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Landscape-scale processes influence riparian plant composition along a regulated river

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ABSTRACT

Hierarchical frameworks are useful constructs when exploring landscape- and local-scale factors affecting patterns of vegetation in riparian areas. In drylands, which have steep environmental gradients and high habitat heterogeneity, landscape-scale variables, such as climate, can change rapidly along a river's course, affecting the relative influence of environmental variables at different scales. To assess how landscape-scale factors change the structure of riparian vegetation, we measured riparian vegetation composition along the Colorado River through Grand Canyon, determined which factors best explain observed changes, identified how richness and functional diversity vary, and described the implications of our results for river management. Cluster analysis identified three divergent floristic groups that are distributed longitudinally along the river. These groups were distributed along gradients of elevation, temperature and seasonal precipitation, but were not associated with annual precipitation or local-scale factors. Species richness and functional diversity decreased as a function of distance downstream showing that changing landscape-scale factors result in changes to ecosystem characteristics. Species composition and distribution remain closely linked to seasonal precipitation and temperature. These patterns in floristic composition in a semiarid system inform management and provide insights into potential future changes as a result of shifts in climate and changes in flow management.

1. Introduction

Riparian landscapes are typically heterogeneous systems in which environmental controls that most strongly affect the riverine community act at different spatial scales (Ward et al., 2002; Wiens, 2002). The composition of riparian plant communities reflects the influences of multi-scale environmental processes, since they are affected by a complex set of filters that govern species presence, persistence, and distributions (Hough-Snee et al., 2015; Lite et al., 2005; Tabacchi et al., 1996). Local-scale effects, including hydrology, channel geomorphology, soils, and adjacent upland conditions, can influence the number and species composition of plants occurring in a particular riparian setting. Landscape-scale effects such as topography, elevation, and climate can also exert a strong influence on species distributions (Goebel et al., 2006; Friedman et al., 2005; McShane et al., 2015; Yang et al., 2011). Evaluating the relative effects of local and landscape-scale variables on species composition facilitates an understanding of vegetation response to environmental change (Ward et al., 2002; Wiens, 2002) and, through formal models, can facilitate prediction, a central goal in plant ecology.

The geographic context of a river influences the biotic composition and richness, as well as the functioning of riparian ecosystems (Wiens, 2002). Regions with high environmental heterogeneity and steep environmental gradients are likely to contain a relatively large number of distinct communities per unit area, due to high variability and interactions among factors such as disturbance, soil chemistry, and geomorphology (Goebel et al., 2006; Gould and Walker, 1999), adjacent land-use (Meek et al., 2010), and water availability (Lite et al., 2005). Conditions can change rapidly along a river's course due to changes in aspect and elevation, variability in depth to the water table, and soil characteristics (Ffolliott and Davis, 2008; Friedman et al., 2006; Nilsson et al., 1994), resulting in differing floristic communities, habitat qualities, and communities with different functional traits (Nilsson et al., 1994; Stromberg et al., 2017).

The surrounding landscape and tributaries can also affect species richness. One important mechanism is through increasing richness longitudinally (upstream to downstream) by supplying water-dispersed propagules (Jansson et al., 2005) from microhabitats and tributaries

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along a river's course. The introduction of seeds from various microhabitats throughout a watershed, and the accumulation of seeds as a function of downstream distance (and the inflow of tributaries) has been described as the 'river accumulator hypothesis' (Nilsson et al., 1994). Alternatively, richness may be limited through a depauperate regional species pool and climatic constraints where even dispersal, hydrochorous or otherwise, is unlimited.

For land areas managed for specific ecosystem services or conservation goals, it is important to identify floristic communities that could respond differently to changing management practices and/or environmental pressures. Management actions applied across a large area have differential effects on plant communities. It is therefore important to assess floristic differences in riparian vegetation due to landscape-scale environmental factors and account for those differences when creating management plans, assessing the status and trends of resources, and predicting ecosystem responses to flow management (Bejarano et al., 2013; Bendix, 1994; Tabacchi et al., 1990). Once landscape-scale influences on vegetation are accounted for, it is possible to gain a clearer understanding of how management activities (e.g., flow alteration, restoration actions) will result in specific changes in riparian vegetation (Bendix, 1994).

Riparian studies that evaluate the relative influence of environmental variables on vegetation at different hierarchical levels typically do not include climate variables (but see Bendix, 1994; Engelhardt et al., 2015; Friedman et al., 2005; McShane et al., 2015; Yang et al., 2011), rather they consider the broad-scale factors to be geomorphology, stream order, or watershed-scale variables (Engelhardt et al., 2015; Goebel et al., 2006; Gould and Walker, 1999; Lite et al., 2005; Wiens, 2002). While these landscape-scale factors are certainly important, climate variables are also known to influence plant distributions (Butterfield and Munson, 2016; Yang et al., 2011) and can operate at an even broader scale than the stream segment or watershed scale (McShane et al., 2015). Drylands in particular have a high likelihood of dramatic floristic change along desert river corridors independent of flow variables. The American Southwest exemplifies this given the presence of four deserts which have differences in temperature and precipitation (MacMahon and Wagner, 1985; Shreve, 1942), the large variation in elevation (Ffolliott and Davis, 2008), and the prevalence of diverse microclimates in large, deep canyons (Stevens, 2012). Considering the influence that elevation, geomorphology, temperature, and precipitation have on species distributions (Butterfield and Munson, 2016; Engelhardt et al., 2015; Yang et al., 2011), the composition of riparian vegetation in western North American arid to semi-arid deserts is likely to change as rivers flow through different geologies and climates (Butterfield and Munson, 2016; McLaughlin, 1989; Yang et al., 2011), drop in elevation (Ffolliott and Davis, 2008; Tabacchi et al., 1990), or enter a different river valley type (Bejarano et al., 2013). Flow management, vegetation rehabilitation efforts, and research on riparian ecosystem processes could be guided by a greater understanding of floristic shifts due to these landscape-scale environmental factors.

The Colorado River within Grand Canyon National Park is ideal for studying floristic change and the effect of landscape-scale factors on riparian species distributions, due to steep environmental gradients, diverse microhabitats, and inputs from tributary streams. Floristic studies conducted by McLaughlin (1989) identified multiple floristic regions that overlap in the Grand Canyon region, primarily with affinities to the Mojave, Sonoran, and Great Basin Deserts, with influences from the Colorado Plateau, a unique physiographic province consisting of a mixture of forests and high deserts. Many regional botanists have acknowledged the contribution of multiple floristic regions to the flora of Grand Canyon (e.g., Clover and Jotter, 1944; Phillips et al., 1987) and early vegetation studies noted a longitudinal transition in plant species along the Colorado River in both upland and riparian plants to more Mojave and Sonoran-like assemblages in the downstream portions (e.g., Clover and Jotter, 1944). Additionally, this river segment drops almost 600 m in elevation, experiences shifts in temperature and precipitation from upstream to downstream (Caster et al., 2014), and contains many different microclimates (Stevens, 2012). This river segment is also characterized by a fairly consistent flow regime due to dam operations, a consistent stream order, and repeating geomorphic features (Schmidt and Graf, 1990). Thus, many of the commonly used landscape-scale factors are constant, allowing for a closer examination of the influence of climate variables.

We hypothesized that plant species composition would transition in the longitudinal (upstream to downstream) dimension in response to changes in climate variables and that changes to plant composition would result in differences in richness and structure of the plant community. If species composition is responding to climate variables, we expect plants with affinities to higher elevations, cooler temperatures, and distributions more closely tied to the Great Basin Desert and the Colorado Plateau to occur in the upstream portion of the river, while plants with affinities to lower elevations, hotter temperatures, and distributions more closely tied to the Mojave and Sonoran deserts to be found in the downstream portion. Although a complete turnover of species is not expected, many of the species that occur in the study area should only occur in the upper reaches or the lower reaches, but not along the entire course. If these floristic patterns are the result of landscape-scale processes, they should be correlated with measurable environmental attributes (e.g., temperature and precipitation). If landscape-scale processes unrelated to flow variables have a greater influence on floristic communities than local-scale conditions, we expect that richness will not increase with distance downstream (suggesting a habitat-related bottleneck for expression of the river accumulator hypothesis). Rather, species will be replaced due to environmental limitations on establishment and survival. The objectives of this study were to 1) determine if the riparian plant assemblages along the Colorado River change longitudinally and, if so, 2) describe how those assemblages differ in floristic composition, richness, and functional diversity, 3) determine if those assemblages are more likely explained by landscape or local factors, and 4) discuss the management and ecological implications of these results.

2. Methods

2.1. Study area

The study area, the Colorado River through Grand Canyon National Park, is located in northwestern Arizona, U.S.A., and consists of the riparian zone between Lees Ferry, Arizona and river kilometer (Rkm) 404, where the backwater influence of Lake Mead becomes apparent (Fig. 1). This is a highly valued, regulated river system in which research and monitoring that informs its management is mandated by law (for summaries of the history, laws, and regulations surrounding the Colorado River downstream from Glen Canyon Dam see Gloss et al., 2005). Glen Canyon Dam is 25 km upstream from Lees Ferry. For the purposes of this study, locations on the river are measured in kilometers downstream from Lees Ferry (Rkm 0). The elevation changes from 950 m at Lees Ferry and drops to 366 m where the river exits the Grand Canyon National Park boundary (Rkm 445). The river trends toward the southwest, but canyon topography controls light availability resulting in variable solar insolation.

The Colorado River through Grand Canyon is a canyon bound river with debris fans at tributaries that create channel constrictions and affect where and how sediment is deposited (Schmidt and Graf, 1990) and thus the distribution and characteristics of substrates for riparian plant growth. Sediment deposits that can support vegetation occur along channel margins, on banks in the pools upstream from channel constrictions, on the boulder dominated debris fans, and as sandbars in eddies downstream from debris fans (Schmidt and Graf, 1990). Variability in water velocity resulting from the debris fan constrictions creates diverse depositional environments with grain sizes ranging from fine sand and some silt (upstream pools) to coarse boulder fields.