Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams

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Protecting hydrologic connectivity of freshwater ecosystems is fundamental to ensuring species persistence, ecosystem integrity, and human well-being. More frequent and severe droughts associated with climate change are poised to significantly alter flow intermittence patterns and hydrologic connectivity in dryland streams of the American Southwest, with deleterious effects on highly endangered fishes. By integrating local-scale hydrologic modeling with emerging approaches in landscape ecology, we quantify fine-resolution, watershed-scale changes in habitat size, spacing, and connectance under forecasted climate change in the Verde River Basin, United States. Model simulations project annual zero-flow day frequency to increase by 27% by midcentury, with differential seasonal consequences on continuity (temporal continuity at discrete locations) and connectivity (spatial continuity within the network). A 17% increase in the frequency of stream drying events is expected throughout the network with associated increases in the duration of these events. Flowing portions of the river network will diminish between 8% and 20% in spring and early summer and become increasingly isolated by more frequent and longer stretches of dry channel fragments, thus limiting the opportunity for native fishes to access spawning habitats and seasonally available refuges. Model predictions suggest that midcentury and late century climate will reduce network-wide hydrologic connectivity for native fishes by 6–9% over the course of a year and up to 12–18% during spring spawning months. Our work quantifies climate-induced shifts in stream drying and connectivity across a large river network and demonstrates their implications for the persistence of a globally endemic fish fauna.

fragmentation | temporary streams | barriers | groundwater extraction

Representing one of the most critically imperiled environments in the world (1), virtually every drop of water is managed, accounted for, and allocated for human use in arid ecosystems of the American Southwest (2). Ephemeral and intermittent streams (hereafter called "dryland streams") that fluctuate between drying and wetting are a distinguishing characteristic of these ecosystems and are associated with a range of important ecological and societal values (3). From a landscape perspective they provide essential hydrologic connectivity during bouts of stream inundation by linking a patchwork of perennial habitats over space and in time. Hydrologic connectivity—here referring to the upstream–downstream longitudinal connection of surface water—is widely recognized as a primary driver of freshwater ecosystem structure and function (3, 4) and is considered fundamental to organic matter and nutrient transport and the persistence of aquatic species by facilitating the repeated recolonization of motile and drifting organisms from isolated stream pools (refuges) to rewetted channel reaches that are intermittently dispersed throughout the river network (5, 6).

Prospects of a rapidly changing climate that include more frequent and severe droughts (7) and human population growth leading to further demand of water resources (8) are poised to increase the spatial and temporal extent of dryland streams that periodically cease to flow. Natural perennial streamflow in the American Southwest has already declined or disappeared completely over the last 2 centuries (9), and future temperature warming and altered climate regimes are predicted to further increase aridity and reduce streamflow (10). Surface flows in dryland streams are particularly vulnerable to even small changes in climate; therefore, with even modest warming and decreased precipitation, there are expected large increases in the frequency and extent of dry streambeds and reduced hydrologic connectivity, especially during prolonged droughts. In addition, increased water demand to meet projected population growth is expected to further reduce surface and groundwater resources, which support streamflow (11). Therefore, habitat changes associated with stream drying are likely to include shifts from perennial to intermittent flow, loss and fragmentation of aquatic habitat, and alterations in nutrient retention, in-stream production, and species assemblages (7).

Despite the fact that dryland streams are a global phenomenon (4) and mounting recognition that their freshwater biodiversity is severely threatened (12), considerable scientific uncertainty exists regarding the fate of these ecosystems in a rapidly changing climate. The Lower Colorado River Basin has been a flashpoint for this predicament, where the highly endemic fish fauna has precipitously declined over the 20th century (three-quarters of the species are listed under the US Endangered Species Act) in response to large-scale hydrologic alteration and land modification (13) and the ecological impacts of invasive species (14). Notwithstanding advances in our general understanding of how climate change may affect freshwater ecosystems (15, 16), we remain poorly positioned to predict local habitat loss from stream drying events and understand how these patterns scale up to shape habitat fragmentation through changes in hydrologic connectivity and affect population persistence of

Significance

We provide the first demonstration to our knowledge that projected changes in regional climate regimes will have significant consequences for patterns of intermittence and hydrologic connectivity in dryland streams of the American Southwest. By simulating fine-resolution streamflow responses to forecasted climate change, we simultaneously evaluate alterations in local flow continuity over time and network flow connectivity over space and relate how these changes may challenge the persistence of a globally endemic fish fauna. Given that human population growth in arid regions will only further increase surface and groundwater extraction during droughts, we expect even greater likelihood of flow intermittence and loss of habitat connectivity in the future.

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endangered species. Disparities in spatial scales between the data output of global and regional climate models (GCMs and RCMs) and the data requirements of local hydrologic models have resulted in only limited advances in these research areas (17), and unlike the dedicated research efforts in terrestrial ecology (18, 19), the ecological implications of climate-induced habitat fragmentation in freshwater ecosystems remain both uncertain and underappreciated.

In the present study we demonstrate that projected changes in regional climate regimes will have significant consequences for patterns of intermittence and hydrologic connectivity in dryland streams of the American Southwest. By simulating fine-resolution streamflow responses to forecasted climate change, we simultaneously evaluate alterations in local flow continuity over time and network flow connectivity over space and relate how these changes may challenge the survival of a globally endangered fish fauna. Given renewed interest in the notion of landscape fluidity and the essential need for organisms to respond to environmental gradients that are shifting through time (20), our investigation uses hydrologic modeling to quantify fine-resolution, landscape-scale changes in habitat size, spacing, and connectance at multiple spatial and temporal scales under forecasted climate change in the Verde River Basin (VRB; Fig. 1), a large tributary to the Lower Colorado River, United States.

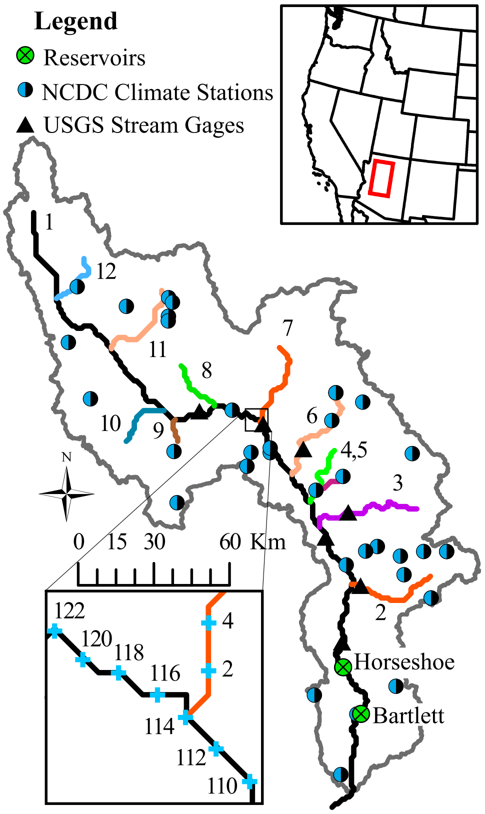

Fig. 1. The study region of the VRB. Numbers are as follows: 1, main stem Verde River; tributaries: 2, East Verde; 3, West Clear Creek; 4 and 5, Wet and Dry Beaver Creek, respectively; 6, Oak Creek; 7, Sycamore Creek; 8, Hell Canyon; 9, Granite Creek; 10, Williamson Wash; 11, Partridge Creek; and 12, Unnamed Tributary included in the hydrologic (SWAT) modeling. Locations of 7 USGS stream gages, 43 National Climate Data Center (NCDC) climate stations, and 2 reservoirs are also identified. Bottom left inset illustrates river kilometer along a portion of the main stem and Sycamore Creek (indicated by 7), which served as the basis for the nodes used in the hydrologic modeling. Crosses refer to river kilometer along river segments increasing in the upstream direction. Top right inset indicates the location of the Verde River Basin in Arizona.

Results and Discussion

Future climate-driven changes in streamflow are predicted to be dramatic in arid ecosystems of the American Southwest. Hydrologic simulations for the midcentury Representative Concentration Pathway8.5 (RCP8.5) climate scenario (*Materials and Methods* and *SI Materials and Methods*) project consistent decreases in streamflow magnitudes throughout much of the river network (Fig. 2) and chronic stream drying (Fig. 3 and *SI Materials and Methods*) in most tributaries and some portions of the main stem in the VRB (late century stream drying patterns are reported in *SI Materials and Methods*). Together, these result in both reduced streamflow continuity over time and connectivity over space. Despite native fishes having evolved life history strategies to cope with the harsh environmental conditions that occur as a result of stream drying events (21), the predicted spatiotemporal changes in streamflow likely will have critical consequences for the distribution, abundance, and persistence of these already highly threatened species into the future.

By midcentury, projected stream drying will result in marked network-wide decreases in streamflow continuity as a consequence of more frequent zero-flow days expressed as frequent stream drying events of prolonged duration (Fig. 3 and *SI Materials and Methods*). Throughout the network, the median number of annual zero-flow days is predicted to increase by 27% (1 to >30 d at individual nodes), with the greatest increase occurring in the spring (45%). Increases of 1–3 zero-flow periods per year at individual nodes reflect a median 17% increase (Fig. 3 and *SI Materials and Methods*). In addition, these stream drying events generally are projected to be of longer duration extending up to 15 d longer at individual nodes (Fig. 3). Increases in stream drying are focused in the upper extent of the tributaries and in both the upper and middle river segments of the main stem (Fig. 3).

Climate-induced loss of streamflow continuity, and the spatiotemporal manner in which these changes are manifested across the river network, could further threaten species persistence and induce community and ecosystem shifts in dryland streams (e.g., refs. 5 and 6). Population persistence of native fishes is compromised during prolonged climatically dry periods due to the combined loss of available habitat and heightened risk of competition with and predation by nonnative fishes (22, 23). Further decreases in streamflow continuity associated with more frequent and intensive channel drying during spring (spawning) and summer low-flow months will effectively reduce the amount of available habitat for reproduction and may eliminate critical summertime refuges. Native fishes in the remaining refuges will face extreme physicochemical stress (i.e., high temperature and low dissolved oxygen concentration) and increased species interactions with nonnative species (6), promoting high local extinction probabilities (24). Climate-induced changes projected for the upper main stem are most concerning for the conservation of spikedace (*Meda fulgida*), which was recently up-listed from threatened to endangered under the Endangered Species Act (US Fish and Wildlife Service, 77 FR 10810, February 23, 2012) and whose designated critical habitat is extremely limited and includes this upper portion of the Verde River. In summary, headwater streams and their connectance to the greater river network are critical to maintaining regional biodiversity in riverine systems (25), and our results suggest that these may be at considerable risk by future climate change.

Chronic stream drying in the future also will reduce network-wide streamflow connectivity for all seasons but more severely for the spring and extending into the early monsoon period (Fig. 4). Decreases in Dendritic Connectivity Index (DCI) values are driven by both the expansion in the length of dry channel fragments and the increased occurrence of these fragments. This results in an overall decrease in the proportion of the river network supporting streamflow (Fig. 5). During the spring, decreased DCI is dominated by an expansion (14% mean increase) in the lengths of dry channel fragments (Fig. 5). Decreased DCI

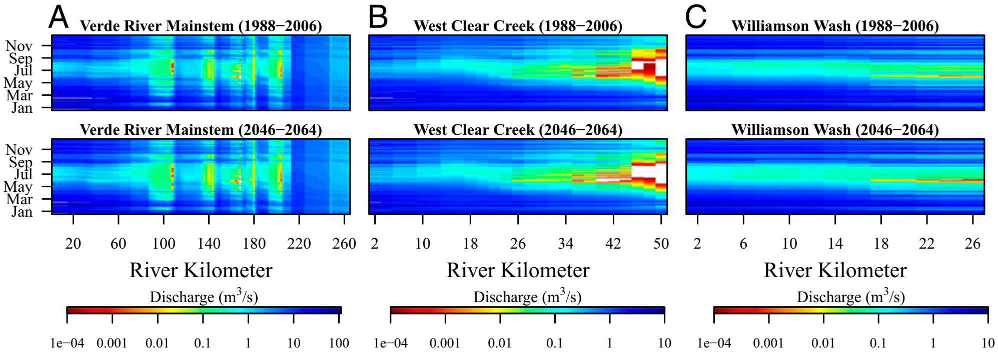

Fig. 2. Mean daily discharge for current (1988–2006) (*Upper*) and future (2046–2064) (*Lower*) climate scenarios for the Verde River main stem (*A*), West Clear Creek (*B*), and Williamson Wash (*C*). Current and future time period values reflect a mean daily discharge values of the CF-adjusted time series used in the hydrologic model. The *x* axis represents river kilometer location increasing in the upstream direction. The *y* axis represents the 365-d calendar year. White space indicates no flow (daily discharge values < 0.0001 m^3/s) at that river location (e.g., node). Discharge magnitude values (m^3/s) expressed by color gradation increasing from red to blue. Color shifts in the future simulation period from green and blue to red and orange and increased area of white reflect decreases in average discharge magnitudes and increased stream drying frequencies.

extending into early summer reflects a failure for dry channel beds to rewet during the monsoon season to the extent of present-day conditions, resulting in moderate increases (5% mean increase) in both the length of the mean daily average dry channel fragment and frequency of these dry fragments (Fig. 5).

Model predictions show that climate change will shrink the length of the remaining flowing reaches, which may further increase species interactions and resource limitations and compromise the ability of these habitats to support native fishes (12). During the spring and early monsoon seasons, flowing regions are projected to diminish between 8% and 20% (Fig. 5). These regions that support flow are increasingly isolated as adjacent dry fragments expand in length and occur more frequently across these seasons. This result has significant consequences for the future of dryland stream fishes given documented associations between stream fragment length and species probabilities of extirpation (26) and ultimately metapopulation persistence and community structure (27, 28).

The Verde River Basin follows a seasonal connectivity regime that exerts strong influences on the physical, chemical, and biological processes throughout the riverine network. Connectivity naturally declines during spring as the snowmelt season progresses and intermittent stream channels go dry (Fig. 4). In the summer monsoon season, river networks experience short episodes of contraction and expansion of wetted areas. During these times, fish become concentrated in available refuges but have opportunities to recolonize habitat upon rewetting of dry channels to take advantage of decreased predation and competition and increased food availability. Winter reflects a resetting of the river system at the network scale, when connectivity is characteristically highest, allowing for organic matter and nutrients to be transported and processed downstream and fish to redistribute across the river network (29). Because winter and spring seasons represent naturally high levels of riverine connectedness, reductions in the spatial extent of available habitat as well as connectivity between these habitats during this time (Fig. 4), especially in the spring (Fig. 5), will both shrink critical opportunities for nutrient transport throughout the system and limit the ability of aquatic organisms to access different necessary resources. Similar stream drying trends in the summertime (Figs. 3–5) may mean that perennial patches, which have served as the only remaining habitats, become even more reduced in size and isolated from each other under climate change.

Climate-induced drying of desert streams will lead to temporal shifts in refuge availability and spacing, where the dispersal capacity of organisms will be a major determinant of refuge use and ultimately population persistence (30). With stream drying, some species may undergo direct migrations to refuges, such as river reaches with permanent water, whereas other species with limited mobility may be confined to nearby pools (6). Our models suggest that midcentury climate will reduce network-wide hydrologic connectivity for native fishes by 4–7% over the course of a year and up to 14% during spring and 5% during monsoon months (Table 1). Although life history strategies of a number of native southwestern fishes include colonization of habitats newly available due to temporary surface flow (29), predicted reductions in hydrologic connectivity may push many species beyond their ability to cope. For example, Gila topminnow (*Poeciliopsis occidentalis*) are highly dependent upon rapid colonization of seasonally available streams and backwaters to expand their populations before retreating into shrinking habitat during dry seasons or drought (31). Longfin dace (*Agosia chrysogaster*) often use intermittent and sometimes ephemeral reaches to reproduce, where fish may make substantial movements into newly wetted reaches after high-flow events to recolonize suitable habitats and reproduce before being forced

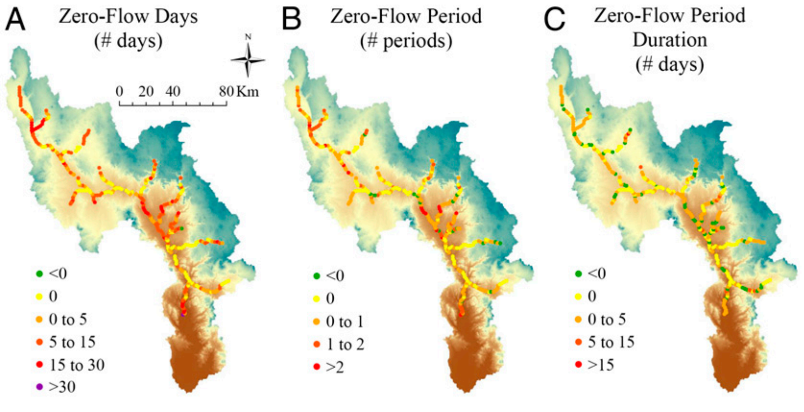

Fig. 3. Difference in mean number of zero-flow days (*A*), zero-flow periods (*B*), and zero-flow period duration (*C*) per year between current (1988–2006) and future (2046–2064) time periods (*Materials and Methods*). Network-wide increases in zero-flow days, zero-flow periods, and zero-flow durations are generally focused in upper reaches of tributaries and along portions of the middle and upper main stem.

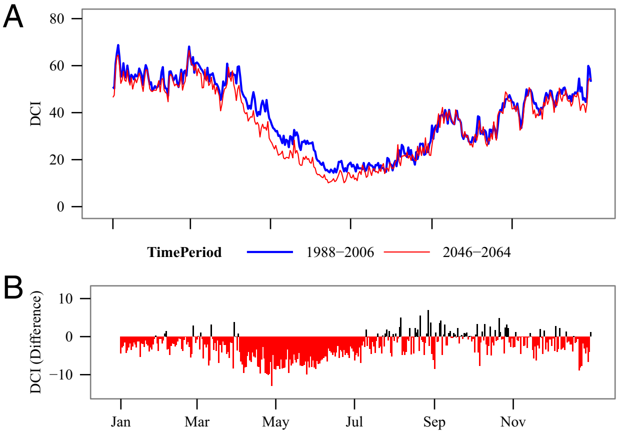

Fig. 4. Dendritic Connectivity Index (DCI) using two-parameter exponential decay function for current (1988–2006) and future (2046–2064) simulation periods (*A*) and differences in mean daily DCI between the two time periods (*B*). Blue solid and red dashed lines (*A*) are mean daily DCI for the current and future time periods, respectively. Differences in mean daily DCI (*B*) are negative (red) or positive (black) for each day. Overall differences between current and future simulation periods reflect a 9% decrease (11% SD) in connectivity under climate change. Seasonal decreases in connectivity include 4% (4% SD) in winter, 17% (10% SD) in spring, and 5% (13% SD) in summer.

out by drying (32). Finally, native sucker species (*Catostomus clarki, C. insignis*) and roundtail chub (*Gila robusta*) can make extensive migrations before spawning (33), and evidence from other dryland streams suggests that reductions in hydrologic connectivity can prevent spawning-related movements (34). Although significant decreases in hydrologic connectivity were predicted across all species, small-bodied species with more limited dispersal abilities may be more challenged in the future.

Our predictions are conservative in that human population growth in arid regions will only further increase surface and groundwater extraction during droughts, causing even greater likelihood of flow intermittence and loss of connectivity (11, 35). The population in Arizona is expected to increase by 50 to ∼100% by 2050 (36). Estimates for this growing population indicate that human water demand in portions of the VRB is equivalent to 50–200% of current base flow volumes depending on the suite of conservation and growth scenarios (8). Projected depletion of groundwater, which supports base flow in the VRB, is dramatic even under moderate population growth scenarios (11). In particular, historical and modern (1910–2005) groundwater pumping in the middle VRB has already resulted in decreased streamflow and is expected to continue into the next century (37). Our models identify this portion of the VRB as especially sensitive to stream drying as a consequence of forecasted climate change.

Our results assess the impacts of climate change on surface runoff but not on base flow supported by subsurface aquifers. The relationship between surface water and groundwater in the basin is complex (11, 38) and affected by both climate and human demands on subsurface water reserves. We expect that our analysis would present more dire increases in stream drying and reductions in connectivity if we could account for the combined pressures of climate-related reductions in groundwater recharge and human-related withdrawals associated with population growth. Therefore, continuity and connectivity estimates are conservative across the basin but particularly for the upper and middle basin that is confronted with high human water demand, low availability of base flow, and expected increases in groundwater pumping.

Protecting the hydrologic connectivity of freshwater ecosystems has been identified as a key principle for ensuring ecologically sustainable water resource development and human well-being (39). Recent decades have witnessed perennial streams and their associated riparian communities contracting or disappearing in many arid and semiarid regions around the world as a result of surface diversions and groundwater extraction (40). The loss of streams and rivers continues to have large social, economic, and ecological consequences. Future climate warming is predicted to increase the frequency of droughts in many regions (7), and here we quantify the spatiotemporal extent of dry riverbeds under climate change and their implications for a globally endangered fish fauna. Compounding these effects will be the challenge for fishes to respond to increasing water temperatures by shifting their distributions in space and time to track thermally suitable habitats (41).

Materials and Methods

Study Region. Our study focused on the VRB (15,800 km^2 catchment area), a large tributary of the Lower Colorado River Basin, Arizona, United States (Fig. 1), characterized by a relatively mild degree of flow regulation and comparatively high representation of endemic desert fishes including federal and state listed fish species (42). Rugged mountains and valleys compose the VRB topography. The climate is arid to semiarid with sharp temperature and precipitation gradients, exhibiting bimodal seasonality composed of a cool, wet winter season (December–March) and a warm summer monsoon season (July–September) (43). Streamflow is derived from a combination of surface runoff and local and regional aquifers (43), resulting in a predominantly perennial main stem with several contributing tributaries of both perennial and intermittent flow (*SI Materials and Methods*). Main stem perennial flow begins at approximately the confluence with Granite Creek [river kilometer (RK) 150] at a run-of-the-river dam, Sullivan Dam; upstream of this location, streamflow is intermittent and ephemeral. Bartlett Dam (94 m height) and Horseshoe Dam (62 m) are located in the lower basin (Fig. 1).

Hydrologic Modeling. We used the hydrologic model Soil Water Assessment Tool (SWAT) to quantify present-day and forecasted streamflow continuity and connectivity. SWAT is a continuous, semidistributed precipitation runoff model developed by the United States Department of Agriculture (44). The model uses spatially explicit elevation, soil, and land cover data coupled with daily precipitation and temperature data to simulate watershed hydrologic processes including evaporation, infiltration, runoff, and streamflow (*SI Materials and Methods*). We used a modified version of SWAT (45)

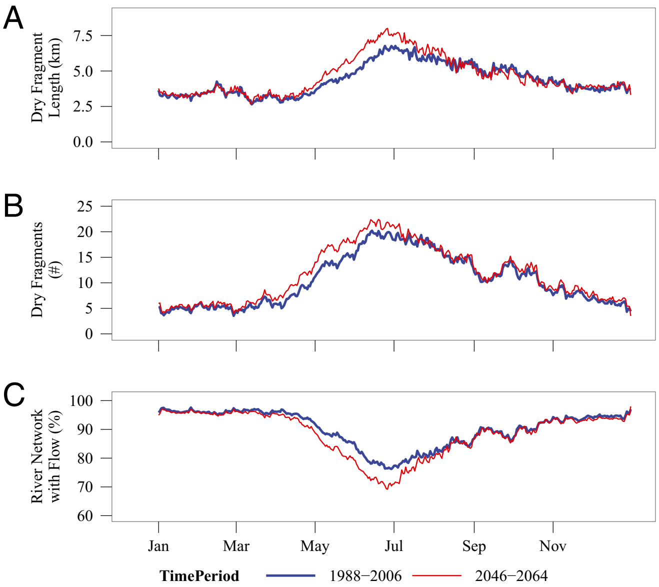

Fig. 5. Mean daily average length (km) of dry channel fragments (*A*), number of dry channel fragments (*B*), and percent of the VRB network that supports flow (*C*). Values are presented for current (1988–2006; blue) and future (2046–2064; red) periods. Increases in both the average length of dry channel fragments and occurrences of dry fragments are projected for the future time period during spring and early summer with associated decreases in proportion of the river network that supports streamflow.

Table 1. Effects of climate-induced changes in hydrologic connectivity on native fish species in the VRB according to estimated median annual dispersal distance of mobile fishes in the population

Species	Median annual dispersal, km	Overall DCI		Percent reduction in DCI			
		Current	Future	Overall	Spawning	Monsoon	Winter
Poeciliopsis occidentalis, Gila topminnow	0.5	57	54 (52)	7 (10)	14 (21)	5 (7)	2 (3)
Agosia chrysogaster, longfin dace	1.0	57	54 (52)	7 (10)	14 (21)	5 (7)	2 (3)
Meda fulgida, spikedace	1.0	57	54 (52)	7 (10)	14 (21)	5 (7)	2 (3)
Rhinichthys osculus, speckled dace	1.3	57	54 (52)	7 (10)	14 (21)	5 (7)	2 (3)
Catostomus clarki, desert sucker	5.7	73	69 (68)	6 (9)	12 (18)	5 (8)	2 (2)
Gila robusta, roundtail chub	10.9	79	76 (74)	5 (7)	10 (15)	4 (6)	2 (2)
Catostomus insignis, Sonora sucker	29.4	82	79 (78)	4 (6)	7 (12)	4 (5)	1 (1)

Overall DCI future values represent the midcentury simulation period. Percent reduction [calculated as $(\mathrm{DCI}_{\mathrm{future}} - \mathrm{DCI}_{\mathrm{current}})/\mathrm{DCI}_{\mathrm{current}} \times 100$] in mean daily DCI values between current and midcentury simulation periods is reported for the entire year (overall) and seasonally according to estimated fish species' dispersal distance. Late century (time period) values for overall DCI and percent change in DCI are reported in parentheses. All percent change values represent a decrease in connectivity for both future simulation periods and therefore are reported as percent reduction.

to account for forecasted changes in CO_2 concentration. We simulated daily discharge (m^3/s) with model output locations, hereafter referred to as "nodes," occurring at an ∼2-km interval along the Verde River main stem upstream of Horseshoe Reservoir (264 km in total) and 11 tributaries (*SI Materials and Methods*). Model modification, calibration, and validation are detailed in *Supporting Information*.

We modeled streamflow in the VRB using values from a multimodel mean (mmm) analysis that included 16 GCMs (16-mmm) for current (1988–2006), midcentury (2046–2064), and late century (2080–2098) time periods. We used a proportional change factor (CF) adjustment that used monthly mean proportions between modeled and observed climate data (46); daily observed data were multiplied by this factor to produce a synthetic downscaled dataset. Three synthetic daily records were generated to represent current, midcentury, and late century time periods. The 16-mmm were under the RCP8.5 scenario, which represents the highest radiative forcing and gas emission scenario and therefore the worst case scenario developed for the Intergovernmental Panel on Climate Change Assessment Report Five (47). We specified a CO_2 concentration of 489 ppm and 800 ppm for midcentury and late century periods, respectively (47, 48). A 19–20 y simulation period maximizes both the available historical data for all of the representative US Geological Survey (USGS) stream gauges and climate stations used to calibrate and validate the hydrologic model (*SI Materials and Methods*). In addition, this simulation period is considered suitably representative for hydrologic analyses as hydrologic metrics tend to stabilize with >15 y of data (49). We report results from hydrologic simulations for the CF-adjusted current and midcentury simulation periods, hereafter referred to as "current" and "future" periods; late century results are summarized in *Supporting Information*.

Quantifying Habitat Loss, Fragmentation, and Fish Persistence Under Climate Change. We evaluate habitat loss and fragmentation by quantifying stream drying characteristics in terms of streamflow continuity (continuous through time) and connectivity (continuous through space), respectively (in the sense of ref. 50). Habitat loss is interpreted as an elimination of surface flow (e.g., stream drying) at discrete nodes through time (i.e., decreased continuity). Habitat fragmentation is interpreted as disruptions in continuous stretches of surface flow along a channel as a result of stream drying (i.e., decreased connectivity). We apply numerous metrics that build on previous work (e.g., refs. 51 and 52) to simulated streamflow from the current and future simulation periods. Habitat loss and fragmentation are based on comparisons of the stream drying continuity and connectivity metrics between the two simulation periods, which are summarized annually and seasonally to capture changes in flow during ecologically relevant time periods for fish and ecosystem processes.

Continuity metrics that quantify habitat loss at individual nodes include the number of zero-flow days (node discharge values < 0.0001 m^3/s), the number of zero-flow periods (discrete unitless periods of consecutive zero-flow days), and duration of zero-flow periods (number of days within a discrete zero-flow period). All three metrics were tallied for each node for the CF-adjusted current and future time periods. Differences between the current and future periods were computed for each node. We report both the individual node differences to illustrate the finer spatial variability in stream drying within a river segment (e.g., the Verde River main stem or a tributary) and summarize across all nodes within a river segment to represent broader-scale patterns of stream drying.

Connectivity metrics to evaluate habitat fragmentation were quantified in terms of the frequency and length of dry channel fragments [which can isolate flowing reaches that serve both as biological refuges during stream drying events and colonization sources when flow resumes (8)] and a DCI after Cote et al. (51). Dry channel fragments represent continuous portions of the stream channel where adjacent nodes simultaneously have zero flow but are separated from other dry fragments by at least one node that supports streamflow for that same time period. The DCI is conceptualized as the probability that a fish originating at a given location in the river network will disperse to any other location within the basin. The index is scaled from 0 (low habitat connectivity and no chance of dispersal) to 100 (high habitat connectivity and high dispersal potential). The index was originally developed to evaluate the impact of culverts as barriers on fish passability at a river basin scale (see ref. 50), but here we modified its formulation by (*i*) considering a dry channel fragment as a temporary barrier to fish movement and (*ii*) applying barrier (i.e., dry channel fragments) passability based on both generalized and system-specific fish dispersal distance (see *Fish Species Sensitivity to Changes in Habitat Fragmentation* and *SI Materials and Methods*).

Fish Species Sensitivity to Changes in Habitat Fragmentation. As habitat fragmentation increases in response to climate-induced changes to streamflow, fish species will be required to disperse through rewetted channels to recolonize suitable habitats containing abundant food resources, meet spawning requirements and access rearing habitats, and avoid predators (32–34, 53). Fish species differ greatly in their mobility, where individuals may rapidly recolonize over many meters or many kilometers from remaining locations of permanent water. Recent studies have supported the idea of heterogeneous movement by fish where populations consist of both stationary (represented by a high peak in the leptokurtic dispersal kernel and linked to the fish home range) and mobile (represented by the fat tail in the leptokurtic dispersal kernel and reflecting long-distance dispersal events) components (54). Mobile fishes are hypothesized to be responsible for facilitating the recolonization (i.e., rescue) of isolated habitats after major disturbance events and thus are decisive for genetic exchange and supporting long-term persistence (55). In our study, we interpret the passability of the temporary dry barrier when surface flow resumes as a function of a mobile fish's ability to disperse the distance of that rewetted channel (12).

First, we assessed network-wide habitat fragmentation by quantifying barrier passability in the DCI based on a generalized fish dispersal curve. Specifically, a two-parameter exponential decay function was used to describe the typical leptokurtic dispersal kernel where the frequency of dispersal decreases with distance from an individual's home range (54). This reflects the phenomenon that although most fish travel only short distances from their home range, a few mobile individuals may travel substantially longer distances, for example, as a consequence of opportunistic movement during a high-flow event or during periods of prolonged hydrologic connectivity.

Next, we evaluate differences in the sensitivity of native fish species in the VRB to habitat fragmentation by calculating DCI barrier passability based on a simple binary threshold. Species-specific thresholds were estimated by fitting leptokurtic dispersal kernels presented in meta-analysis by Radinger and Wolter (56) where median annual movement rate (km) of mobile individuals is predicted as a function of fish morphology (body length and aspect ratio of the caudal fin) and river characteristics (Strahler stream order). We took the conservative approach (i.e., maximizing estimated dispersal) by setting body length to the maximum recorded value for the species; aspect ratio was derived from photographs of prepared specimens in the literature, and stream order was defined as the maximum stream of the VRB or 6 (*SI Materials and Methods*). We apply the estimated annual dispersal distance as a binary threshold distance, for which the length of a dry channel reach is considered passable if it is less than or equal to the estimated dispersal distance or not passable if the length exceeds the estimated dispersal distance.

We generate a network-wide DCI using both calculation methods—generalized species dispersal (continuous function) and species-specific dispersal (binary threshold)—for every day in the current and future simulation periods. Mean daily DCI values for each simulation period represent DCI values for each calendar day averaged across all years within the simulation period. We report differences in mean daily DCI between current and future simulation periods both annually and seasonally.

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