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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.

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 mm yr^{-1}, while those locations that receive greater than 650 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 coexistence, 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 continent-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