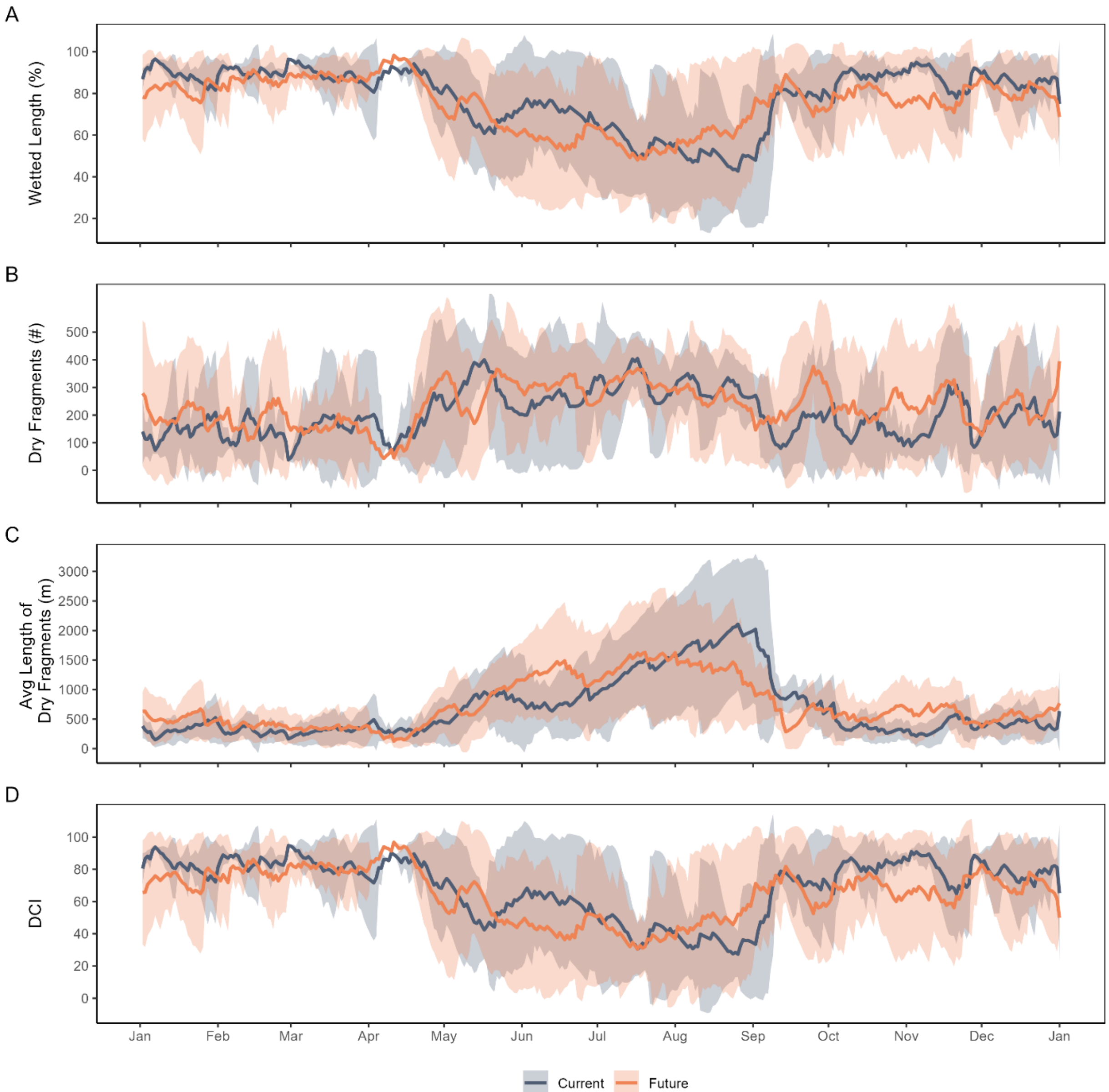

Figure S1-10. Daily percent wetted length (A), number of dry fragments (B), average length of dry fragments (C), and connectivity (D) for current (2010-2029) and future (2060-2079) periods from hydrologic model driven by MIROC5 GCM for RCP 4.5. Plots show mean (line) and IQR (shaded).

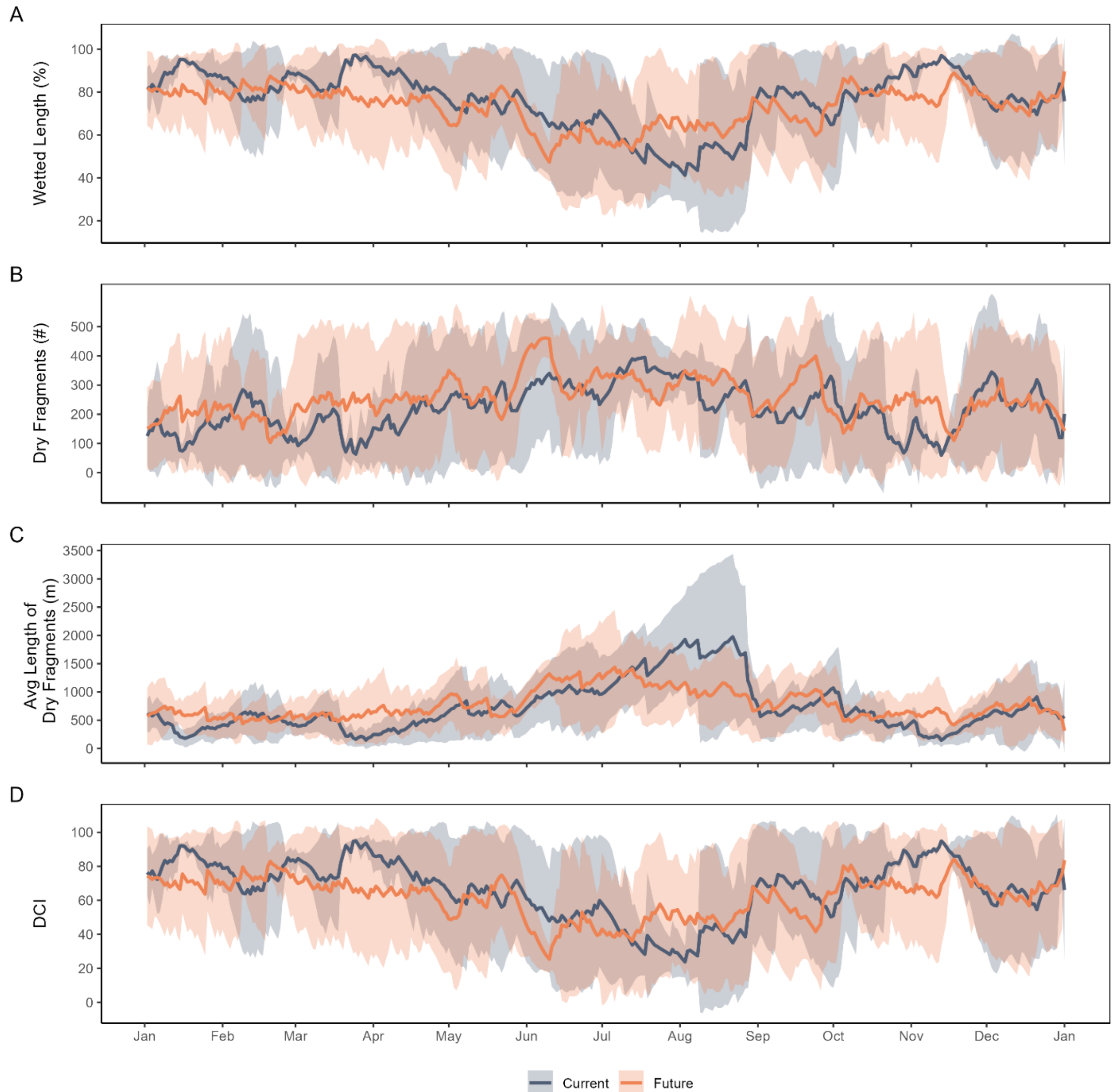

Figure S1-11. Daily percent wetted length (A), number of dry fragments (B), average length of dry fragments (C), and connectivity (D) for current (2010-2029) and future (2060-2079) periods from hydrologic model driven by MIROC5 GCM for RCP 8.5. Plots show mean (line) and IQR (shaded).

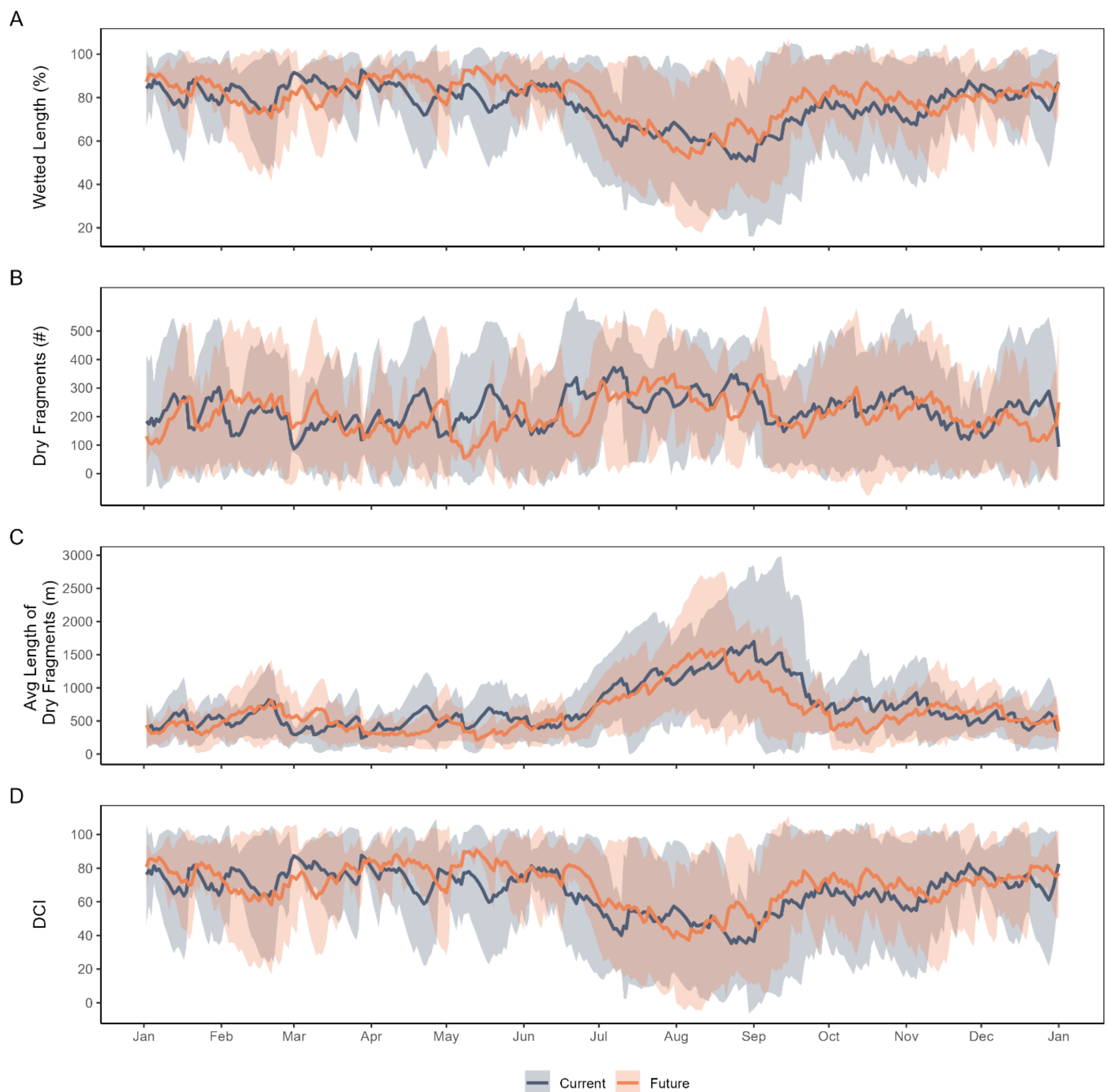

Figure S1-12. Daily percent wetted length (A), number of dry fragments (B), average length of dry fragments (C), and connectivity (D) for current (2010-2029) and future (2060-2079) periods from hydrologic model driven by MPI_ESM_LR GCM for RCP 2.6. Plots show mean (line) and IQR (shaded).

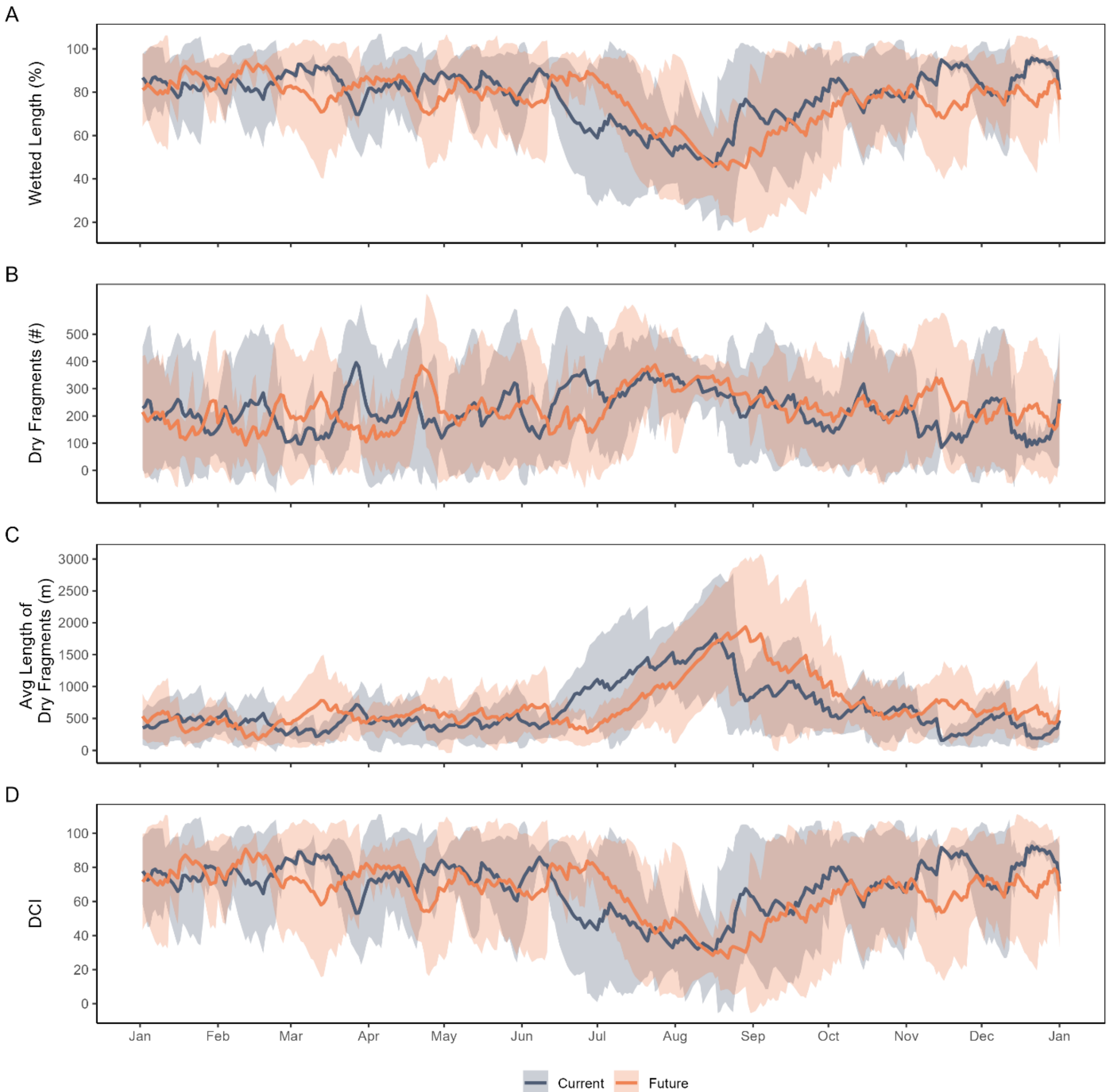

Figure S1-13. Daily percent wetted length (A), number of dry fragments (B), average length of dry fragments (C), and connectivity (D) for current (2010-2029) and future (2060-2079) periods from hydrologic model driven by MPI_ESM_LR GCM for RCP 4.5. Plots show mean (line) and IQR (shaded).

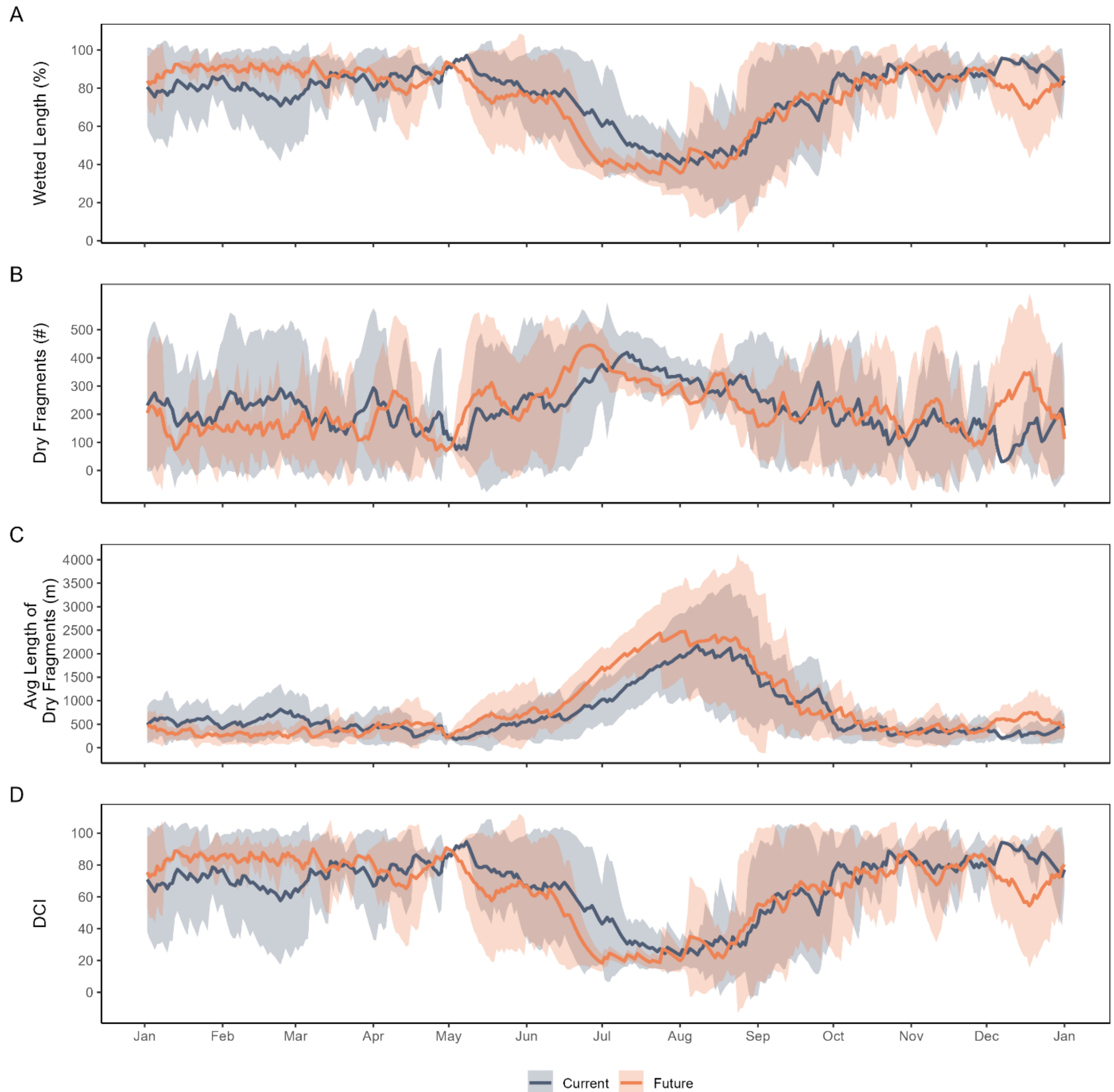

Figure S1-14. Daily percent wetted length (A), number of dry fragments (B), average length of dry fragments (C), and connectivity (D) for current (2010-2029) and future (2060-2079) periods from hydrologic model driven by MPI_ESM_LR GCM for RCP 8.5. Plots show mean (line) and IQR (shaded).

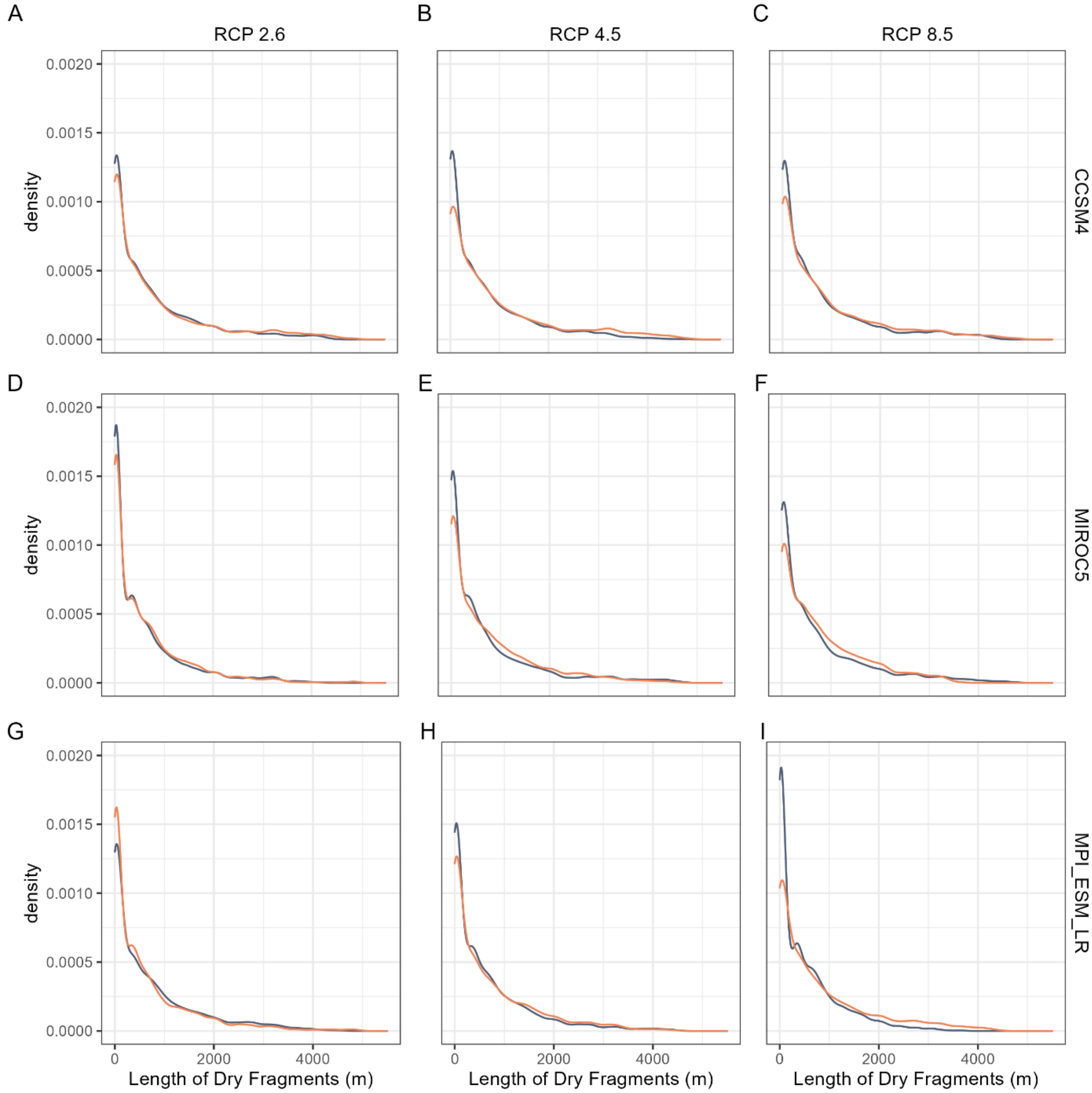

Figure S1-15. Distribution of daily average dry fragment length during current (blue) and future (orange) climate scenarios. Climate scenarios result from all combinations of three GCMs (rows) and three RCPs (columns).

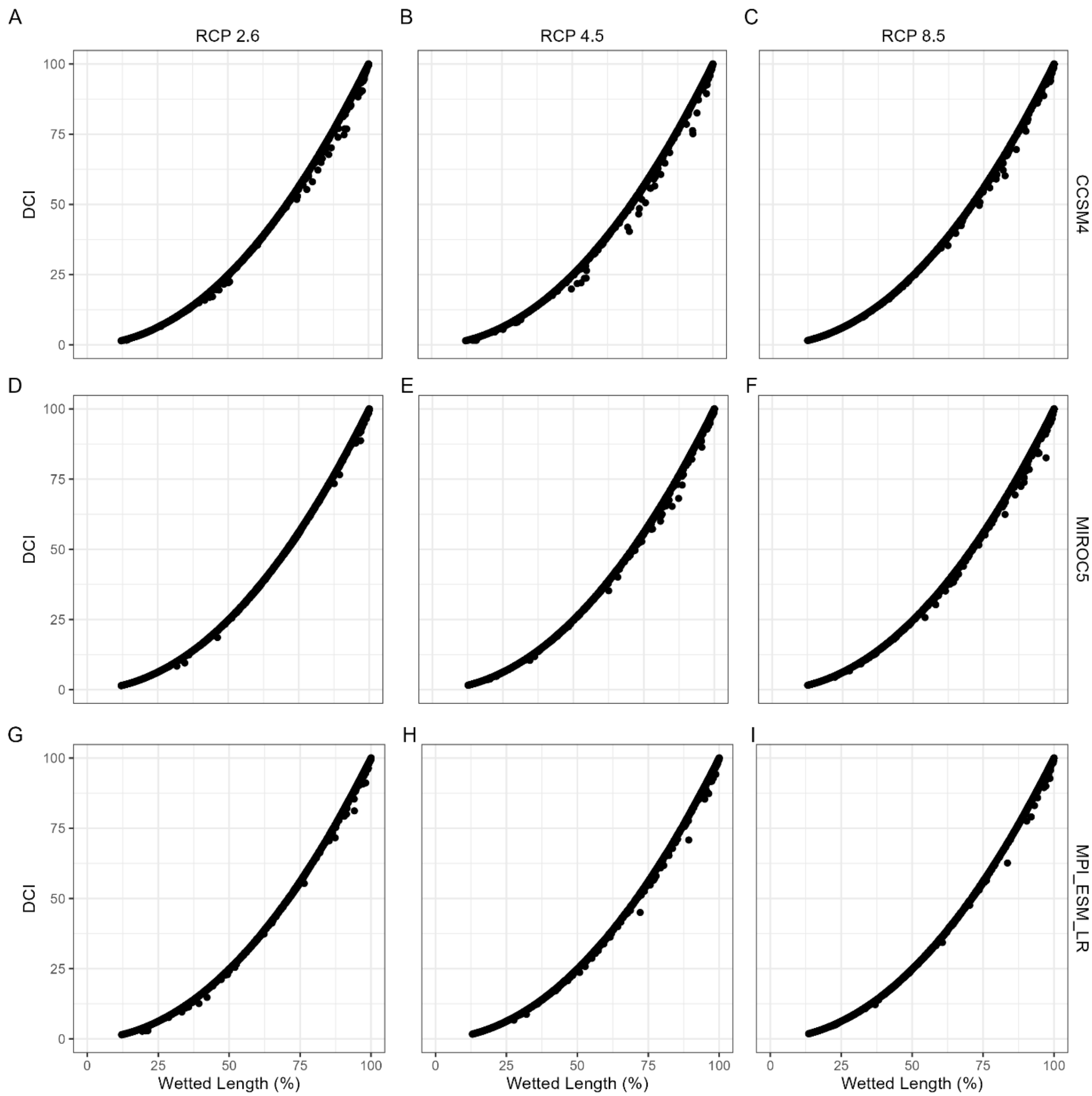

Figure S1-16. Relationships between wetted length and connectivity for nine climate scenarios (r = 0.99, $p < 0.05$). Climate scenarios result from all combinations of three GCMs (rows) and three RCPs (columns).

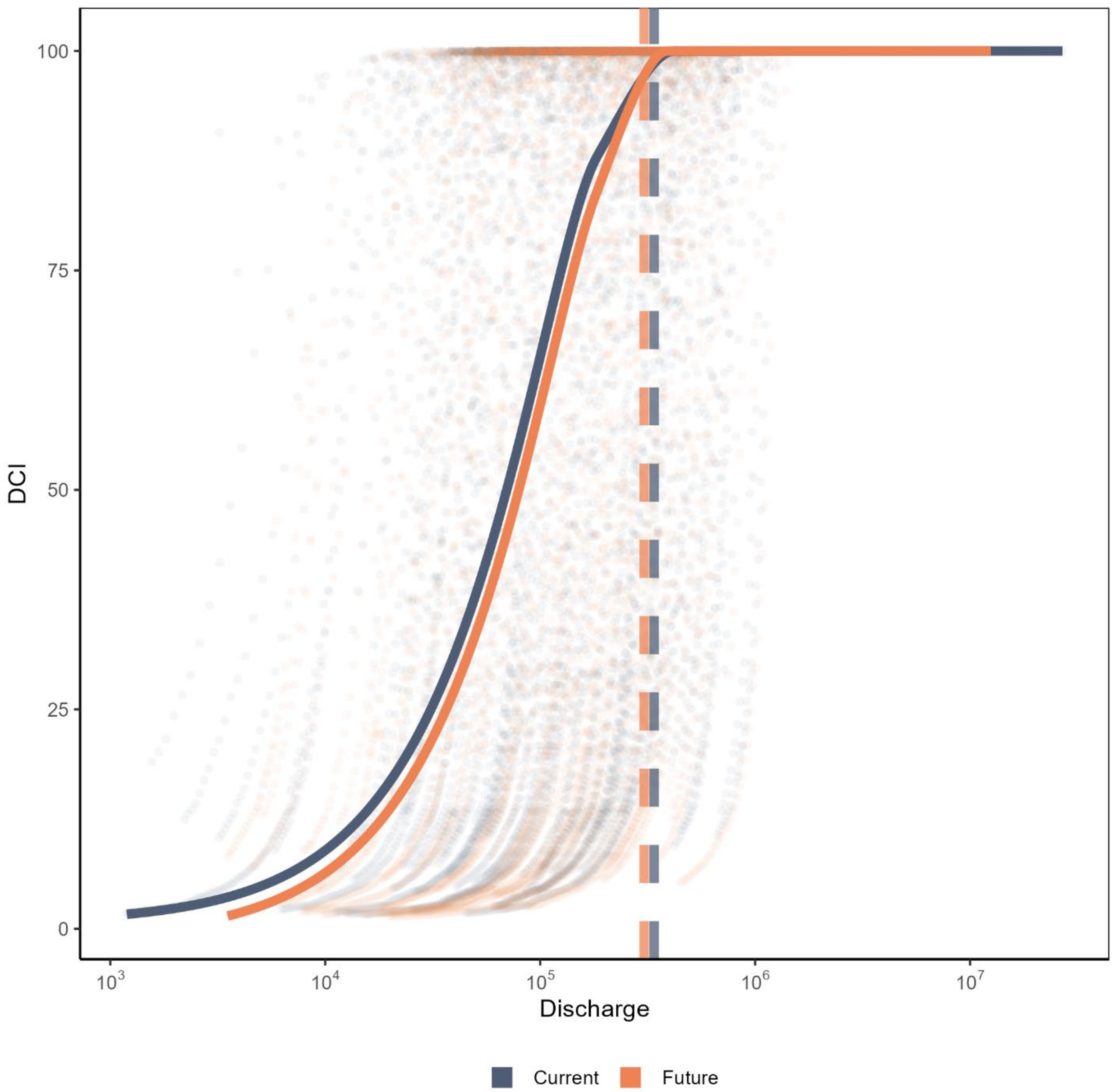

Figure S1-17. Relationship between watershed daily discharge (m^3/day) and connectivity for the hydrologic model driven by CCSM4 GCM for RCP 2.6 for the current and future study periods. Points represent days and lines represent relationship modeled using smoothing splines. Dashed lines represent mean daily discharge for current and future study periods.

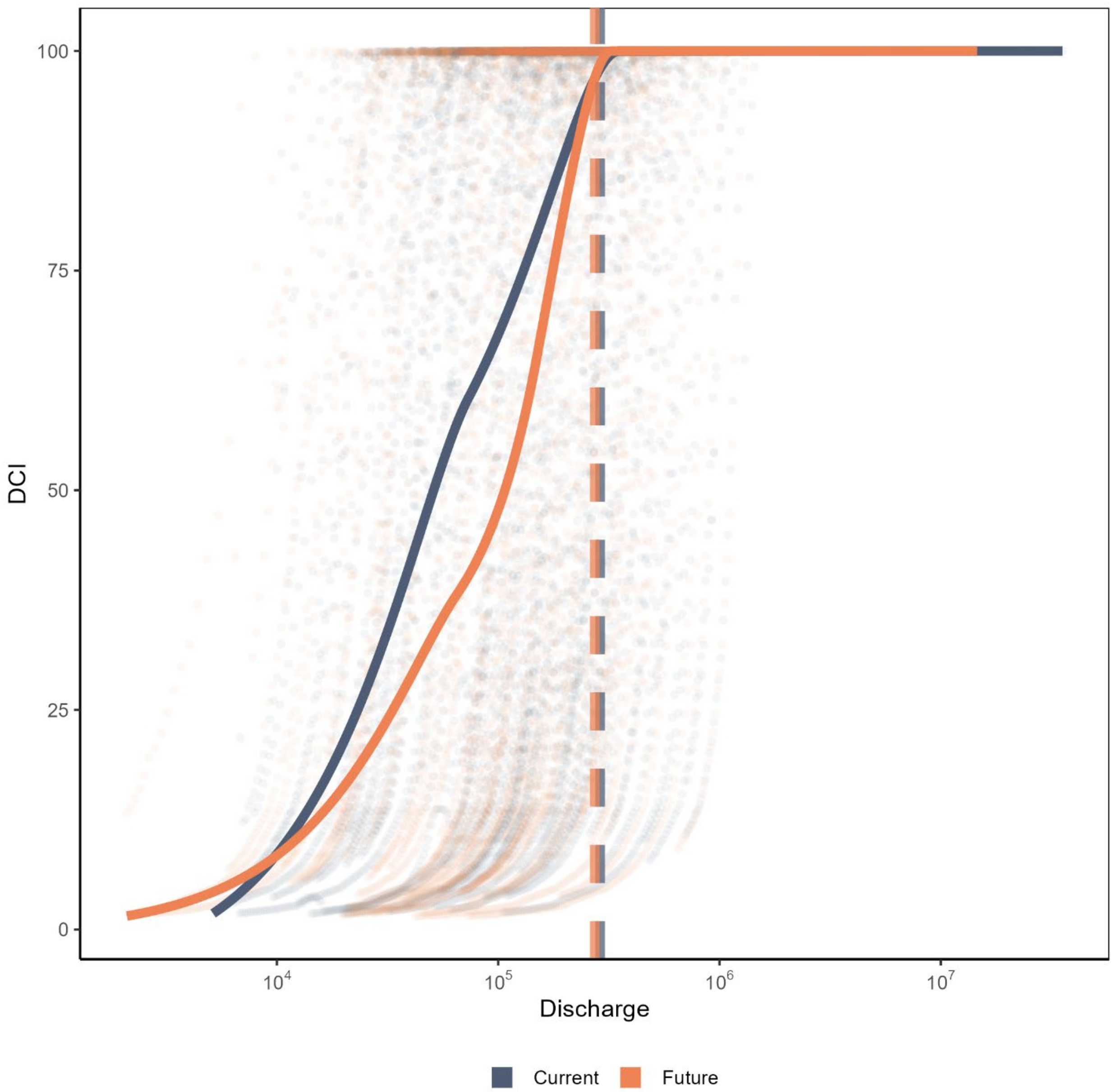

Figure S1-18. Relationship between watershed daily discharge (m^3/day) and connectivity for the hydrologic model driven by CCSM4 GCM for RCP 8.5 for the current and future study periods. Points represent days and lines represent relationship modeled using smoothing splines. Dashed lines represent mean daily discharge for current and future study periods.

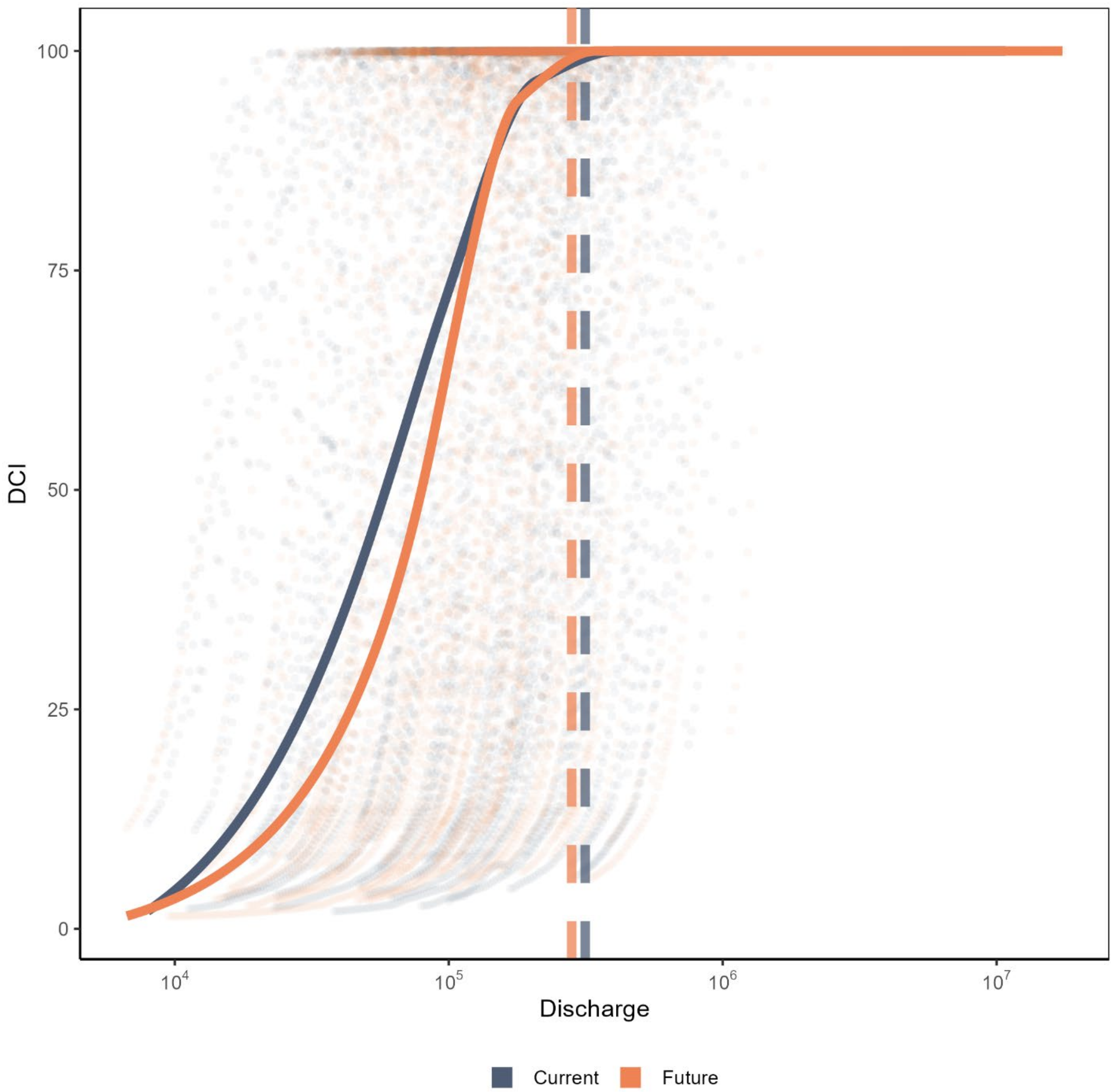

Figure S1-19. Relationship between watershed daily discharge (m^3/day) and connectivity for the hydrologic model driven by MIROC5 GCM for RCP 2.6 for the current and future study periods. Points represent days and lines represent relationship modeled using smoothing splines. Dashed lines represent mean daily discharge for current and future study periods.

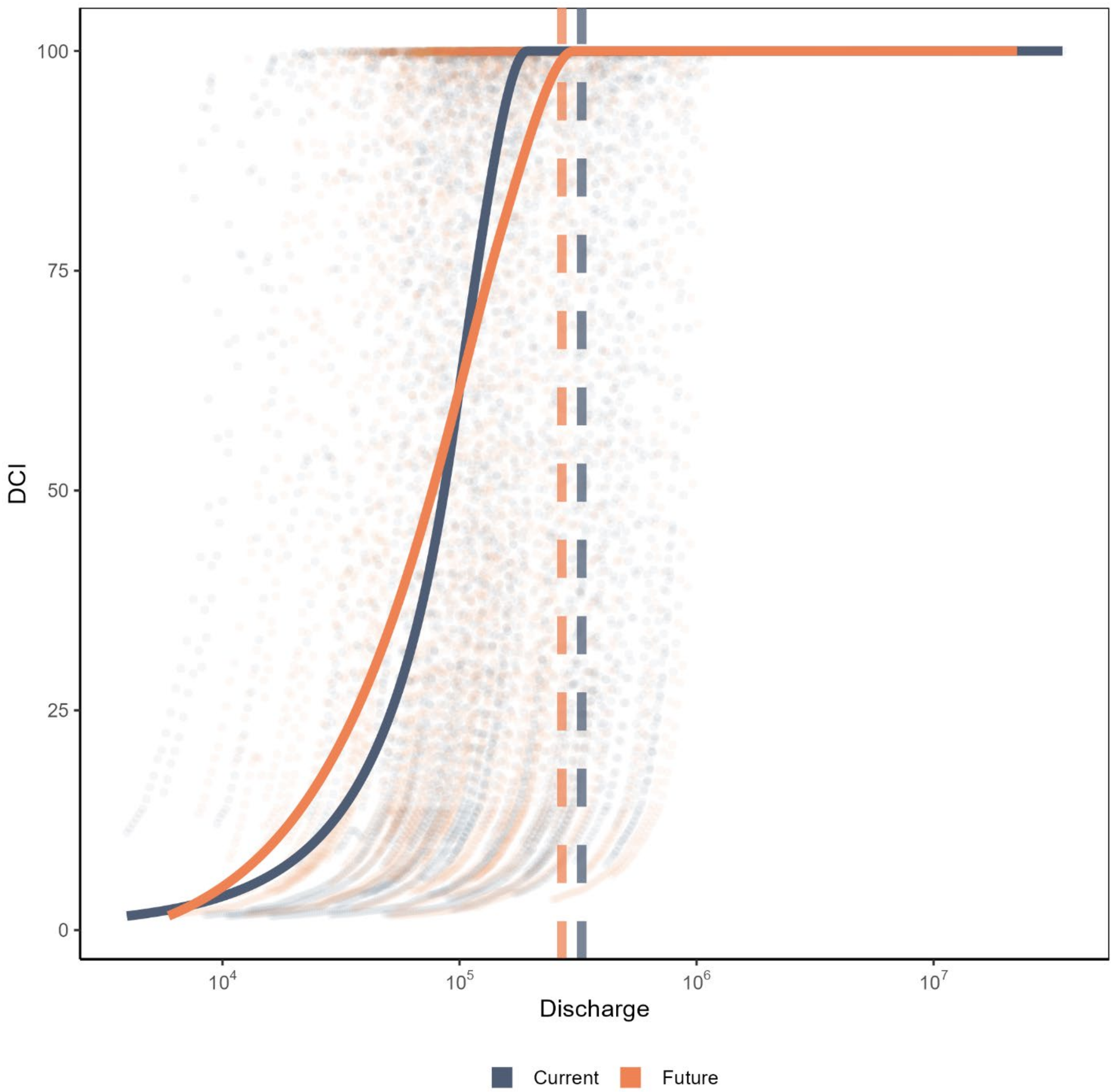

Figure S1-20. Relationship between watershed daily discharge (m^3/day) and connectivity for the hydrologic model driven byMIROC5 GCM for RCP 4.5 for the current and future study periods. Points represent days and lines represent relationship modeled using smoothing splines. Dashed lines represent mean daily discharge for current and future study periods.

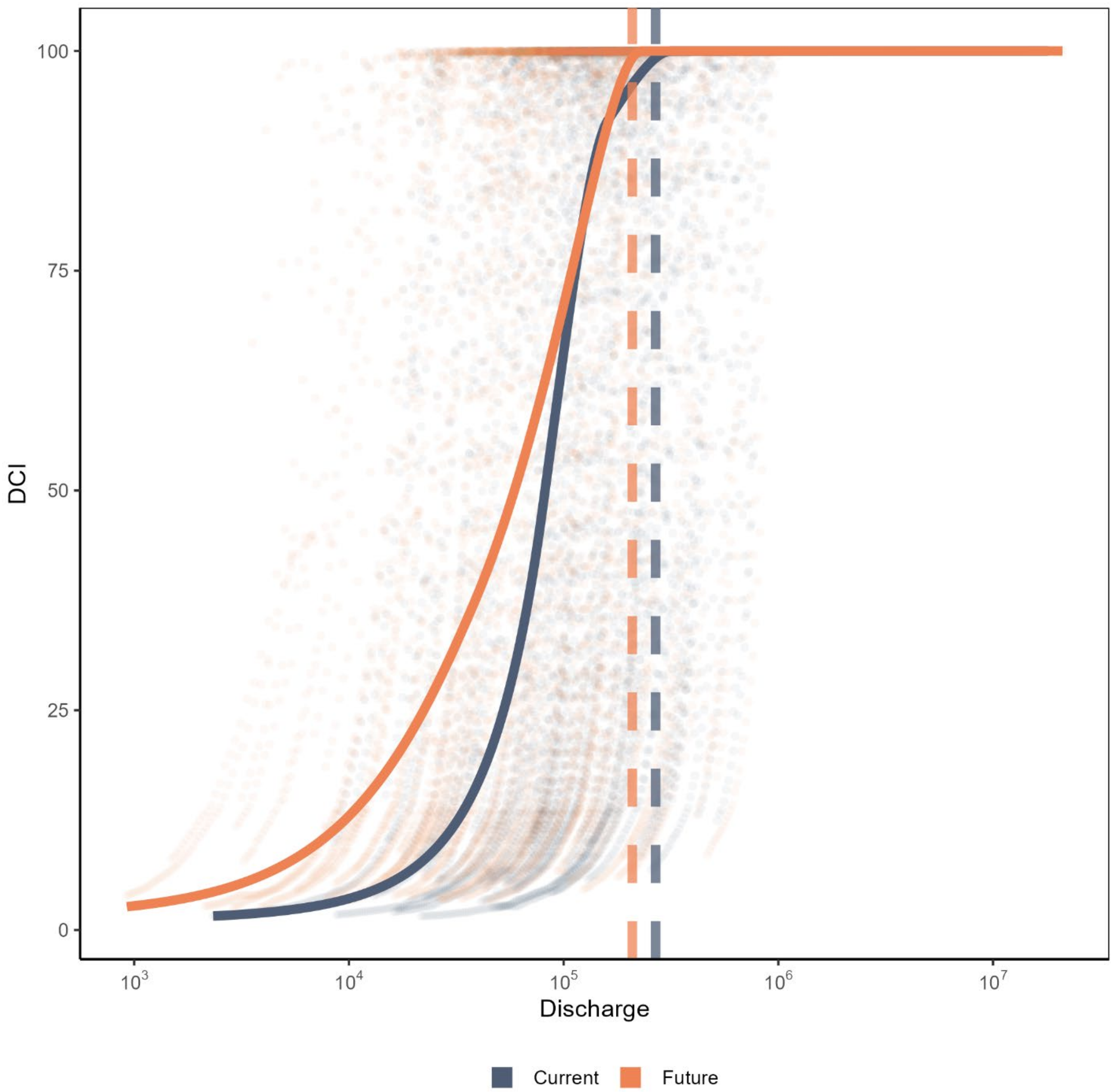

Figure S1-21. Relationship between watershed daily discharge (m^3/day) and connectivity for the hydrologic model driven by MIROC5 GCM for RCP 8.5 for the current and future study periods. Points represent days and lines represent relationship modeled using smoothing splines. Dashed lines represent mean daily discharge for current and future study periods.

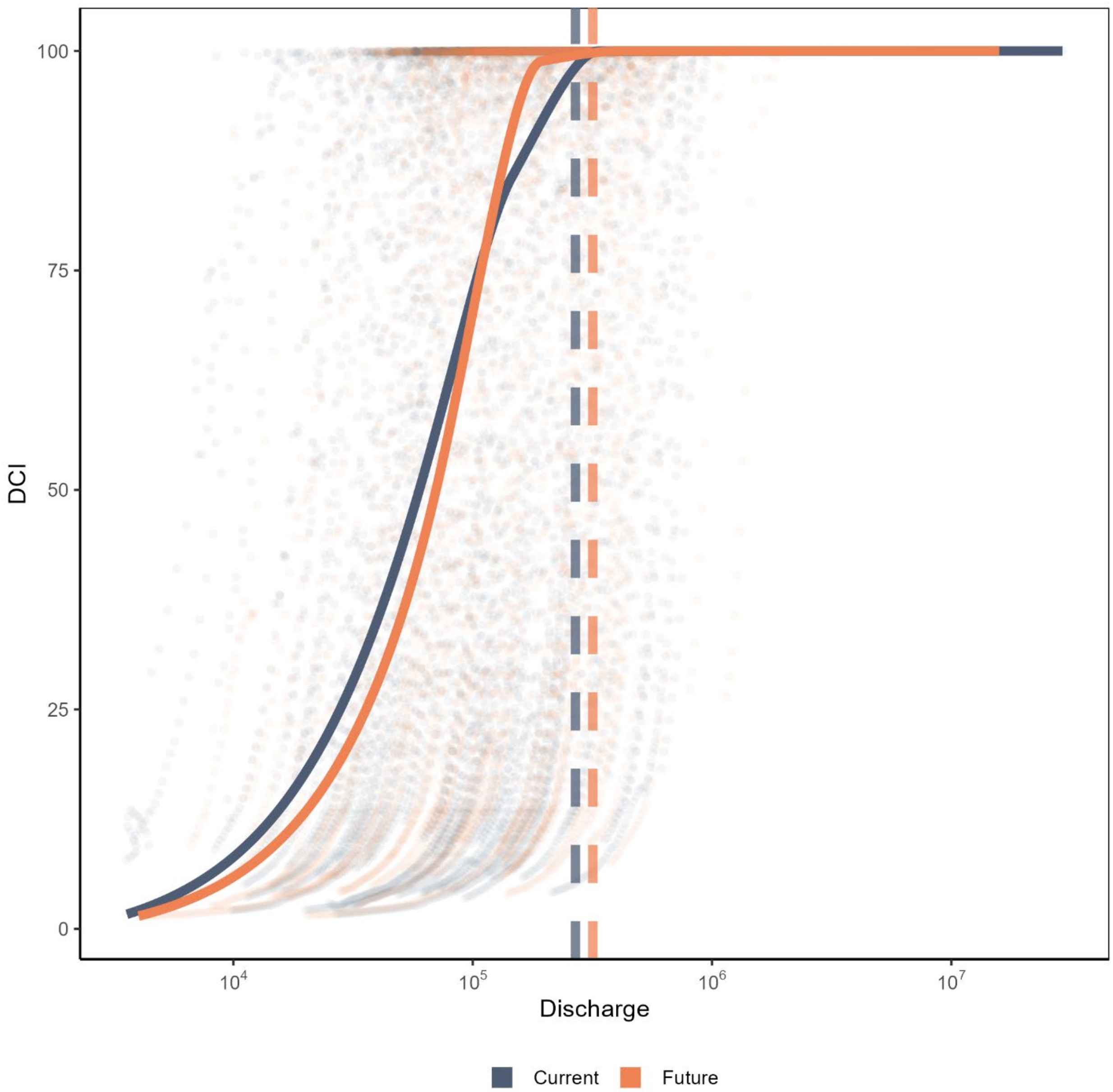

Figure S1-22. Relationship between watershed daily discharge (m^3/day) and connectivity for the hydrologic model driven by MPI_ESM_LR GCM for RCP 2.6 for the current and future study periods. Points represent days and lines represent relationship modeled using smoothing splines. Dashed lines represent mean daily discharge for current and future study periods.

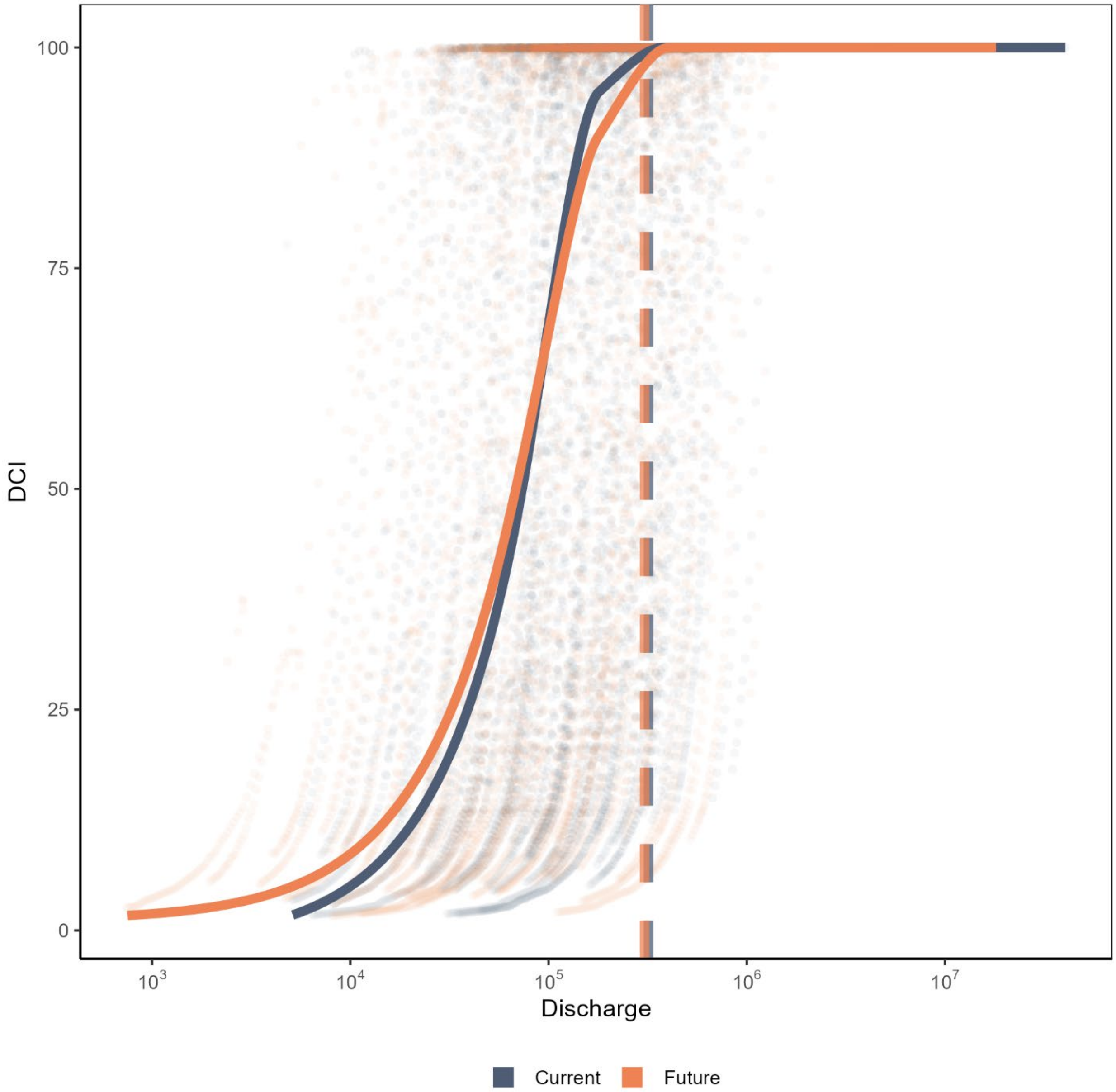

Figure S1-23. Relationship between watershed daily discharge (m^3/day) and connectivity for the hydrologic model driven by MPI_ESM_LR GCM for RCP 4.5 for the current and future study periods. Points represent days and lines represent relationship modeled using smoothing splines. Dashed lines represent mean daily discharge for current and future study periods.

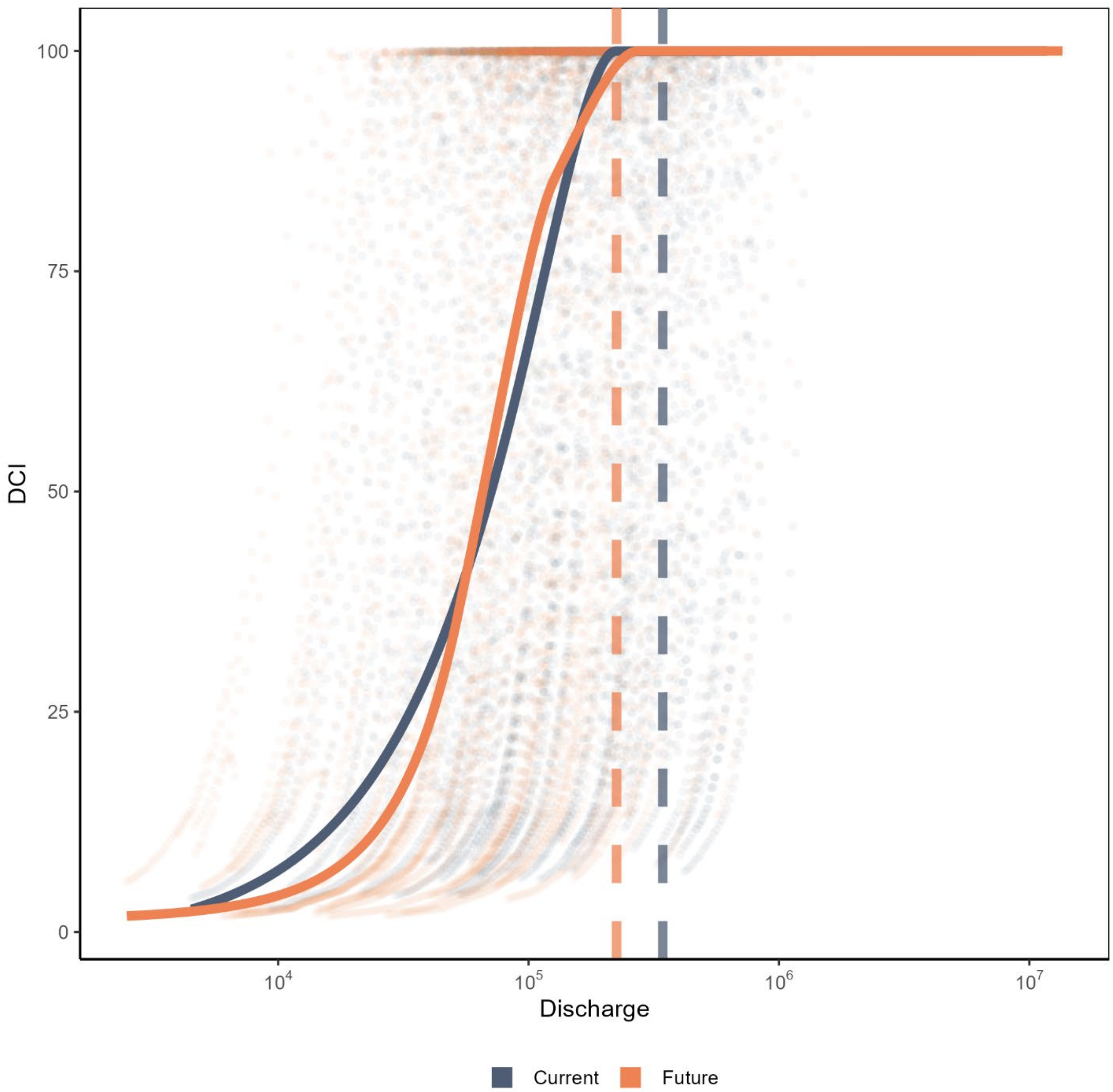

Figure S1-24. Relationship between watershed daily discharge (m^3/day) and connectivity for the hydrologic model driven by MPI_ESM_LR GCM for RCP 8.5 for the current and future study periods. Points represent days and lines represent relationship modeled using smoothing splines. Dashed lines represent mean daily discharge for current and future study periods.

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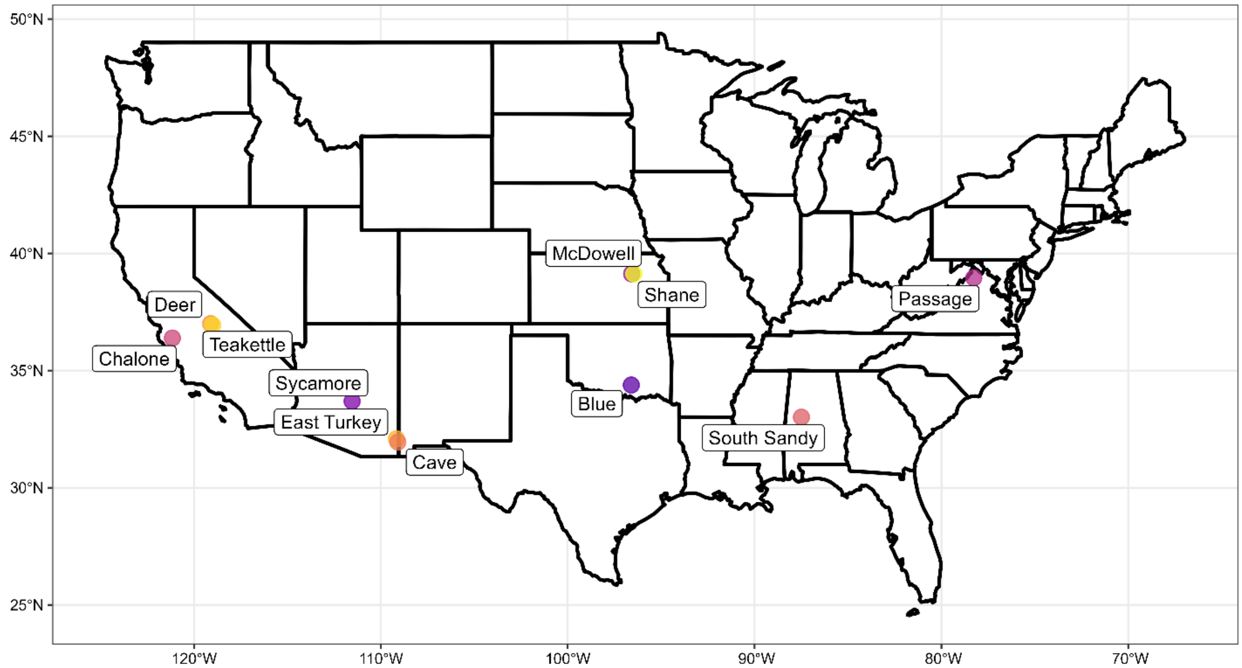

Figure S2-1. Locations of the study stream networks.

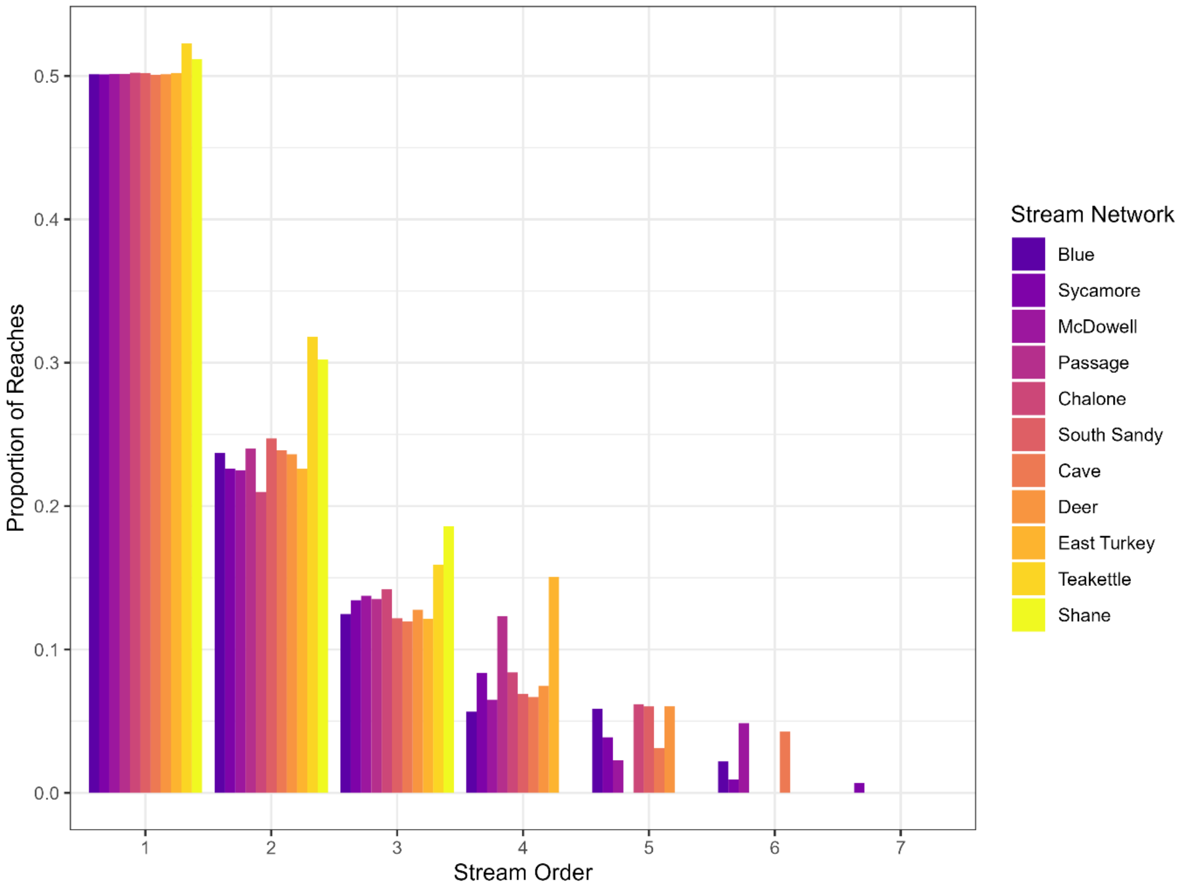

Figure S2-2. Composition of each stream network by Strahler stream order.

Table S3-1. Mean daily discharge (m^3/day) and dendritic connectivity index (DCI) values under current and future climate scenarios, and the p-value resulting from t-tests comparing each climate scenario. Blue indicates significant increases in daily discharge or DCI. Red indicates significant decreases in discharge or DCI. Stream networks are ordered from most arid to least arid.

Stream Network	Mean Discharge (Current)	Mean Discharge (Future)	Mean DCI (Current)	Mean DCI (Future)
Sycamore	11567	16634	2.8	3.9
East Turkey	1118	1290	4.9	4.6
Chalone	11051	12652	9.2	9.3
Cave	3829	4360	6.6	5.8
Deer	117060	115687	82.9	80.8
Teakettle	10851	9976	83.6	81.7
McDowell	129165	178408	17.8	20.9
Shane	1181	2124	17.0	20.3
Blue	189015	245374	25.1	24.7
Passage	133050	156623	68.4	65.4
South Sandy	178257	206002	50.9	47.8