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Dryland Riparian Ecosystems in the American Southwest: Sensitivity and Resilience to Climatic Extremes

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Introduction

Drylands make up over 40% of the earth's land surface (Noy-Meir 1973; Reynolds and others 2007). In these arid and semiarid landscapes, surface and subsurface water flows create mesic riparian environments (Kingsford 2006; Stromberg and Tellman 2009). Dryland riparian areas sustain water-limited plants and animals that cannot withstand upland conditions year-round, thereby supporting regional diversity (Sabo and others 2005; Lite and others 2005). Dryland rivers are also characterized by occasional large, high-intensity floods that rework the bed geomorphology and increase riparian heterogeneity. This combined variation in water availability and flood disturbance creates spatiotemporally complex and unique landscapes (Soykan and Sabo 2009; Soykan and others 2012).

The hydrology of desert riparian ecosystems has been extensively altered by human activities including stream diversion and groundwater extraction, and is expected to undergo further change in response to changing climates (Patten 1998). Globally, increasing temperatures associated with climate change are expected to intensify the water cycle, leading to greater rates of evapotranspiration, more water in the atmosphere, and more-frequent intense storms (Huntington 2006; IPCC 2007). More intense storms are likely to increase flood intensity over the next 50 years (Dominguez and others 2012). In the American Southwest in particular, warmer sea surface temperatures could spur stronger and more-frequent El Niño-associated winter storms (Garfin and Lenart 2007). Perhaps of greater importance are projected increases in aridity. Average precipitation is expected to increase at a global scale, but some regions, including the American Southwest, are expected to experience substantial decreases in average annual rainfall as well as increases in frequency and intensity of droughts (Seager and others 2007). As aridity increases, streams and riparian zones undergo declines in surface flow and depth to groundwater; there are declines, as well, in the extent of river segments with perennial (vs. intermittent or ephemeral) stream flow.

Given that rivers and their riparian corridors function as keystone elements of arid and semiarid landscapes, climate change will have far reaching effects on regional biota (Stromberg and others 2010). Nevertheless, the extent of biotic change for riparian ecosystems in coming decades will be tempered by the fact that for desert rivers, climatic and hydrologic variation is the norm (Milly and

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others 2008). Surface flows vary widely among seasons and years, reflecting the diverse regional patterns of storm tracks and multi-year climatic cycles. For some rivers, the predominance of seasonal flood types has shifted at multi-decadal scales, in response to complex air-sea interactions (Hirschboeck 2009). Most rivers in the American Southwest have undergone periodic severe drought (for example, 1890s, 1950s, and 2000s) and periodic extreme floods. Thus, these systems may have great potential for autonomous adaptation to climate change, bringing us to the purpose of this article: to briefly review mechanisms of both sensitivity and resilience of dryland riparian ecosystems to climate change, with a focus on riparian plant and animal communities in the American Southwest.

Sensitivity and Resilience of Riparian Vegetation

Many desert riparian organisms have traits allowing persistence in adverse and variable conditions. One adaptive strategy, seen in the many annual and short-lived perennial plants that typify desert riparian zones, is the capacity to escape seasonal, annual, and decadal droughts as viable seeds in soil seed banks. This strategy confers resilience to human alterations such as river diversion and increased climate variability (Boudell and Stromberg 2008; White and Stromberg 2009). The capacity of seeds to be mobilized by flood waters further increases resilience to changing flow conditions, by enabling dispersal of propagule types capable of growing under differing environmental conditions (Nilsson and others 2010).

In contrast, at short-term scales, many riparian herbaceous plants are highly sensitive to drought. Sustained reductions of surface and sub-surface water flows cause significant changes in productivity, functional-type composition, and species diversity, highlighting the potential sensitivity of these ecosystems to climate change (Stromberg and others 2007). One threshold occurs as perennial streams become intermittent. As reduced groundwater inflow causes cessation of base flows in the summer dry season, a cascade of effects occur. Shallow-rooted macrophytes decline sharply in abundance, and the river channel widens without the soil-binding root masses of the wetland plants. Species richness along the low-flow channel declines, although, owing to tradeoffs between competition and colonization and to high influx and storage of seeds in soils, herbaceous species richness can increase over the long-term (multiple seasons and years) at sites with intermittent, rather than perennial, flow (Katz and others 2012).

The pioneer trees *Salix* and *Populus* are the structural dominants in the floodplains of many desert rivers, and they strongly influence many ecosystem processes from transpirational cooling to habitat provision for riparian birds. One adaptive strategy of these trees is long-life span ($>$100 years) coupled with annual production of large numbers of widely dispersed seeds. The trees regenerate episodically, with seedling establishment keyed into large, long duration winter floods. Their population sizes can fluctuate widely through time in response to temporal variation in frequency, magnitude, and duration of flood flows (Friedman and Lee 2002; Lytle and Merritt 2004). Long-term persistence of these trees in a dryland environment, however, requires continued availability of baseflows or shallow, stable alluvial groundwater levels. On the floodplain, if the water table deepens and shows more seasonal and annual variation in response to increased aridity or water extraction, the tall, phreatophytic pioneer trees (*Populus*, *Salix*) decline in productivity and abundance. As the water table drops below their root zones, they are replaced by more deeply rooted and shrubbier taxa, such as naturalized *Tamarix* spp. (Stromberg and others 2010).

Yet other adaptations of riparian plants to spatial and temporal variation in water availability include flexibility in biomass allocation and plant architecture. Persistence of the moderately shallow-rooted *Populus* and *Salix* hinges on near-continuous availability of shallow groundwater; yet, other woody taxa, including *Prosopis* and naturalized *Tamarix*, exhibit high plasticity in canopy height and root depth and distribution. This allows them to grow in a wide range of riparian settings, including areas with shallow or deep water tables, as well as along streams with ephemeral flow where flood pulses create perched water tables.

Sensitivity and Resilience of Riparian Animals

Birds have been a major focus of study in desert riparian ecosystems, in part because these linear oases are key components of migratory flyways (Skagen and others 1998). The abundant bird life (resident and migratory) that typifies Southwestern gallery forests changes compositionally in tandem with linked changes in hydrology and vegetation. Some obligate riparian birds decline in the absence of reliable surface water, but many others can be sustained in areas with intermittent flows as long as

Populus-Salix forests are present. Collectively, though, the simplification of community structure, decline in productivity, and loss of the tall *Populus-Salix* canopy following extensive water table and base flow decline result in declines in bird abundance and diversity (Brand and others 2010, 2011). Nevertheless, areas that have shifted to *Tamarix* shrublands and or *Tamarix/Prosopis* forests do sustain substantial bird life, with *Tamarix* currently providing key nesting habitat for an endangered riparian songbird (Sogge and others 2008). The functional role of *Tamarix* in Southwestern riparian zones is a controversial topic, with some recognizing its value as habitat for riparian songbirds and others waging war to rid the landscape of an ''invasive exotic'' (Stromberg and others 2009).

For many dryland riparian animals, little is known about how they survive adverse and variable conditions. Many species found in abundance in desert riparian zones of the southwestern US are not endemic to deserts, but are common in more mesic environments (McCluney and Sabo 2012). Given that desert riparian animals must survive juxtaposed periods of low water availability and intense disturbance from large floods (Miller and others 2003), behavioral coping adaptations are important. Mobile animals move between riparian areas and uplands, tracking food and water availability and avoiding periods of high disturbance (Soykan and Sabo 2009). However, during dry periods, trophic interactions intensify as riparian animals without surface water consume greater amounts of moist food (vegetation, prey) to meet water demands (Sabo and others 2008; McCluney and Sabo 2009). Multiple predator and prey species are forced into close contact near surface water and this may alter behavior and species interactions (Valeix and others 2008). These behavioral coping mechanisms enable riparian animals to persist in the face of rapid environmental variation.

Riparian arthropods are affected in complex ways by stream drying. Even with loss of perennial stream flow, *Populus* and *Salix* trees, as phreatophytes, may deliver sufficient groundwater via greenfall to sustain large populations of aboveground consumers such as crickets (Sabo and others 2008) (Figure 1). However, despite the buffering effects of these tree species on responses of floodplain animals to declines in water availability, even short-term declines in flow reduce diversity and alter composition of near-stream arthropod assemblages (McCluney and Sabo 2012). These arthropod communities are likely responding to both declines in water availability and a reduction of riverine subsidies to the terrestrial food web

Figure 1. Damp-loving field crickets (*Gryllus alogus*) consuming freshly fallen moist leaves (greenfall) under dry conditions in the riparian floodplain forest along the San Pedro River in southeastern Arizona, USA. These crickets can meet water demands solely by consuming greenfall under dry conditions, but eat very little greenfall under moist conditions. Photo by K. McCluny.

(Nakano and Murakami 2001; Greenwood and McIntosh 2010). Thus, dryland riparian plants and animals have numerous adaptations to variable environmental conditions associated with climate change, taking advantage of the spatiotemporal heterogeneity inherent in dryland riparian zones. But, extreme levels of environmental conditions, within the potential scope of climate change, could push these organisms and the riparian plant communities upon which they are dependent, beyond thresholds, leading to substantial ecosystem change.

River Setting, Feedbacks, and Other Areas of Uncertainty

Sensitivity to climate change differs among rivers and reaches, varying in part with hydrogeological setting. Many rivers of the Basin and Range Province are classified as interrupted perennial—with interspersed perennial and intermittent to ephemeral reaches—that derive their flows largely from rain that falls within mountainous headwaters. Some perennial reaches are buffered by shallow bedrock that forces water in the aquifer very close to the surface. Other reaches, however, are more sensitive to watershed-scale inputs of precipitation. Surface and subsurface flow paths and travel times are difficult to unravel in areas of complex geology. The magnitude of drought in the headwaters that would dewater perennial sections of rivers that flow through the desert basins remains one of many unanswered questions for the US Southwest

Figure 2. Flood-induced widening of the channel of a formerly perennial reach of the San Pedro River, Arizona. Photo by M. Denslow.

and other dryland regions (Jobbágy and others 2011).

There are other areas of uncertainty. One set of questions revolves around the degree to which feedbacks and interactions between ecosystem components will buffer or exacerbate climate change effects. As water tables decline due to groundwater pumping or drought, the capacity of near-stream soils to store flood waters is increased. This enables flood waters to infiltrate and be utilized at a later time by vegetation or to help sustain summer base flows (Baillie and others 2007; Simpson and Meixner 2012). Further, negative feedbacks may exist between riparian vegetation and base flows, with lower groundwater depth leading to reduced evapotranspiration and ameliorating some of the declines in base flows under increasing aridity. On the other hand, increased flood intensities could have positive feedbacks on disturbance processes, by shifting plant communities toward species with less ability to stabilize sediments (Figure 2). The combination of severe drought and floods could lead to nonlinear geomorphic changes, such as renewed cycles of significant channel down-cutting, extreme channel widening, and loss of floodplain ecosystems, as occurred on many southwestern rivers in the late nineteenth and early twentieth centuries (Turner and others 2003).

Conclusion

As aridity increases in the American Southwest, riparian zones will become increasingly important for maintaining regional diversity and ecosystem services. At the same time, on rivers with dams, diversions, and ground water extraction, increased aridity could heighten conflicts between human and riverine ecosystem needs for dwindling water supplies (Palmer and others 2009). Management to maintain segments with perennial flows distributed throughout river basins will be important for promoting ecosystem resilience in the face of climate change. Restoring or maintaining longitudinal connectivity between stream segments, lateral connectivity between channels and floodplains, and vertical connectivity between groundwater and surface water are all essential. With hydrology as the key factor regulating dryland riparian ecosystem condition, and with the coping strategies of plants and animals dependent on spatiotemporal hydrologic variability, the degree of river regulation and groundwater withdrawal will likely be key factors influencing the adaptive capacity of these ecosystems to future climate change.

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