



## Hydrology as a driver of biodiversity: Controls on carrying capacity, niche formation, and dispersal

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### ABSTRACT

A synthesis is presented highlighting the importance of hydrologic variables and dynamics to biodiversity patterns. The focus of this paper is the key hydrologic controls crucial towards quantifying the impacts of climate changes on the distribution of species. Specifically, we highlight the hydrologic controls operating on the carrying capacity, niche formation, and dispersal dynamics. This synthesis will facilitate avenues of future research and is connected to issues of major practical importance, such as the integration of the structure of river networks into conservation strategies and the evaluations of the impacts of climate change on biodiversity.

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### 1. Introduction

Maintenance of biodiversity across multiple scales has been of basic interest to the biological and ecological sciences for decades [43,41,31]. The debate over the ultimate controls on biodiversity is a contentious one and indeed the numerous papers investigating them rarely reach solid conclusions. However, it is without debate that patterns exist across taxa, geographical areas, and geological eras [67]. With the ever growing body of literature detailing the benefits provided by biodiversity [12,14,21,30], increasing attention is being paid towards its fundamental drivers and how changes to key components could affect specific patterns of biodiversity. Additionally, increased global species loss [58] has made it critical to better understand the processes that govern biodiversity.

The principal threats to biodiversity vary widely depending on geographic location and the complicating effects of differences in spatial and temporal scale. At present, the principal threats to biodiversity are the effects due to land use change and associated habitat loss and fragmentation, as they act on a much shorter time scale than other processes [28,19,55,56]. Several global modeling scenarios show that land use changes will continue to be the principal reason for terrestrial biodiversity loss until at least 2050 [34,56,71,72]. However, climate change is likely to be the major reason for biodiversity loss worldwide after 2050 [48,75,76].

While the predicted ultimate percentage loss of species due to climate change varies widely from study to study (e.g. [44,77]), the IPCC reports that 20–30% of animal and plant species are likely to be at high risk of extinction with a global mean annual temperature rise of 2–3 °C [75]. Indeed, research has shown that despite the numerous possible explanations for changes in biological patterns and communities, climate change effects are already influencing biodiversity through range shifts and alteration of phenology [19,56]. This loss of biodiversity has the ability to produce a multitude of consequences, such as the loss of ecosystem functioning and reduction or elimination of goods and services [56]. Many of these responses may be nonlinear and difficult to predict [5], leading to rapid transitions or sudden shifts in ecosystem states [56,20,74].

One of the major pathways through which climate change will impact biodiversity patterns is through altered hydrologic patterns and processes [83]. It is well known that climate change will impact global precipitation patterns [53,75], resulting in increased variability in rainfall regimes in both time and space [54], which, in turn, change the hydrologic conditions that regulate ecological processes [13,67,59,46]. This is one of the reasons why it is important to focus on the specific mechanisms through which hydrology impacts biodiversity. In this paper, we present a synthesis of some of the most important hydrologic controls on biodiversity, with an eye towards understanding the potential impacts of climate change. Note that we make no attempt to summarize the vast literature that relates to the many and varied interactions between hydrology and species diversity. Instead, we focus on hydrologic

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controls that can be used to quantify the impacts of climate changes on biodiversity.

While the role of hydrology on biodiversity within freshwater ecosystems may seem self evident, hydrologic controls also play a vital role in structuring and maintaining terrestrial ecosystems [16,65,73]. Hydrology has been shown to play a vital role in structuring terrestrial vegetation, particularly in water-limited ecosystems. In water-limited ecosystems, soil moisture controls the availability of nutrients and limits plant transpiration [64,65]. In humid ecosystems, the interactions between water and energy cycles increases in importance, and the diversity of trees is influenced by evapotranspiration [13]. Vegetation communities in riverine systems are often structured by hydrogeomorphological interactions [2]. Hydrologic disturbances, including droughts and floods, play an important role in the maintenance of both aquatic and floodplain ecosystems [38]. Likewise, droughts and floods are important determinants of vegetation diversity in terrestrial systems [78].

Hydrology is not the only factor impacting biodiversity patterns and processes. For example, it is well known that the species richness of almost all life forms increases from high to low latitudes and along elevation gradients. This latitudinal diversity gradient is thought to be generated by several mechanisms, such as the availability of energy, historical perturbations, and interactions between species, but may simply be a consequence of more land area in the tropics [66,67]. The biogeography of plants in mid- to high latitudes may best be explained by the space–time patterns of the shortwave radiative flux [17]. Determining the ultimate controls on biodiversity patterns is complicated by the fact that the specific underlying mechanisms and their importance may differ across both spatial and temporal scales. Hydrologic processes act with considerable variability across multiple spatial and temporal scales, which is one of the reasons why biodiversity is likely influenced by some aspect of hydrology at most scales of analysis [13,63,59].

In this paper we focus on three specific determinants of diversity for which hydrology may play an important role and which can be used to quantify potential climate change impacts. In Section 2, we describe the hydrologic control of the spatial pattern of carrying capacity in some ecosystems. Section 3 discusses the hydrologic control of niches favoring or restricting the existence of different species. Section 4 describes the hydrologic control of dispersal mechanisms, with a focus on lotic populations in river networks. We look to the future in Section 5.

## 2. Hydrologic control of carrying capacity

‘Carrying capacity’ is defined as the maximum number of individuals or units of organisms that can be maintained in a given area on a long-term basis. Some habitats are far more productive than others and, in general, more productive areas support more individuals and more species [13]. However, this pattern is often complicated and may follow a non-monotonic relationship in many systems [67]. For this reason, we draw examples from natural systems for which an increase in the carrying capacity has been shown to lead to more species. The focus of this section is the hydrologic control of the spatial distribution of carrying capacity.

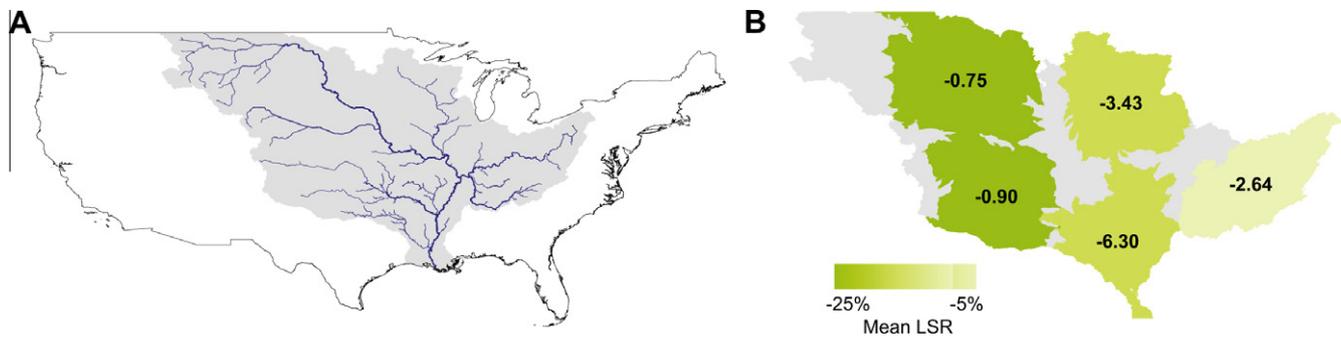
The relationship between hydrology and carrying capacity has been established for quite some time [81,25,62]. Both terrestrial and aquatic ecosystems with more freshwater resources tend to support more individuals. Here, we focus on the controlling influence of hydrology in both aquatic and terrestrial ecosystems: namely, the influence of precipitation on the carrying capacity of trees and the impact of flow characteristics on the carrying capacity of fish.

Recently, mean annual precipitation was found to be the major determinant of potential woody cover in African savannas [73]. Sankaran et al. [73] demonstrate that maximum fractional woody cover, which proxies for the carrying capacity of trees, is primarily controlled by moisture limitation. They conduct a continental-scale analysis of Africa in an effort to determine whether savannas are primarily climatically determined or disturbance driven, finding that savannas are predominantly water limited in locations with less than approximately  $650 \text{ mm yr}^{-1}$ , while those locations that receive greater than  $650 \text{ mm yr}^{-1}$  are disturbance driven. Thus, mean annual precipitation controls the upper bound on woody cover, although disturbance regimes and soil characteristics do impose significant controls on woody cover below the bound [73].

Recent research builds upon the work of Sankaran et al. [73] and utilizes mean annual precipitation as a driver of carrying capacity to model distributions of tree species diversity. Konar et al. [39] demonstrate that a neutral meta-community model, coupled with an appropriate representation of tree carrying capacity, effectively reproduces empirical patterns of tree diversity. The model was not able to reproduce empirical tree diversity patterns without a spatial representation of tree carrying capacity based on rainfall [39,11]. This analysis was conducted for the Mississippi Watershed (shown in grey in Fig. 1A), showing that mean annual precipitation appropriately characterizes the carrying capacity of trees in humid ecosystems. Note that forest cover was used as a proxy of tree carrying capacity in Konar et al. [39], rather than woody cover as in Sankaran et al. [73], which accounts for differences in functional form. Additionally, Sankaran et al. [73] focus on savannas, which, by definition are regions with tree-grass co-existence, i.e. tree cover never reaches 100% in savannas. Two hydrological variables were considered for use as a driver of forest cover in Konar et al. [39]: evapotranspiration and mean annual precipitation. The relationship between forest cover and mean annual precipitation exhibited a more well-defined relationship than that between forest cover and evapotranspiration. Additionally, projections of mean annual precipitation under climate change scenarios are readily available, making this variable desirable for projection purposes.

Importantly, the modeling approach used in Konar et al. [39] has predictive powers, since it allows for the direct linkage of large-scale biodiversity patterns to environmental forcings. Projections of mean annual precipitation under different climate scenarios were used to obtain new values of tree carrying capacity for the Mississippi Watershed. With these resulting new carrying capacities, Konar et al. [39] determine how various climate change scenarios are projected to affect tree diversity patterns in the Mississippi Watershed. 15 climate change scenarios are implemented in the model. Here, the spatially-explicit impacts under the most dramatic species-poor scenario are shown in Fig. 1B. Note that the probability of any particular outcome in large-scale macrobiodiversity patterns is heavily reliant on the probabilities associated with the projected precipitation patterns provided by the global climate models. For this reason, the patterns should be interpreted as envelopes of plausible biodiversity scenarios, rather than as predictions of biodiversity outcomes. Tree diversity patterns are impacted more under the species-poor scenarios than under the species-rich scenarios, with the exceptions of a few select regions, where impacts are of comparable magnitudes under both scenarios. Additionally, rare species are disproportionately impacted under climate change [39], a finding shared with niche-based models [50].

Recent research indicates that the timing and intensity of rainfall may be a more important driver of carrying capacity than sheer quantities of rainfall in some systems [70,22,1]. In a continental-scale analysis of Africa, Good and Caylor [22] build upon the work of Sankaran et al. [73] and demonstrate that the quantity and intensity of rainfall events influences the upper limit of woody



**Fig. 1.** (A) Map of the Mississippi Watershed within the continental United States. The Mississippi Watershed is highlighted in grey and the network structure in blue. (B) Impact of climate change on region-averaged local species richness (LSR) in sub-regions of the Mississippi Watershed. Shades of green indicate the percentage change in the region-averaged local species richness under climate change, with dark green indicating a higher percentage lost. The general trend is that a higher percentage of species are lost in the west with a decreasing trend to the east. The change per local community in region-averaged local species richness under climate change is indicated for each region by the bold numbers. The species-rich regions east of the 100°W meridian lose more species, though these species represent a smaller percentage of species in these regions. The mean local species richness in the South is anticipated to decrease by 6.3 species under climate change, the largest loss of all sub-regions. Taken and modified from Konar et al. [39] and Bertuzzo et al. [4]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

vegetation cover. They show that areas with similar seasonal rainfall totals have higher fractional woody cover if the local rainfall climatology consists of frequent, less intense precipitation events. This distinction is crucially important since climate change is projected to lead to more intense, less frequent storm events, with important repercussions for vegetation. Similarly, Bartholomeus et al. [1] demonstrate that increased extremes in soil moisture, similar to those likely to be observed under climate change, will impact plant functional groups, though this study does not address the impact of hydrologic variation on species diversity directly. To our knowledge, there has not yet been a study that quantifies the impact of hydrologic variation on species diversity, so this represents an important area for future research. Thus, although hydrologic averages may drive the carrying capacity and diversity in some systems, spatial and temporal variability may prove more important in other ecosystems.

The carrying capacity of organisms in river systems is strongly impacted by the gradient of a number of physical factors connected to the drainage network [81]. In fact, the flow of water, which is strongly correlated with other physical variables, can be considered a “master variable” that limits the distribution and abundance of organisms in rivers [63,59]. Recent research on fish biomass demonstrates the importance of flow characteristics. Halls et al. [27] developed a flood index that accounts for the extent and duration of flooding during the entire flood period of the Tonle Sap River, Cambodia. Fish biomass varied by almost a factor of 5 in response to the flood index over the last decade [27]. The Mekong River is subject to rapid development, with the construction of several large-scale hydropower dams and reservoirs [40]. The related flow alterations will have significant impacts on productivity and numbers of fish in Tonle Sap ecosystem, with significant repercussions for fish diversity.

Taking advantage of the relationship between the number of fish and river flow, Xenopoulos et al. [84] analyze the projected impacts of climate change and future water withdrawals on fish diversity at a global scale. To address this issue, they present the first coupling of a global hydrological model with a freshwater biodiversity model. A species-discharge regression model was used to produce scenarios of fish species loss. Species richness generally increased with increased mean river discharge, in a similar manner to the species-area curve of terrestrial ecosystems [84].

Fig. 2 illustrates the 52 watersheds that Xenopoulos et al. [84] show will lose more than 10% of their fish species. The combination of increased evapotranspiration and decreased precipitation as a result of climate change (specifically, under the IPCC SRES A2 scenario

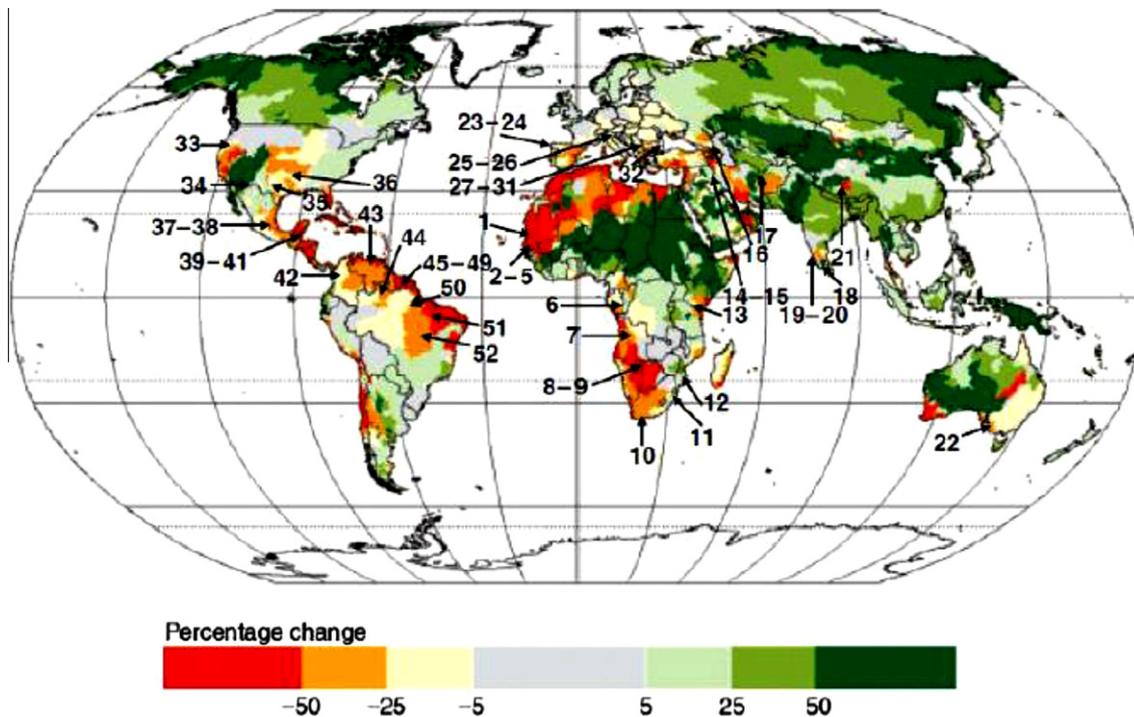
[75]) is the most important driver of freshwater fish loss. However, the impact of water withdrawal for human consumption on fish diversity is particularly important in certain watersheds. For example, consumptive water use in the Euphrates and Cauvery Rivers was the major driver of fish species losses in these watersheds. Xenopoulos et al. [84] present an excellent first approximation to the projected impacts of climate change and human modification on fish diversity. However, as with all species-distribution models, there are inherent problems in making projections based on correlations with current environmental regimes (see e.g. Pearson and Dawson [57]). For this reason, a model based upon ecological processes would be a most beneficial addition to the literature.

In this section, we have shown that hydrologic variables are important to the carrying capacity of trees and fish. Recent research demonstrates the influence of hydrology on carrying capacity [73,27,22], as well as how to utilize this relationship to quantify the impact of climate change on biodiversity patterns [84,39,1].

### 3. Hydrologic control of niches

‘Niches’ refer to segments of ecosystems that have been partitioned in both space and time and that are available for utilization by different organisms. The number of niches that a given ecosystem contains has long been thought to be a major driver of species diversity [32,67]. The hydrologic control of niches occurs across both terrestrial and aquatic environments, but may be best displayed within wetlands, as they have been a principal location for studying the relationship between hydrology and the structuring of vegetation communities [49]. Due to their dynamic hydrology, climate change impacts in these areas could be particularly severe, as slight changes in water availability may have profound influences on the surrounding biodiversity. The focus of this section is the influence of hydrology on niche structure and the role climate change may have in altering these relationships.

The hydrology of a wetland environment can be described by multiple factors, but is most often described by its hydroperiod or hydroperiod, a combination of the periodicity of inundation events for a given location along with the length and depth of inundation. One such environment where these relationships have been extensively studied is the Everglades, with multiple studies showing a relationship between the hydroperiod and vegetation communities of a given area [15,26,87]. Nevertheless, the role of hydrology in structuring vegetation communities in wetlands is difficult to determine due to a suite of interacting variables [6,69,86].



**Fig. 2.** Impact of change in water discharge from climate change and water consumption on fish diversity at a global scale. Colors display the percentage change in fish diversity, where red indicates approximately 50% loss of diversity and green indicates roughly 50% gain in diversity. The 52 watersheds that are projected to lose more than 10% of their fish species are numbered. Climate change is projected to decrease fish diversity more than water withdrawals in most watersheds. However, in a few watersheds, such as the Euphrates and Cauvery, fish species losses due to water withdrawals will be more severe. Taken and modified from Xenopoulos et al. [84]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

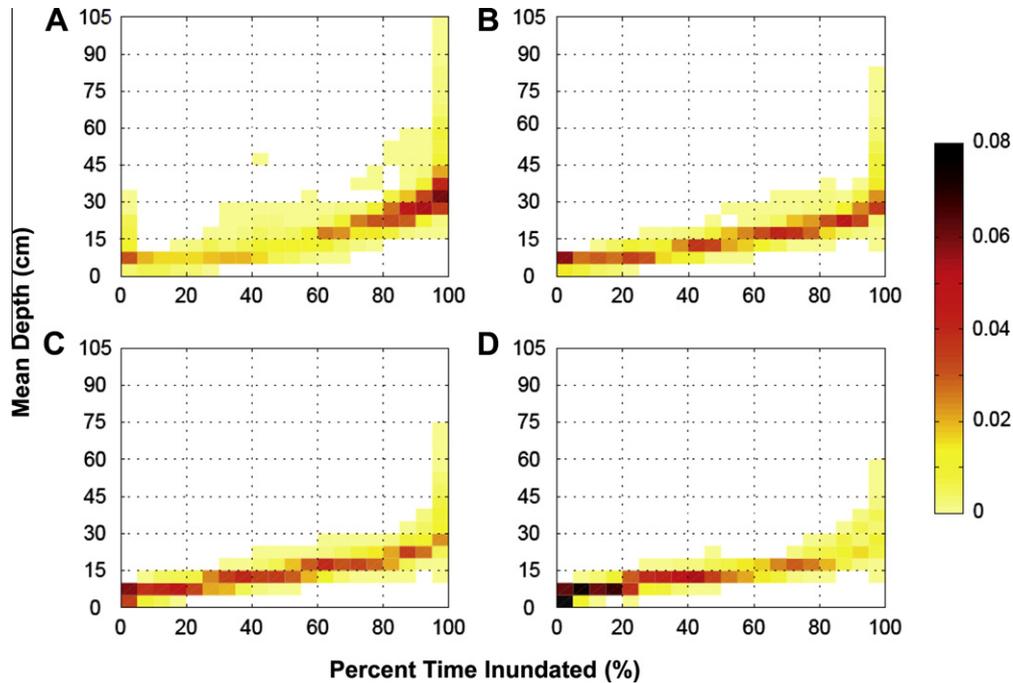
Additionally, the lack of long term temporal and wide spatial coverage data presents a further complication to understanding the role of hydrology in structuring vegetation communities.

Todd et al. [79] examine the hydrologic control of niches across a long temporal and wide spatial scale of the entire Everglades National Park (ENP). This analysis quantifies the hydrological niches of the dominant vegetation communities. Mean hydroperiod depth and percent time inundated best describe the vegetation niches. For instance, muhly grass occurs most often at shallower depths and at locations that are not inundated for long period of time. In contrast, bay-hardwood scrub favors more hydric locations. However, results for sawgrass, by far the most common vegetation community across the ENP, supported earlier studies that hydrology is not the only variable structuring sawgrass niches [26,29]. Thus, the work of Todd et al. [79] showed that, while multiple factors can influence the landscape distribution of vegetation communities, hydrology plays a principal, if not dominant role, in many cases. Most importantly, this work indicates that hydrology structures vegetative niches at large spatial and temporal scales, reinforcing the results of many studies conducted previously at smaller scales.

In an effort to gauge the impacts of projected changes in precipitation on plant diversity, Todd et al. [80] used the relationships between vegetation communities and hydrologic variables developed in Todd et al. [79]. Specifically, Todd et al. [80] utilized projected precipitation values for this region under various climate change scenarios to model future hydroperiod characteristics. Projected values of mean depth and percent time inundated are then used to determine impacts to vegetation communities, based upon the relationships described by Todd et al. [79]. Under increasing emissions scenarios, precipitation decreased across the ENP by as much as 8% from present scenarios, leading to an associated decrease in mean depth and percent time inundated (refer to Fig. 3). These

changes in hydroperiod were then used to project changes to vegetation communities. Thus, vegetation communities that favor xeric conditions increased in abundance and communities that favor hydric conditions became scarcer (refer to Table 1). For instance, the relative abundance of muhly grass, which favors xeric conditions, increased by 15% under the high emissions scenario. In contrast, the relative abundance of bay-hardwood scrub, which favors hydric environments, decreased by 66%. Thus, Todd et al. [80] utilizes the previously established relationships between hydroperiods and species distributions [79] to project the potential impacts of climate change on plant diversity at large spatial scales.

Another wetland region that has undergone intense research regarding the influence of changing climate on vegetation community structure and biodiversity is the Prairie Pothole Region of North America. This region has numerous wetlands covering a suite of inundation regimes from temporary (one to two months) to semipermanent (inundated throughout most years). Associated with these varying inundation regimes, the vegetation found therein shows complex zonation dynamics. Through the years, various models have been developed to simulate vegetation dynamics across a range of hydrologic parameters including precipitation, runoff, potential evapotranspiration, snowpack and subsurface inflow [60,61,37]. These models generally did a satisfactory job of reproducing hydrologic and vegetation conditions of these wetlands. When incorporating climate change scenarios of increases in temperature as compared to historic levels, these wetlands showed marked hydrologic changes. In general, the wetlands experienced earlier snowpack melting, decreased water depths and volume, diminished hydroperiods, and reduced peaks from snowmelt and rainfall unless rainfall across the region increases 5–7% per degree of warming [37]. However, the influence of these changes was not uniform across wetland type with seasonal wetlands being the most affected. These seasonal wetlands normally persist into



**Fig. 3.** The joint probability surface of percent time inundated and mean depth for (A) present conditions and under (B) low (B1), (C) middle (A1B), and (D) high (A2) climate emissions scenarios. The value of each pixel represents the relative frequency of all pixels across the Everglades National Park meeting both hydrologic conditions. These hydrologic scenarios were used to determine the impact of climate change on plant communities in the Everglades National Park, provided in Table 1. Taken from Todd et al. [79].

**Table 1**  
Percent coverage of dominant vegetation types within Everglades National Park under the present and high emissions scenarios. The percent change of dominant vegetation types between the present and high emissions scenarios are also provided. Only those vegetation types constituting more than one percent of the total landscape are listed. Taken from Todd et al. [79].

Vegetation type	Present	High	% Change
Sawgrass	60.68	55.21	-9.0
Mixed Gramminoids	6.55	8.82	34.7
Tall Sawgrass	5.80	2.24	-61.4
Muhly Grass	4.07	10.25	152.0
Spike Rush	2.98	1.38	-53.5
Red Mangrove Scrub	2.16	0.92	-57.4
Bayhead	1.72	0.83	-51.7
Pine Savanna	1.59	5.17	224.3
Willow Shrublands	1.47	1.36	-7.9
Dwarf Cypress	1.45	0.69	-52.1
Bay-Hardwood Scrub	1.44	0.49	-66.1
Brazilian Pepper	1.22	2.50	104.4
Cattail Marsh	1.09	0.29	-73.5
Slash Pine with Hardwoods	0.88	2.96	237.2
Hardwood Scrub	0.71	1.57	121.9
Subtropical Hardwood Forest	0.75	1.43	91.1

the summertime months, but suffered shortened hydroperiods due to the enhanced evaporative demand of a warmer climate.

The changes in hydroperiod structure in the Prairie Pothole Region had a marked effect on the habitat available for migratory waterfowl. Johnson et al. [36] utilized the WETSIM model, a process-oriented, deterministic model that simulates wetland surface processes and vegetation dynamics, to quantify suitable waterfowl niche space. Three future scenarios were run in WETSIM to quantify the impacts of climate change on wetland hydrology and corresponding waterfowl habitat availability. These scenarios are (1) a 3 °C temperature increase with no change in precipitation, (2) a 3 °C temperature increase with a 20% increase in precipitation, and (3) a 3 °C temperature increase with a 20% decrease in precipitation. From Fig. 4, it is clear that all three scenarios lead to

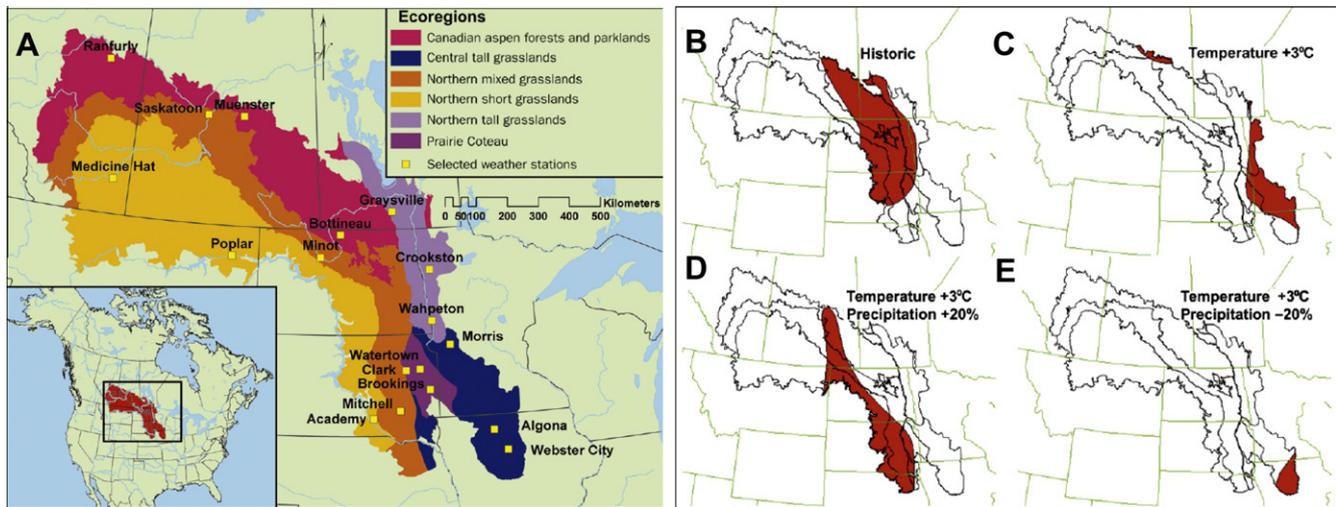
marked geographic shifts in the availability of waterfowl habitat. The scenario with increased temperature and decreased precipitation led to the most dramatic contraction in suitable habitat (Fig. 4E).

Many of the studies investigating the role of hydrology in structuring vegetative niches implement climate change as a long, gradual process, with a trend towards elevated temperatures and associated changes in hydrology. However, it is important to note that in dynamic environments, such as wetlands, changes in the occurrence of extreme precipitation events may play an important role [35]. Additionally, increased variability in rainfall patterns, leading to flooding and droughts, may have profound influences on vegetation [85,47]. As an example, Zedler [85] investigated the influences of floods and droughts on wetland vegetation over thirty years, showing that biodiversity richness and evenness was reduced abruptly due to sequential, catastrophic floods.

In this section, we have described the important role that hydrology plays in structuring niches in wetland ecosystems for both vegetation and migratory birds. Recent research quantifies the hydrologic niches of plants [15,26,79,87] and waterfowl [36] and has recently been used to quantify the potential ecological impacts of climate change [36,80,85].

#### 4. Hydrologic control of dispersal mechanisms

'Dispersal' of organisms refers to their movement from one habitat to another and has long been recognized as an important driver of biodiversity patterns. Dispersal tends to increase the diversity of local communities [43], but systems with high rates of dispersal tend to have lower global diversity [31]. The dispersal distance [8] and shape of the dispersal kernel [68] are important determinants of diversity patterns as well. Empirical evidence suggest that the dispersal kernels of seeds have fat-tails [9], which indicates that dispersal is likely to occur if there is an available pathway. Dispersal of organisms through heterogeneous landscapes also



**Fig. 4.** A. The Prairie Pothole region of central North America (inset map) and six eco-regions. Yellow symbols represent weather stations (three per eco-region) used in WETSIM analyses. Simulated waterfowl habitat across the Prairie Pothole region under historic (B) and future scenarios of climate change (C, D, and E). Taken from Johnson et al. [36]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

impacts the distribution of organisms. This is because organisms adapt their dispersal strategies based upon the underlying landscape structure [52].

There are a number of hydrologic variables and hydrologic dependent landscapes which may impact dispersal. Here, we focus on systems with hydrologically determined carrying capacities and habitat connectivity, since organisms adapt their dispersal strategies to both factors [52]. River systems present a unique opportunity to explore how dispersal is influenced by the combination of the spatial distribution of carrying capacity and the landscape connectivity structure (i.e. riverine topology). This unique landscape structure, in turn, makes it possible to explore how ecological dispersal might be impacted by human modification. The focus of this section is recent research that quantifies how river topology influences dispersal and diversity and, subsequently, how human modification to river topology may impact diversity patterns.

With increased variability in rainfall regimes under climate change and increased demands on freshwater, not only will river flows be altered, but it is likely that human modification of river systems will intensify, in an effort to stabilize water supplies for human consumption, agriculture, and industry [82]. For example, inter-basin water transfer projects, in which man-made canals transform the river connectivity to provide water to areas where demand exceeds supply, are anticipated to become more prevalent [42], as are water withdrawal projects [84]. River topology is an important element of dispersal, particularly for aquatic organisms. In fact, fish and other entirely aquatic organisms are constrained by the landscape imposed dispersal constraints embedded in river networks [18].

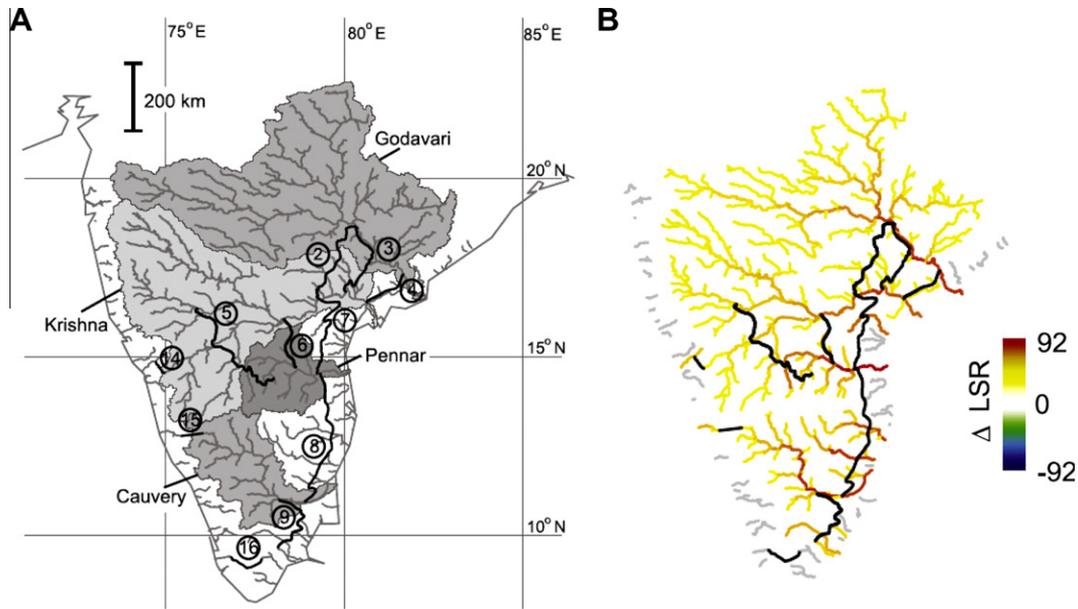
River networks impose constraints on population processes, such as spread, growth, and survival [23]. Thus, straight line distances in 2-D space may be very different to distances as measured through the river network. In other words, “as the crow flies” may be different to “as the trout swims” [18]. For this reason, one of the principal consequences of the riverine structure is to alter the landscape through which organisms disperse. For example, the river network structure may influence population extinction risk, slow the spatial spreading of exotic organisms, enhance diversity at confluence points of the network [23], and impact the persistence of species [3].

Muneepeerakul et al. [51] present a neutral model of fish diversity in the Mississippi Watershed that is based upon ecological processes. In this metacommunity model, the fish disperse based upon the underlying river network topology. The model produced

excellent fits to the empirical data, once the spatial distribution of carrying capacity was appropriately characterized and the dispersal process was constrained to follow the river network. The model effectively reproduced several key diversity patterns; namely, the profile of local species richness, the local species richness frequency distribution, the rank-occupancy curve, and the  $\beta$  diversity as characterized by the Jaccard’s similarity index [51]. Additionally, Bertuzzo et al. [4] demonstrate that the model is able to reproduce spatially explicit biodiversity patterns; namely, the environmental resistance, which quantifies the spatial loss of community similarity and is useful in identifying biogeographic regions. Remarkably, the model produced a good fit to this spatial pattern with no further calibration [4].

The process-based model presented in Muneepeerakul et al. [51] demonstrates that the dispersal of fish in the Mississippi Watershed is controlled by the combination of the spatial distribution of carrying capacity and river network structure. Interestingly, the model results indicate that fish do not exhibit biased dispersal and the majority travel locally, though an important fraction do travel very long distances [51,4]. The river network structure is an essential component of the model; fish dispersal is dramatically impacted by the drainage structure, since fish offspring are constrained to follow the ecological corridors defined by the network [51]. Thus, river network structure, a key hydrologically influenced landscape, is an important controlling feature of the dispersal of fish.

Inter-basin water transfer projects restructure river connectivity and have the potential to alter landscape-scale patterns of species distributions by introducing new dispersal routes. The landscape constraints imposed by river topology are essential in determining the dispersal characteristics and diversity of entirely aquatic organisms (i.e. those constrained to solely ‘within-network’ movement). However, the unique topology of river networks does not entirely control the dispersal of aquatic organisms capable of ‘out-of-network’ movement [23,24]. For example, salamanders utilize both ‘out-of-network’ and ‘within-network’ movement, which acts to stabilize their populations [24]. Thus, the network structure is not as important in the dispersal of organisms that are able to travel out-of-network, such as salamanders or trees [24,39]. Changing the connectivity structure of river networks with man-made canals for inter-basin water transfer projects is an extreme example of ‘out-of-natural-network’ movement, most likely to impact entirely aquatic organisms.



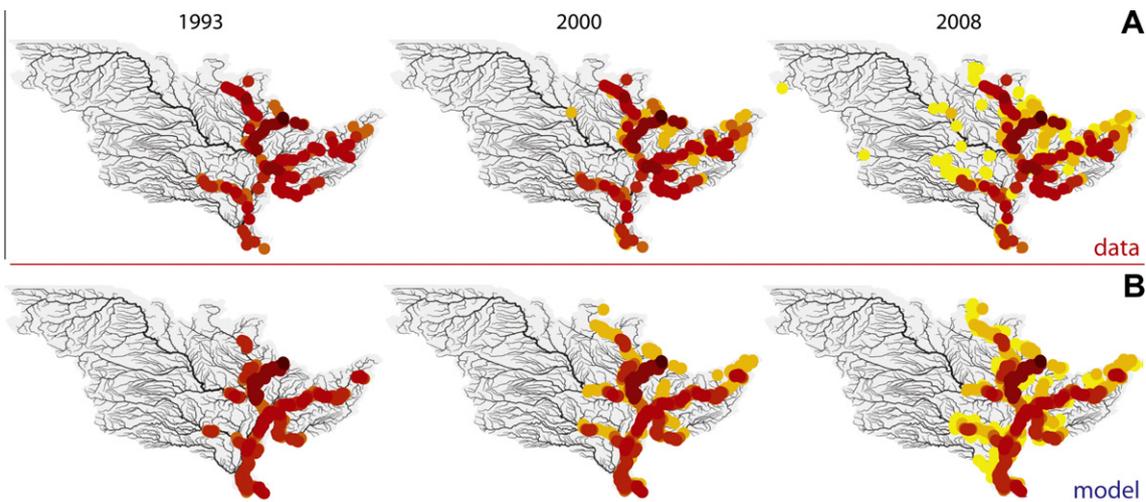
**Fig. 5.** (A) Map of the Indian Peninsula. Major rivers are shown in gray, and the 11 proposed links considered in the analysis are shown in black. The four major river basins involved are shaded and labeled. The links are numbered according to enumeration assigned by India’s National Water Development Agency. (B) Impact of the 11 proposed interbasin water transfers on local species richness (LSR) for the Indian Peninsula river network. The absolute differences (after minus before) in LSR are shown for each link in the river network. Taken and modified from Lynch et al. [42].

A neutral metacommunity model of fish in river networks, similar to that of Muneeppeerakul et al. [51], can be used to determine the impacts of inter-basin water transfer projects on fish diversity. With this approach, Lynch et al. [42] quantify the potential ecological impacts of the proposed inter-basin water transfers in India. Although the neutral model is not able to predict how the proposed inter-basin transfer project will impact specific species, it is a suitable framework to evaluate the potential landscape-scale consequences of changes to river connectivity [42].

Changes in species richness due to the 11 proposed inter-basin water transfers are quantified and shown in Fig. 5. Their study demonstrates the fragility of reaches in close proximity to the proposed canals. Note that local diversity increases throughout India with increased connectivity, which is anticipated under the null scenario of habitat fragmentation [7]. However, global diversity

in the system becomes spatially more homogenous with a notable decrease in  $\beta$  diversity. Additionally, rare species decrease with the introduction of the proposed canals [42]. In other words, more species are present in each location, but this is because certain species become widespread and dominant when otherwise distant basins are linked through human modification. This increase in common species comes at the expense of endemic and rare species. The study by Lynch et al. [42] is the first to examine the impact of changing network connectivity on basin-wide patterns of biodiversity and species richness.

We can look to the past to observe how human introduction of exotic organisms into river networks has exacerbated biological invasions. Invasive species are known to displace native species, usually decreasing species diversity in the system as a whole [10]. Mari et al. [45] show that anthropogenic drivers of dispersal



**Fig. 6.** Dynamics of the zebra mussel invasion of the Mississippi Watershed. (A) Empirical data on zebra mussel spread over time. (B) Model snapshots of zebra mussel spread. Note that the model (B) reproduces the data (A) very closely when both the connectivity structure of the river network and human interferences in zebra mussel spread are taken into account. Human-mediated dispersal impacts the spread of zebra mussels through commercial and recreational boating activities. Taken and modified from Mari et al. [45].

(i.e. commercial navigation) in combination with the river network topology provide the best fit to the spatio-temporal dynamics of invasion of zebra mussels. In Fig. 6, model estimates of zebra mussel invasion in space and time provide excellent fits to the data of zebra mussel invasion. Dispersal in the model was constrained to follow the river network, but zebra mussels were transported at an accelerated rate and to regions of the network that may have been outside their range by ships. The study by Mari et al. [45] illustrates that human-mediation of dispersal is of great importance, particularly when temporal dynamics are taken into account in river network context, where natural ecological distances are constrained to follow the topology.

In this section, we have presented examples of how network connectivity can be used to hind-cast or fore-cast the potential impacts of re-routing the connectivity structure of river systems. Examples of human-mediated dispersal in both India and the Mississippi Watershed indicate changes to river network topology may have disastrous consequences for species diversity, largely through the introduction of invasive species. As increased pressures are placed on global freshwater resources from population growth and climate change [82], it is likely that human modification of riverine systems will intensify. It is imperative to understand how water withdrawals and modifications to the connectivity structure of river networks will impact ecological dispersal, in order to properly evaluate the projected biodiversity impacts. This is particularly relevant since policy makers and resource managers are more able to directly impact water withdrawals and river engineering projects than global climate.

## 5. Looking forward

It is imperative to understand the key relationships between hydrologic processes and biodiversity as global freshwater resources are subject to increasing pressures from both population growth and climate change. There is certainly a vast literature that relates to the many and varied interactions between hydrology and species diversity that we do not cover in this paper. Instead, we have outlined some of the major hydrologic drivers of biodiversity: carrying capacity, niche formation, and dispersal. In this synthesis, we have chosen to focus on hydrologic controls that can be used to quantify the impacts of climate changes on biodiversity.

Forecasting the potential impacts of climate changes on biodiversity is of increasing importance. For this reason, the focus of this paper is research that uses hydrologic processes to quantify changes in species compositions. Going forward, there is a clear need to develop a mechanistic model linking rainfall dynamics and biodiversity. While the mean annual precipitation may be the major driver of the distribution of species in some cases, it is clear that rainfall timing and intensity will play a major role as well [22]. For this reason, the development of a model that integrates species diversity processes with rainfall dynamics would make a valuable contribution to the literature. Similarly, recent research has highlighted the importance of soil moisture variability to plant functional groups [64,1]. It is important that future research continue to develop the relationship between soil moisture processes and plant diversity.

As global water resources are increasingly constrained, water withdrawals, transfer projects and dams will become increasingly popular. Understanding the ecological impacts of proposed engineering projects is particularly important and challenging. The impact to fish diversity due to withdrawals and changes in river network connectivity have only recently been examined quantitatively. In the future, these modeling approaches could be improved by incorporating a more comprehensive set of relationships between hydrologic variables and the carrying capacity of fish.

Of course, the major hydrologic drivers that we have highlighted do not act in isolation. For example, changes to global precipitation patterns will impact the spatial distribution of carrying capacities of certain organisms. This, in turn, may lead those organisms to adapt their optimal dispersal strategies accordingly. Similarly, increased variability in rainfall regimes may lead to enhanced niche spaces, which may, in turn, affect the carrying capacity and diversity of certain species. Thus, accounting for the interplay between the major hydrological drivers of biodiversity is an important and challenging task going forward.

Additionally, the interaction between these hydrologic and other abiotic variables should be taken into account when appropriate [33]. In particular, research that mechanistically links hydrologic processes with other factors, such as nutrients and temperature, will be of increased importance in the future, particularly as the scientific community strives to understand the multitude of interactions between a changing climate and the diversity of biological systems.

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