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Why is small mammal diversity higher in riparian areas than in uplands?

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ABSTRACT

Riparian areas are valued in arid regions for supporting wildlife diversity. We examined relationships between small mammal diversity and riparian areas and mechanisms facilitating higher small mammal diversity in riparian areas. Riparian areas were identifiable from uplands by higher plant cover and supported higher small mammal abundance. Small mammal abundance was related to plant cover and decreased away from riparian habitat. Riparian and upland habitats supported different species, contributing to higher gamma diversity via species turnover between habitats. Differences in plant $\delta^{13}C$ between riparian and upland habitats were used to track assimilation of riparian resources by small mammals. Voles and shrews derived significant portions of their carbon from riparian vegetation. Sagebrush vole and woodrat hair was relatively low in $\delta^{13}C$, likely the result of assimilating forbs and annual grasses in upland habitat. Deer and harvest mice were abundant in riparian habitat but assimilated little riparian vegetation indicating that the riparian corridor provided resources other than food. In addition to food resources, plant cover likely provided protection from predators and a moderate microclimate. To our knowledge this is first use of $\delta^{13}C$ to trace riparian resources into a vertebrate community and show $\delta^{13}C$ as a good proxy for riparian vegetation assimilation.

1. Introduction

Riparian areas are terrestrial habitats adjacent to aquatic ecosystems. Riparian areas are greatly influenced by their proximity to water and the primary controlling factor for riparian areas is the availability of water from in-stream or groundwater sources (Stromberg et al., 1996). In arid regions, riparian corridors are well developed along streams and form narrow, linear contrasts of dense, highly productive vegetation against the sparsely vegetated precipitation dependent upland matrix. In water limited environments, riparian areas are scarce and constitute less than 1% of most arid landscapes (Patten, 1998).

Riparian resources, such as food, vegetative cover, and water, are often unavailable in the xeric, precipitation dependent upland matrix. Despite their low areal extent, riparian areas have a strong influence on wildlife diversity (Gregory et al., 1991). High plant biomass available in riparian areas is an abundant high quality food source for herbivores (Case and Kauffman, 1997) and also provides protection to wildlife from predators (Peles and Barrett, 1996). High plant cover in riparian areas moderates the riparian climate, increases shade, decreases solar insolation, lowers temperatures and increases humidity (Naiman and Decamps, 1997).

Small mammals are ecosystem engineers in arid areas. Seed caching by small mammals enhances plant germination (McAdoo et al., 1983), burrowing aerates soils (Huntly and Inouye, 1988), cycles nutrients (Sirotnak and Huntly, 2000), and maintains early seral stage plant communities (Kitchen and Jorgensen, 1999). As the prey base for many predators, small mammals are an important

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trophic link in food webs (Glaudas et al., 2008).

Small mammal diversity is often higher in riparian habitat than in uplands. For example, higher small mammal richness (Falck et al., 2003), abundance (Macdonald et al., 2006), evenness (Oaten and Larsen, 2008), and increased turnover (Soykan and Sabo, 2009) are found in riparian habitats across a range of geographic areas, spatial scales, and time spans. Riparian habitats exhibit a high level of structural and compositional diversity relative to uplands (Gregory et al., 1991) and higher small mammal diversity is often attributed to increased vegetative complexity (Bateman and Ostoja, 2012). Alternatively, lack of diversity differences are attributed to a lack of heterogeneity between habitats (Macdonald et al., 2006).

Habitat heterogeneity in of itself cannot provide a mechanistic explanation for trends in small mammal diversity. Although the link between riparian areas and small mammal diversity is pervasive, causal mechanisms are not yet established. Habitat heterogeneity suggests several testable hypotheses related to resource availability, such as forage, cover, and microclimate. Increased resource availability in riparian areas and the general pattern of higher small mammal diversity in the riparian corridor lead us to a series of questions meant to clarify mechanisms responsible for higher small mammal diversity in riparian habitat. Our questions are followed with a series of predictions.

(1) Is small mammal diversity related to the availability of riparian habitat or proximity to streams? The relationship between small mammal diversity and riparian habitat is widespread and general. We expect higher abundance, richness and evenness in riparian habitat and high turnover between upland and riparian habitats. Higher diversity indices may result from differential availability in resources such as food, cover, and microclimate in riparian habitat. In arid regions, differences between riparian and upland habitats should maximize habitat heterogeneity, potentially maximizing contrasts in small mammal diversity.

(2) Do riparian and upland vegetation differ in stable isotope composition? If so, can stable isotopes be used to trace riparian resources? Phreatophytic vegetation in the Great Basin occurs where groundwater is available and the presence of phreatophytes is a defining characteristic of riparian areas (Bren, 1993). At higher water availabilities, plants are more efficient at discriminating against the heavier ^{13}C isotope (Farquhar et al., 1989). Therefore we expect that riparian vegetation will be lower than upland vegetation in carbon isotope ratios due to greater availability of soil moisture and groundwater near streams. If riparian and upland vegetation differ, stable carbon isotopes can be used to trace feeding and assimilation of riparian food sources by small mammals.

(3) Do small mammal isotope ratios suggest a diet of riparian vegetation? Stable isotopes can quantify the direct assimilation of food into the tissues of consumers (Phillips, 2012). Given a difference between riparian and upland plants, small mammal consumers assimilating riparian vegetation should be distinct relative to species assimilating upland vegetation. Assimilation of vegetation may occur directly by consumption of vegetation or secondarily by consumption of primary consumers such as insects.

(4) What proportion of riparian vegetation is assimilated by the small mammal community? The proportion of riparian vegetation assimilated should be related to habitat use. Species and individuals with access to riparian resources should assimilate a higher proportion of riparian carbon than those lacking access, i.e., upland species.

2. Materials and methods

2.1. Study area

The South Snake Range encompasses Great Basin National Park (N – 38.98°, W – 114.30°; 31,201 ha) and is located in east central Nevada in the Great Basin desert. Elevations in the South Snake range vary from 1621 m in the town of Baker to over 3982 m at the summit of Wheeler Peak. The climate is cool and arid and varies dramatically with elevation. In Garrison, Utah (elevation – 1609 m) mean annual precipitation is 19 cm and mean annual temperature is 10 °C (Western Regional Climate Center, unpublished data). At the Lehman Caves Visitor Center, Nevada (elevation – 2832 m) annual precipitation is 33 cm and the mean annual temperature is 9 °C (Western Regional Climate Center, unpublished data). Although there are no weather stations on Wheeler Peak, mean annual precipitation is estimated between 76 and 89 cm (Western Regional Climate Center, unpublished data). Ten perennial streams originate at high elevations in the South Snake Range and are recharged primarily by groundwater and snowmelt.

2.2. Study design

Three watersheds (Lehman, Snake Creeks, and Strawberry Creek) were sampled with four transects per watershed. Transects were randomly located within the watersheds using a stratified sampling design. Transects were oriented perpendicular to streams and extended through the riparian corridor, across the stream, and approximately 450 m into the uplands. Total transect length was approximately 520 m. Within a watershed the average distance between transects was 651 m (sd = 143 m). Watersheds were separated by approximately 7 km and all streams were first order.

2.3. Riparian and upland habitat delineation

To quantitatively delineate riparian and upland habitats, we measured plant and ground cover using a line-point intercept method (Herrick et al., 2005). To avoid measuring trampled vegetation, sampling points were offset from transects by 5–10 m. At each sampling point (31 per transect), an observer tossed a pin flag to their left or right, with the direction determined by coin flip. The first azimuth for the pin drop was randomly chosen by spinning a compass. The other sampling points were 90°, 180°, and 270° relative to the first point for a total of four samples at each sampling point. The observer then stood at the pin flag location, closed their eyes and lowered the pin flag. Pin flag contacts were recorded as bare soil, rock (rock >10 cm), litter (any organic matter in contact with the soil), herbaceous vegetation (grasses or forbs), shrub (woody vegetation <3m in height), or tree (woody vegetation >3 m in height). The numbers of hits were tallied for each location (0, 1, 2, 3, or 4) and the total cover values calculated. Cover values were summed across sampling points and converted to percentages. Cover values were additive and could exceed 100% for total cover.

2.4. Plant isotopes

Plant samples were collected along transects in August 2007–2009. Samples were oven dried at 50 °C, ground in a Wiley Mill, and analyzed for stable carbon isotope ratios. Plant species and distance from streams were recorded for each sample.

2.5. Stable Isotope Analysis

Carbon isotopes (δ^{13}C) were analyzed with Brigham Young