A Seed Bank Study of Southwestern Riparian Areas:

Temperature Effects and Diversity

by

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ABSTRACT

Throughout the Southwest, complex geology and physiography concomitant with climatic variability contribute to diverse stream hydrogeomorphologies. Many riparian plant species store their seeds in soil seed banks, and germinate in response to moisture pulses, but the climatic controls of this response are poorly understood. To better understand the ecological implications of a changing climate on riparian plant communities, I investigated seed bank responses to seasonal temperature patterns and to stream hydrogeomorphic type. I asked the following questions: Are there distinct suites of warm and cool temperature germinating species associated with Southwestern streams; how do they differ between riparian and terrestrial zones, and between ephemeral and perennial streams? How does alpha diversity of the soil seed bank differ between streams with ephemeral, intermittent, and perennial flow, and between montane and basin streams? Do streams with greater elevational change have higher riparian zone seed bank beta-diversity? Does nestedness or turnover contribute more to within stream beta-diversity?

I collected soil samples from the riparian and terrestrial zones of 21 sites, placing them in growth chambers at one of two temperature regimes, and monitoring emergence of seedlings for 12 weeks. Results showed an approximately equal number of warm and cool specialists in both riparian and terrestrials zones; generalists also were abundant, particularly in the riparian zone. The number of temperature specialists and generalists in the riparian zones did not differ significantly between perennial headwater and ephemeral stream types. In montane streams, alpha diversity of the soil seed bank was highest for

ephemeral reaches; in basin streams the intermittent and perennial reaches had higher diversity. Spatial turnover was primarily responsible for within stream beta-diversity—reaches had different species assemblages. The large portion of temperature specialists found in riparian seed banks indicates that even with available moisture riparian zone plant community composition will likely be impacted by changing temperatures. However, the presence of so many temperature generalists in the riparian zones suggests that some component of the seed bank is adapted to variable conditions and might offer resilience in a changing climate. Study results confirm the importance of conserving multiple hydrogeomorphic reach types because they support unique species assemblages.

DEDICATION

This thesis is dedicated to my partner Aaron Rockwell for his love and support, and for putting up with me during this process, and to my father Paul Setaro, who has always believed in me; my grandmother, Shirley Burney, who is one of the most loving supportive people I've had the pleasure of having in my life; and to my brother Dylan Burney for his unwavering belief in me.

I also dedicate this work to the members of my family who couldn't be here to witness the occasion: Cathey Burney, James Burney, Lisa Burney, and Holly Burney—I love and miss you all.

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DEFINITIONS

For stream hydrology, I am using the same terminology found in the report by Levick et al. (2008):

- Ephemeral: A stream or portion of a stream which flows briefly in direct response to precipitation in the immediate vicinity, and whose channel is at all times above the ground-water reservoir.
- Intermittent: A stream where portions flow continuously only at certain times of the year, for example when it receives water from a spring, ground-water source or from a surface source, such as melting snow (i.e. seasonal). At low flow there may be dry segments alternating with flowing segments.
- Perennial: A stream or portion of a stream that flows year-round, is considered a permanent stream, and for which baseflow is maintained by ground-water discharge to the streambed due to the ground-water elevation adjacent to the stream typically being higher than the elevation of the streambed.
- Riparian area or riparian zone: the strip of vegetation along an ephemeral, intermittent, or perennial stream, which is of distinct composition and density from the surrounding uplands

CHAPTER 1: THE IMPORTANCE OF SEED BANKS

BACKGROUND

Plants reproduce sexually via seeds or spores, and/or asexually (vegetative) via shoots, bulbs, corms, rhizomes or other similar vegetative structures. Along with other environmental and biological factors the strategies and rates of plant reproduction directly impact the development of plant communities. Plants have evolved these diverse reproductive strategies to ensure their survival through space and time. For many plant species the diaspore (sexual dispersal unit) is the key structure of plant reproduction. Diaspores usually consist of the seed(s), but may also include additional structures, such as fruits or cones. A primary survival strategy of many plant species is the storage of diaspores, or propagules (often used specifically in reference to vegetative dispersal units, but is sometimes used to generally refer to any type of dispersal unit; sometimes diaspore and propagule are used interchangeably), in the environment via a "bank".

Plants utilize many storage strategies for retaining diaspores/propagules through space and time. A soil seed bank is made up of the viable seeds in the soil and leaf litter and is a collection of ungerminated seeds that have the potential to replace adults as they die (Leck et al 1989). There are also bud or propagule banks which consist of bulbs, corms, or offshoots from rhizomes (Leck et al 1989). Some forested regions may have a sapling bank – trees remain small until there is an opening in the forest canopy. Some plants utilize aerial seed banks, such as pine trees that have serotinous cones that release seeds when heated by fire (Coker 1909). Another example is the desert annual

Agriophyllum squarrosum (Chenopodiaceae) that lives on sand dunes in China (Gao et al 2014). The dead plants retain a large portion of seeds that remain on the canopy becomes buried by wind driven sand.

The interactions between a seed bank, the extant vegetation, and other biotic and environmental factors can be complex (see Leck et al 1989). There are many environmental factors that can add to or remove seeds from the soil seed bank. Seed bank composition is influenced by disturbances, seed burial, pathogens or predation, physiological seed death, and germination— failed or successful. Germination in turn is affected by other factors including light, temperature, water availability, exposure to oxygen, exposure to chemical influences, and mechanical disturbances. Germinants can then grow into adults or they can be maintained in a sapling or seedling bank. If they mature into adults and become part of the extant plant community they can then reproduce via seeds and/or vegetative propagules, which may then be removed by predation. Surviving seeds are then retained as part of an aerial seed bank or dispersed and become part of the soil seed bank, repeating the cycle.

There are two common methods for studying soil seed banks. In both cases the soil is collected from the environment first. After soil collection the seeds can either be extracted from the soil and counted (seedling extraction method), or the soil can be placed in a growth chamber or greenhouse to allow the seeds in the soil to germinate (seedling emergence method) (Leck et al 1989; Price et al 2010; Baskin and Baskin 2014). If the seed extraction method is employed, the seeds should then be tested for viability.

There are some important considerations that must be made when conducting seed bank studies. Collection time of the soil must be taken into account, and will depend on the species being investigated and the regional climate. Due to different types of dormancy some seeds might first need to be cold stratified or heat incubated to germinate. To capture the plant species that have transient seed banks it is also best to count and germinate seeds right away instead of storing them (Baskin and Baskin 2014).

To better understand seed bank dynamics for different plant species and the factors that affect them, many classification systems have been devised over time (Leck et al 1989; Csontos and Tamas 2003; Baskin and Baskin 2014). The seed bank classification systems are based on the two primary criteria of seed dormancy type and seed longevity. Some of the classification systems include other ecological and physiological such as timing of seed release, seasonal time of germination (including temperature and water availability), light and dark requirements, the dispersal mechanisms and plant life history. Disturbance regimes including flooding, fire, and grazing history have also been included when classifying seed banks (Csontos and Tamas 2003).

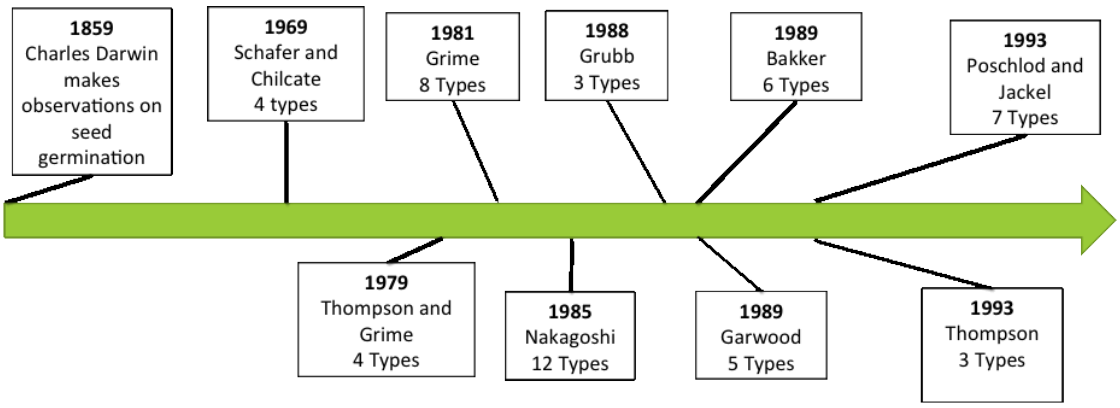


Fig. 1 Seed bank classification systems through time by author, with number of different classifications for each system

SEED DORMANCY

Baskin and Baskin (2014) recognize five primary classes of seed dormancy: physiological, morphological, morphophysiogical, physical, physical plus physiological. Physiological dormancy is due to a mechanism of the embryo that prevents radical emergence, like seed structures that cover the embryo and prevent oxygen from reaching it, restrict the growth, or have some kind of inhibitor. There are multiple levels of physiological dormancy. Morphological dormancy is caused by embryos being immature at the time of dispersal. Morphophysiological dormancy occurs in seeds with rudimentary or linear embryos that also have some type of physiological dormancy. Physical dormancy is generally due to seed coats preventing water uptake.

Temperature can play a role in dormancy for all five dormancy classes. Many seeds prefer, or even require, alternating diurnal temperatures in order to germinate. Certain species can require a large (sometimes $\geq$ 10 ºC) difference between daily maximum and minimum temperatures, however others only require a small temperature difference. The optimal daily maximum and minimum germination temperatures are species dependent. A smaller proportion of species require constant temperatures in order to germinate. Even the rate of temperature change can be important for some species. Many seeds can require longer term cold or heat stratification over weeks or months in order to break dormancy. Often times a combination of longer term temperature stratification followed by alternating diurnal temperatures can be required for dormancy break depending on the species. For many seeds the proper levels of light (including ratio of light to dark), moisture, and temperature, all in combination are

required to break dormancy. For example, spring annuals often require light in combination with low winter temperatures to germinate. In some species the requirement for light changes as temperature changes.

SEED LONGEVITY AND CLASSIFICATION OF SEED BANKS

Most classification systems consider a species that produces seeds with longevity of less than one year or that of one germination season to form a transient seed bank, whereas longevity of greater than one year or at least two germination seasons is considered a persistent seed bank (Csontos and Tamas 2003; Walck et al 2005; Baskin and Baskin 2014). Persistent seed banks are sometimes divided into short-term (two to five germination seasons) and long-term (six germination seasons). Determining seed age can be difficult but can be done by conducting seed burial studies, herbarium studies, exclusion studies, and radiocarbon dating (Leck et al 1989; Bekker et al 1998; Csontos and Tamas 2003; Baskin and Baskin 2014) .

Understanding seed bank classifications can be especially helpful when conducting conservation and/or restoration because seed banks conserve genetic variability caused by selection pressures (Templeton and Levin 1979; Aikio et al 2002). Studying seed banks and seed germination allows us to understand phenotypic plasticity over time in traits like leaf area, biomass allocation, and germination timing (Angert et al 2010; Gremer and Venable 2014). An example of genetic variability that might be observed in a seed bank is the adaptation that occurs due to selective pressures on the seed banks of annuals and perennials. The seeds of the annual species would be genotypes from favorable years whereas the seeds of the perennial species would be of

genotypes that had persisted through all conditions (Leck et al 1989). Seed banks can also allow species or morphs that would normally compete with each other to coexist in the same plant community by utilizing staggered germination strategies (Ellner 1987; Leck et al 1989; Aikio et al 2002).

SEED BANKS AND ECOSYSTEM RESTORATION

Seed banks have been shown to have restoration value or the potential for restoration in many different plant types of communities, from calcareous grasslands to wetlands and riparian areas (Blanckenhagen and Poschlod 2007; Boudell and Stromberg 2008a; Stroh et al 2010; Hong et al 2012) Restoration using seed banks is most effective in plant communities that have a larger portion of long term persistent species. In some plant communities the dominant species have primarily transient seed banks, so although some amount of restoration is possible via the seed bank additional efforts would be needed to ensure the desired species assemblages were present (Bekker et al 2000; Stroh et al 2010). Due to the fact that seed viability decreases thought time, seed bank restoration potential may decreases as time goes on, illustrating the need for conservation and proper management (Bekker et al 2000; Boudell and Stromberg 2008a). Understanding the potential regeneration capacity of a seed bank can ultimately allow for more precise management practice.

CHAPTER 2: EFFECTS OF SEASONALITY ON SEED BANKS OF SOUTHWESTERN RIPARIAN AREAS

INTRODUCTION

Latitude, elevation, topography, and geographical location relative to the Pacific Ocean, Gulf of California, and Gulf of Mexico are all important abiotic factors that influence climate in the Southwestern, United States and produce variation in the amount and timing of precipitation (Sheppard et al 2002). Historically winter and fall rains in the Southwest have been more consistent than summer rains in their timing and quantity. Summer rains in the Southwest often occur as sudden downpours and the timing and quantity of precipitation from these storms, or monsoons, can be highly variable across the Southwestern region. Much of this variability is due to the effects of the El Niño Southern Oscillation and the Pacific Decadal Oscillation, often in combination (Sheppard et al 2002). Warming sea surface temperatures in the Pacific Ocean increases the frequency of winter storms in the Southwest. In Arizona annual precipitation varies according to region: Western Arizona is dominated by winter, central by bimodal (winter and summer) and Southeastern by summer precipitation (Adams and Comrie 1997). In Arizona and New Mexico up to 50% of the annual rainfall can be from monsoons (Sheppard et al 2002).

Seasonality of flood pulses shapes riparian biotic communities (Baker et al 2004; Levick et al 2008), yet a recent causal-criteria analysis revealed many unanswered questions about its effects on plant processes including dispersal and germination (Greet

et al 2011). Some regions have regionally distinct groups of hydrochorous species that disperse and germinate in time with corresponding seasonal floods (Capon 2007; Greet et al 2012; Kehr et al 2014). Many overstory riparian trees—*Populus fremontii, Salix goodingii, and Platanus wrightii* in the Southwest—have short-lived seeds with transient seed banks and they rely on seasonal floods for dispersal at time of seed release as well as germination (Fenner et al 1984; Siegel and Brock 1990; Pettit and Froend 2001; Nilsson et al 2010).

Most of the plant species that grow in wetland or riparian habitats are herbaceous species, many of which produce persistent seed banks (Stromberg et al 2008; Kehr et al 2014). Hydric herbaceous species have specific seed characteristics, such as mass and shape, and germination requirements that include not only moisture, but also temperature, light, and pH (Freas and Kemp 1983; Thompson and Grime 1983; Stromberg et al 2008; Stromberg and Boudell 2013; Baskin and Baskin 2014). In comparison to their dryland counterparts, hydric species tend to have smaller, lighter, rounder, faster germinating seeds that can germinate either in the water or on soil surfaces readily when exposed to light (Thompson and Grime 1983; Stromberg et al 2008; Leyer and Pross 2009; Stromberg et al 2011; Stromberg and Boudell 2013). Given the high diversity of species found in riparian zones, however, temperature ranges for germination remain unknown. We suspect that many have wide temperature ranges for germination, as an adaptation to the seasonally variable timing of the flood pulses that moisten river floodplains. Alternatively, given that there are defined cool-season and warm-season floods, riparian zones may have a high percentage of temperature specialists. Germination stimulated by exposure to light/dark cycles and adequate moisture in combination with temperature

variation—both diurnal and seasonal—allow riparian plants to control for seed dispersal and/or burial linked with flood pulses (Thompson and Grime 1983; Leyer and Pross 2009).

In the Southwest, precipitation and snowpack have already decreased, thus reducing stream flows throughout the region; the summertime temperatures are already increasing, and are likely to continue to increase, as will unpredictable flooding events and wildfires (Karl et al 2009; Garfin et al 2014). Upon reexamination of Robert Whittaker's 1963 study in the Santa Catalina Mountains of southern Arizona Brusca et al (2013) found that the trend of lower elevation species moving into higher in elevations and elevational range contractions for many species were significant. In her study of herbarium specimens Bowers (2007) indicated that flowering phenology of Sonoran Desert shrubs might have shifted anywhere from 20 to 41 days earlier between the years of 1894 to 2004, especially between 1990 and 1999. The transition of flowering, fruiting, and seed dispersal to an earlier time of the year would cause seeds to be in the soil longer, which increases vulnerability to herbivory. This decrease of certain seeds in the seed bank during subsequent seasons may affect populations of desert shrubs and their associated plant communities. The number of frost free days have increased, and for plants this can lead to early bud burst and frost damage, heat stress, and increased herbivory because pests are not killed by off by cold winter temperatures (Garfin et al 2014).

Diffenbaugh et al (2008) have persistently identified the Southwestern United States and Northern Mexico as climate change hotspots using multiple climate models. Dominguez and Rivera (2012) predict, based on their climate models, that the

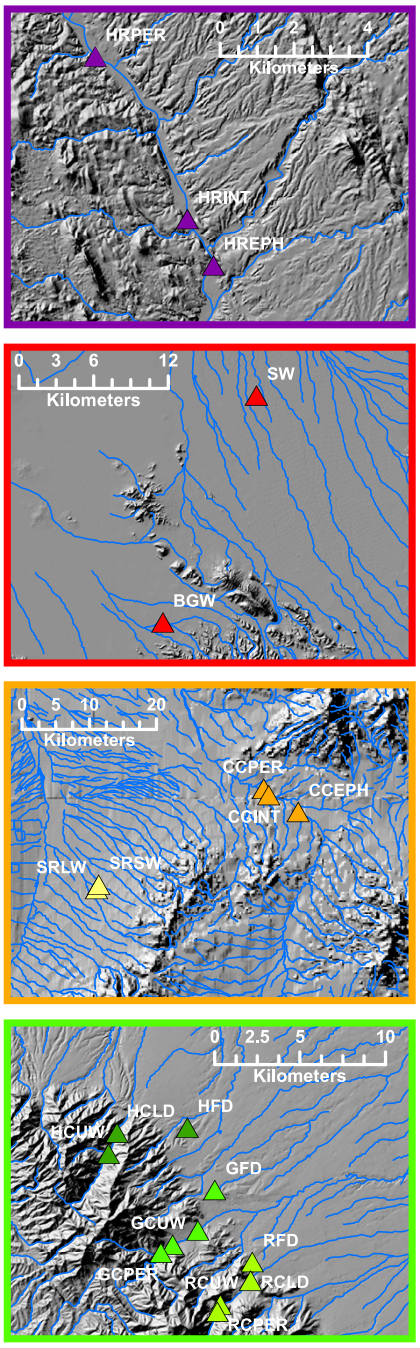
Southwestern and Coastal areas of the United States will have a decrease in the mean annual winter precipitation by approximately 7.5%, however the entire Southwestern region is predicted to have an increase in extreme winter precipitation events. Therefore, the Southwest should expect more unpredictable storm events with a decrease in overall precipitation. The seasonality of flood pulsing is an integral abiotic factor that plays a significant role in shaping Southwestern riparian zone plant communities, thus climate change related stressors are a major cause for concern going forward.

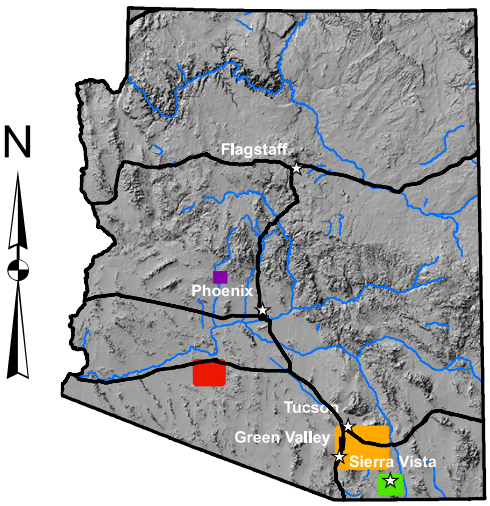
With climate as a growing concern, increased understanding of ecosystem functioning in Southwestern riparian areas will allow decision makers to make more informed land use and conservation choices for Southwestern riparian areas, including ephemeral and intermittent streams, their surrounding habitats, communities, and the industries that they support. To increase our level of knowledge about and the effects of temperature on germination within Southwestern riparian seed banks, I asked the following questions 1) Are there distinct suites of warm temperature and cool temperature germinating species in the soil seed banks of Southwestern streams? a) Does the number of temperature specialists differ between riparian and terrestrial (upland) zones? b) Does the number of temperature specialists differ between ephemeral streams and those with perennial headwaters?

STUDY AREAS

I collected soil seed bank samples from a total of twenty-one study sites in central and Southeastern Arizona that varied in elevation, climate, and hydrogeomorphology to discern the possible affects that a changing temperature regime might have on seed

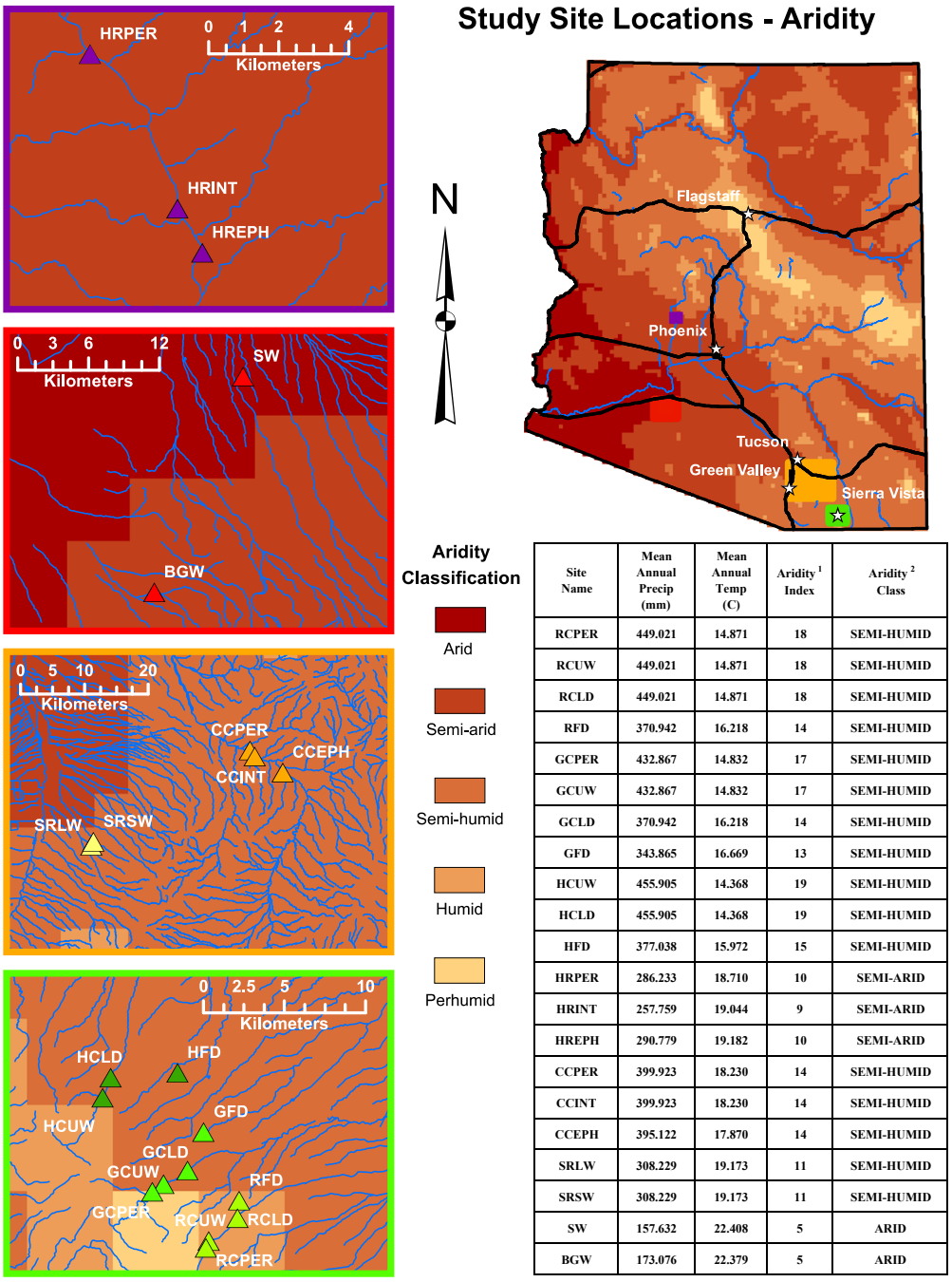
germination in southwestern riparian. The study sites were 250 m to 300 m long sections of stream. Their elevation ranged from 249 m to 1797 m. They were situated in arid, semiarid, or semi-humid climate zones. I calculated aridity zone using the de Martonne Aridity Index (mean annual precipitation in mm divided by mean annual temperature in °C plus a constant of 10) (Quan et al. 2013). In this system, a value of less than five is arid, five to 10 is semi-arid, 10 to 20 is semi-humid, 20 to 30 is humid, and greater than 30 is per-humid. Seven of the sites are located on ephemeral streams. The remaining fourteen sites are located along spatially intermittent streams that have perennial, intermittent, and ephemeral-phreatic reaches. Stream flow permanence at the sites was determined either from prior studies that used monthly site visits to assess flow presence/absence (Katz et al. 2012) or from electrical resistance sensors placed in the stream channel (Blasch et al 2002; Stromberg et al 2015).





Site	Upstream Elevation (m)	Downstream Elevation (m)
SW	258	249
BGW	324	322
HREPH	561	559
HRINT	568	564
HRPER	596	596
SRSW	956	949
SRLW	958	955
CCPER	1029	1026
CCINT	1054	1035
CCEPH	1083	1076
HFD	1452	1429
GFD	1505	1501
RFD	1539	1531
GCLD	1545	1545
GCUW	1593	1572
RCLD	1596	1573
HCLD	1606	1592
GCPER	1631	1620
HCUW	1671	1659
RCUW	1755	1729
RCPER	1797	1768

Fig. 2 Elevation map showing site locations by major geographical areas. Table lists sites from lowest to highest elevation for upstream end of site



Site Name	Mean Annual Precip (mm)	Mean Annual Temp (C)	Aridity [1] Index	Aridity [2] Class
RCPER	449.021	14.871	18	SEMI-HUMID
RCUW	449.021	14.871	18	SEMI-HUMID
RCLD	449.021	14.871	18	SEMI-HUMID
RFD	370.942	16.218	14	SEMI-HUMID
GCPER	432.867	14.832	17	SEMI-HUMID
GCUW	432.867	14.832	17	SEMI-HUMID
GCLD	370.942	16.218	14	SEMI-HUMID
GFD	343.865	16.669	13	SEMI-HUMID
HCUW	455.905	14.368	19	SEMI-HUMID
HCLD	455.905	14.368	19	SEMI-HUMID
HFD	377.038	15.972	15	SEMI-HUMID
HRPER	286.233	18.710	10	SEMI-ARID
HRINT	257.759	19.044	9	SEMI-ARID
HREPH	290.779	19.182	10	SEMI-ARID
CCPER	399.923	18.230	14	SEMI-HUMID
CCINT	399.923	18.230	14	SEMI-HUMID
CCEPH	395.122	17.870	14	SEMI-HUMID
SRLW	308.229	19.173	11	SEMI-HUMID
SRSW	308.229	19.173	11	SEMI-HUMID
SW	157.632	22.408	5	ARID
BGW	173.076	22.379	5	ARID

Fig. 3 Aridity map showing study site locations by major geographical areas. [1] Aridity = Mean annual precip.(mm)/(Mean annual temp. (C) +10). [2] Aridity classifications: < 5: arid; 5–10: semi-arid; 10–20: semi-humid; 20–30: humid; >30: perhumid

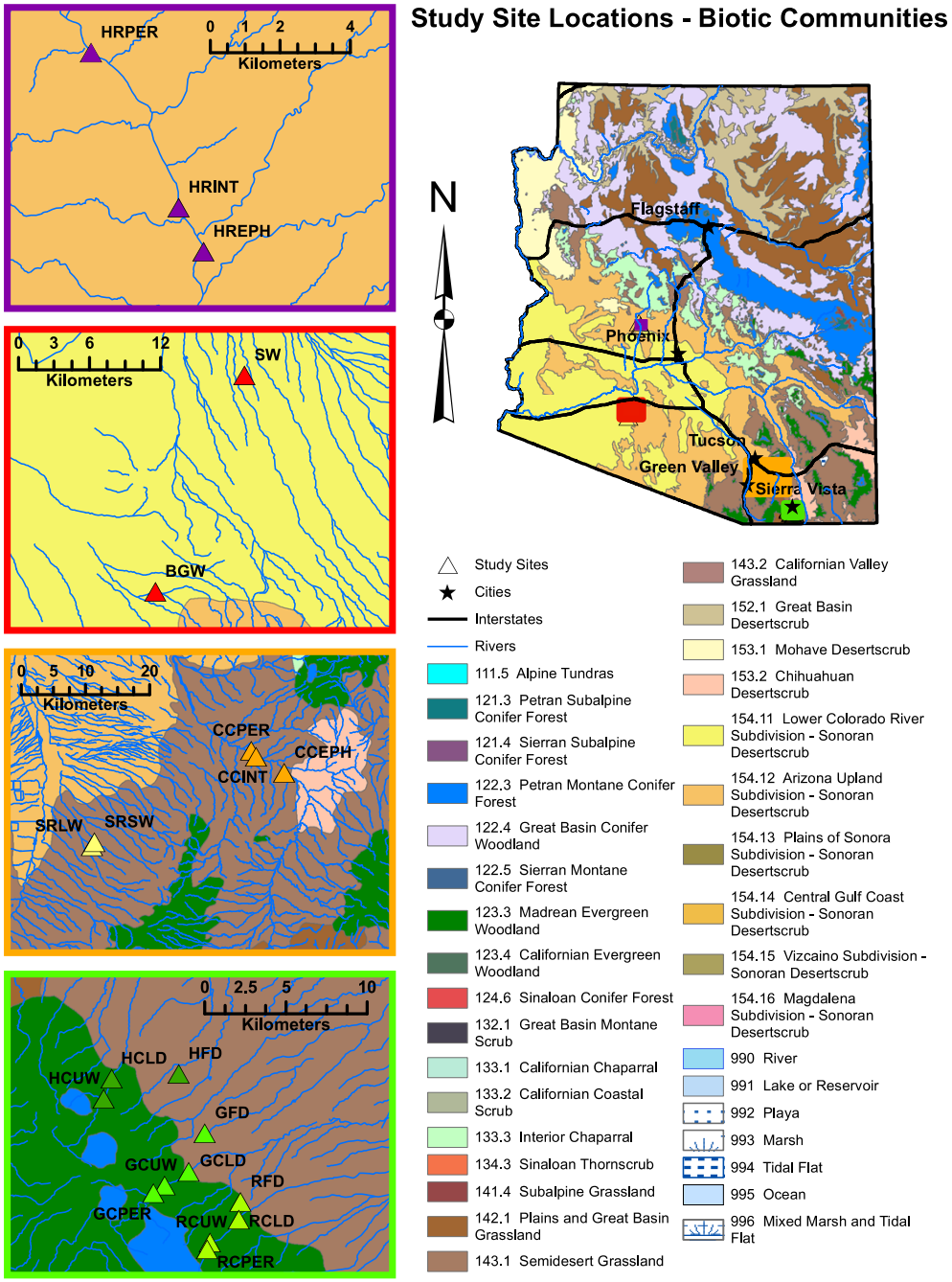


Fig. 4 Biotic communities map showing site locations by major geographical areas

Barry M. Goldwater Air Force Range

One study area was located on the Barry M. Goldwater Air Force Range, just west of Gila Bend in central Arizona. The sites in this study area were along two ephemeral washes: Sauceda Wash and Black Gap Wash (SW and BGW); they were the lowest elevation sites in the study and the most arid. Based on the aridity calculations both are arid. They were both hydrogeomorphically classified as basin ephemeral stream types. The vegetation in this region is of the Lower Colorado River Subdivion Sonoran Desertscrub (Brown 1994). The perennial vegetation in the narrow riparian zones of these washes consists primarily of *Prosopis juliflora* var. *velutina, Parkinsonia florida, Acacia greggii, Olneya tesota,* and *Larrea tridentata*. The perennial vegetation in the terrestrial zones surrounding these washes consists of *Larrea tridentata*, with some scattered *Ambrosia dumosa* and *Ferocactus wislizeni*. The annual vegetation in both zones consisted primarily of cool-season plants such as *Amsinckia* spp., *Camissonia* spp *Caulanthus lasiophyllus, Cryptantha* spp., *Erodium* spp., *Euphorbia* spp., *Lepidium lasiocarpum,* and *Pectocarya* spp.

Hassayampa River Preserve

The Hassayampa River (HR) is a spatially intermittent, lower elevation river that flows underground for the majority of its length and is located in the basin and range area of central Arizona, near Wickenburg. I selected three study sites along this river that vary in flow permanence from perennial (HRPER), to intermittent (HRINT), to ephemeral-phreatic (HREPH). The sites that I selected were within the Hassayampa River Preserve, which was owned and operated by The Nature Conservancy. Due to

geographical and property constraints the terrestrial zone was only sampled at the ephemeral-phreatic study site. These three sites were the second lowest in elevation and aridity, and were classified as semi-arid.

The vegetation of this area is classified as Arizona Upland Subdivision – Sonoran Desertscrub (Brown 1994). The most abundant perennial vegetation in the riparian zones consists primarily of *Baccharis salicifolia, Eleocharis* spp.*, Juncus* spp., *Mimulus* spp., *Populus fremontii, Prosopis juliflora* var. *velutina, Salix goodingii, Schoenoplectus* spp., *Typha domingensis,* and *Veronica anagallis-aquatica* along the perennial and intermittent sections. The perennial vegetation in the riparian zone of the ephemeral-phreatic section is primarily *Acacia greggii, Ambrosia salsola, Ambrosia monogyra, Baccharis salicifolia, Baccharis sarothroides, Celtis pallida, and Prosopis juliflora* var. *velutina*. *Ambrosia* spp., *Atriplex* spp., *Cylindropuntia* spp., *Gutierrezia sarothrae, Isocoma acradenia*, and *Opuntia* spp. are some of the species that comprise the perennial vegetation in the terrestrial zone in this study area. There are many annual and biennial species in the study area; *Bromus* spp., *Calibrachoa parviflora, Euphorbia* spp., *Hordeum murinum, Melilotus* spp., *Pluchea odorata, Polypogon monspeliensis*, and *Pseudognaphalium* spp. are some of the more abundant of these species.

Santa Rita Experimental Range

The Santa Rita Experimental Range (SRER) is a conservation area of a little over 53,000 acres established in the early 1900's and managed and maintained by the University of Arizona. It is located on the Northwest side of the Santa Rita mountains, about 35 miles South of Tucson. Much of the area consists of alluvial fans crossed with

washes and gullies. Historically most of the area was Semidesert Grassland (Brown 1994) however much of the grassland has been invaded by woody shrubs (primarily *Prosopis juliflora* var. *velutina*) and some cacti (*Opuntia* spp. and *Cylindropuntia* spp.), as well as *Eragrostis lehmanniana*—an introduced non-native grass. Two basin ephemeral washes (SRSW and SRLW) were selected as study sites in this area. The washes are classified as semi-humid.

The perennial vegetation in the riparian zones of these washes consists primarily of *Acacia greggii, Celtis pallida, Parkinsonia florida, Prosopis juliflora* var. *velutina*, and *Ziziphus obtusifolia*. Some of the dominant perennial species in the terrestrial zone are *Aristida* spp., *Bouteloua* spp., *Cylindropuntia* spp., *Ephedra trifurca, Eragrostis* spp., *Muhlenburgia* spp., *Opuntia* spp., and *Prosopis juliflora* var. *velutina*. The annual vegetation in both the riparian and terrestrial zones consists of different groups of forbs and grasses, depending on the season. *Amsinckia* spp., *Boerhavia* spp., *Bouteloua aristidoides, Cryptantha* spp., *Eschscholtzia californica, Euphorbia* spp., *Pectocarya* spp., *Portulaca* spp., *vulipia octoflora,* and *Tidestromia lanuginosa* and were some of the more common annual species found at these sites.

Ciénega Creek Natural Preserve

Ciénega Creek is an alluvial Basin and Range stream located in Southern Arizona, Southeast of the Tucson area. Ciénega Creek supports riparian plant community types including mesquite bosques and cottonwood-willow forests, and provides important habitat for many endangered fish, birds, reptiles, and amphibians. Much of the perennial section of the stream is now protected by the Ciénega Creek Natural Preserve, which is

where I selected three study sites along the creek that vary in flow permanence from perennial (CCPER), to intermittent (CCINT), to ephemeral-phreatic (CCEPH). Only the intermittent site (CCINT) had seed bank samples taken in both the riparian and terrestrial zones. These study sites are all classified as semi-humid based on aridity calculations.

These three study sites are all located in the Semidesert grassland plant community (Brown 1994). The vegetation of this area is classified as Arizona Upland Subdivision – Sonoran Desertscrub (Brown 1994). The most abundant perennial plants in the riparian zones are *Baccharis salicifolia, Celtis reticulata, Eleocharis* spp., *Juncus* spp., *Mimulus* spp., *Muhlenbergia rigens, Populus fremontii, Prosopis juliflora* var. *velutina, Salix gooddingii, Schoenoplectus* spp., *Sorghum halapense, Sporobolus wrightii, Typha domingensis,* and *Veronica anagallis-aquatica*. In some areas the riparian areas have multiple terraces due to incisement of the stream channel. Common terrace species include *Acacia greggii, Baccharis sarothroides, Celtis pallida*, *Prosopis juliflora* var. *velutina,* and *Ziziphus obtusifolia.* Common perennial species in the terrestrial area are *Ambrosia* spp., *Cylindropuntia* spp., *Dasyochloa pulchella, Gutierrezia sarothrae, Isocoma* spp., *Larrea tridentata, Opuntia* spp. Common annual and/or biennial species that occur in the study area are *Bromus* spp., *Calibrachoa parviflora, Erigeron canadensis, Euphorbia spp., Hordeum murinum, Juncus bufonius, Melilotus* spp., *Polypogon monspeliensis,* and *Pseudognaphalium* spp.

Huachuca Mountains

The Huachuca Mountains are located in Southeastern Arizona just southwest of Sierra Vista and are considered part of the biogeographical province known as the

Madrean Archipelago, or "Sky Islands". The large range in elevation, variation in geology and hydrogeomorphology (including slope and aspect), and water availability all contribute to a rich flora—994 species when the last flora of the region was completed, almost 70% of which is comprised of Madrean species (Bowers and McLaughlin 1996). The sky islands are a biodiversity hotspot; home to large number of endemic plant, bird, butterfly, reptile, fish, mammal, and amphibian species (Karl et al 2009). The area is a well-known destination for hiking, birding, and butterfly watching.

Eleven sites were selected from the Huachuca Mountains and the surrounding foothills located along three spatially and temporally intermittent streams that have perennial reaches: Ramsey, Garden, and Huachuca canyons (RC, GC, and HC). The sites on the canyon streams include reaches of perennial (RCPER and GCPER), intermittent (RCUW, GCUW, and HCUW), and ephemeral-phreatic (RCLD, GCLD, and HCLD) flow. The upstream (perennial) canyon sites are the highest elevation sites in the study. (Seed bank samples from the perennial site on Huachuca Canyon (HCPER) were not germinated because the location where the soils were collected ended up being intermittent instead of perennial.) The terrestrial zones at the perennial sites were not sampled due to the steepness of the Canyon walls. Sites on three ephemeral washes (RFD, GFD, and HFD) in the foothills near each canyon stream were also selected. The aridity index for all eleven sites is semi-humid.

The canyon sites in this study area are in the Madrean Evergreen Woodland biotic community, along with one of the foothills sites—RFD—that is right near the transition into the Semidesert Grassland community, where the other two foothills sites (HFD and GFD) are located (Brown 1994). The perennial species of the riparian zones at the

canyon sites consist mainly of *Arbutus arizonica, Juglans major, Juniperus deppeana, Pinus* spp., *Piptochaetium fimbriatum, Platanus wrightii, Quercus emoryi, Q. grisea, Q. hypoleucoides, Rhus trilobata*. In addition to those species, the upstream canyon site riparian zones also include *Abies concolor, Acer grandidentatum*, and *Pseudotsuga menziesii.* The perennial species that dominate the uplands at the canyon sites are *Arctostaphylos pungens, Eragrostis* spp., *Juniperus deppeana, Muhlenbergia* spp., *Pinus* spp., *Piptochaetium fimbriatum, Quercus emoryi, Q. grisea, Q. hypoleucoides,* and *Rhus trilobata.* The perennial species in the riparian zones of the foothills sites include *Agave* spp., *Aristida* spp., *Bothriochloa barbinodis, Bouteloua* spp., *Calliandra eriophylla, Disakispermum dubia, Elionurus barbiculmis, Eragrostis* spp., *Evolvulus* spp., *Mimosa aculeaticarpa* var. *biuncifera, Prosopis juliflora* var. *velutina, Schizachyrium* spp., and *Trachypogon spicatus*; most of the same perennial species occur in the uplands at these sites. The sites all have a large number of annual/biennial species, some of the more common of which include *Acalypha* spp., *Bidens* spp., *Desmodium* spp., *Diodia teres, Eriochloa acuminata, Euphorbia* spp., *Heliomeris* spp., *Mitracarpus breviflorus, Mollugo verticillata, Panicum hirticaule,* and *Urochloa arizonica.*

METHODS

Seed Bank Study

Soil seed bank samples were collected in January and early February of 2012. Two subsamples of soil were collected at four random locations from both the right and left banks of the stream at each study area in both the riparian and terrestrial zones. At each random location approximately 700 ml of soil for each of the two subsamples was

collected to ensure enough soil was collected. Each of the subsamples were collected by taking multiple soil cores from the top 5 cm of soil within a one square meter area using a standard bulb corer (including small litter and duff) until the container had approximately 700ml of compressed soil. A 19mm sieve was used to remove larger debris from the sample on site.

The soil samples were stored in a cold room at 4 °C until two environmental growth chambers were available to conduct the experiment. One set of subsamples were assigned to the warm temperature treatment (25 – 35 °C) and the other set was assigned to the cool temperature treatment (10 – 20 °C). During sample preparation approximately 1 cm (~200 ml) of soil from each subsample was layered on top of a 3 cm (~500 ml) layer of autoclaved base soil (sandy loam) in small flats. The samples were placed in the growth chambers on January 31, 2013. After a seven-day dry-down period the samples were fully saturated for three days and then allowed to dry out until they were damp. Samples were then watered as necessary to maintain moist soils and to ensure that water availability was not limited.

Temperature within each growth chamber was programmed to change temperature seven times within each 24-hour cycle coinciding with major diurnal fluctuations in temperature; there was a daytime maximum of 35°C and nighttime minimum of 25°C for warm treatment and 20°C and 10°C for the cool treatment. Day-length was programed to simulate the day length for the time of year associated with the temperature bands (http://www.ncdc.noaa.gov/cdo-web/). The seed bank samples were grown for twelve weeks in the two environmental growth chambers. While in the growth chambers, individuals were harvested/collected as they became identifiable. After the

twelve-week experimental period, the remainder of the samples were transferred to greenhouses and grown until the plants were mature. Plants were identified to the most specific taxonomic level possible; "species" that were identifiable as a single taxon but not able to actually be determined were given a morpho-species number. Plant identification was conducted using *Arizona Flora* (Kearney et al 1979), *Canotia*, *Journal of the Arizona-Nevada Academy of Science*, and *The Jepsons Manual* (Baldwin and Goldman 2012), and utilizing the collection at the Arizona State University Herbarium.

Statistical and Graphical Analysis

I used ArcGIS® to make the three site maps (ArcMap 10.2.1 software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. www.esri.com) to create all site maps. The aridity site map Fig. 3 created by mapping PRISM data downloaded for the site locations (http://prism.nacse.org/historical/). To conduct my statistical and graphical analyses I used R version 3.3.1 (https://cran.r-project.org) and R studio 1.0.44 (https://www.rstudio.com), with multiple R packages including Vegan, BiodiversityR, SpadeR, betapart, dplyr, tidyr, agricolae, Cairo, hclust, Hmisc, car, and ggplot2.

To determine if there were different temperature dependent germination groups I used the ChaoShared function from the SpadeR package, which estimates the number of shared species between pairs of data sets. I calculated the similarities between the warm and cool treatments within each zone (riparian and terrestrial) for each site. Based on a species abundance matrix (by summing the columns (community/sample) and rows

(species) and then comparing those numbers) the ChaoShared function in the SpadeR package can calculate the total number of communities, the total number of individuals per community, the total number of species per community, and the number of species each community has in common. Using these similarity totals I calculated the number of cool, warm, and both cool and warm (generalist) germinating species within each zone at each site. To detect significant differences between the number of species found in each temperature germination group for the riparian and terrestrial zones, as well as between ephemeral washes and streams with perennial headwaters I conducted Kruskal-Wallis and associated post-hoc non-parametric tests (O'Hara and Kotze 2010).

RESULTS

Question 1

The similarity data that I calculated between the temperature treatments for each zone at each site showed that there were distinct warm and cool germinating species in the soil seed banks along Southwestern streams, as well as temperature generalists that germinated in both temperature treatments. When comparing the three temperature germination groups between the riparian and terrestrial zones for all sites an average of 6.0 species per site were riparian cool germinants, 5.8 species were riparian warm germinants, and 2.3 were riparian generalists. When comparing the three germination groups for both zones for only those sites that had both riparian and terrestrial samples, an average of 5.6 species per site were riparian cool germinants, 6.1 species were riparian warm germinants, and 2.6 were riparian generalists. For the terrestrial zone (same for either analysis), the respective numbers were 4.8 (cool germinants), 4.2 (warm germinants), and 2.5 (generalists) (Fig. 5, Fig. 6, Table 1).

Based on both of the statistical analyses—all sites and sites with samples in both zones—there were significant differences between the mean ranks for some of the germination groups (Table 2). There were two primary subsets that were significantly different from each other: the Cool-Riparian, Warm-Riparian, and Cool-Terrestrial germination groups were in one subset (not significantly different from each other), vs the Warm-Terrestrial and Generalist-Riparian germination groups in the other subset (not significantly different from each other). The Warm-Terrestrial germination group was not significantly different from either of those two primary subsets.

In the collective seed bank as a whole there were a large number of temperature specialists, and the riparian zone had a larger number of temperature generalists as compared to the terrestrial zone. For the seed banks from all sites amassed as a collective the riparian zone had a total of 136 taxa germinants; 88 taxa were cool temperature germinants, 91 taxa were warm temperature germinants. In the terrestrial zone a total of 79 taxa germinated; 52 taxa were cool temperature germinants, 42 taxa were warm temperature germinants. Although the average number of species per germination group by site within and between zones was not always significantly different, the composition of each germination group as a whole was different; there were many taxa unique to each group. Comparing the warm and cool temperature germinants within the riparian zone there were 45 taxa found specifically in the cool treatment that were not found in the warm treatment and 48 taxa were found specifically in the warm treatment that were not found in the cool treatment, and there were 43 riparian generalists. Within the terrestrial zone there were 37 taxa specifically found in the cool treatment that were not found in the warm treatment and 27 taxa specifically found in the warm treatment that were not found in the cool treatment, and there were 15 terrestrial generalists.

A comparison made between the warm and cool germinating taxa for both the riparian and terrestrial zones revealed that there were distinct suites of taxa within each group for each zone: 36 riparian cool specialists, 36 riparian warm specialists, 20 terrestrial cool specialists, and 14 terrestrial warm specialists. There were 16 riparian generalists not found in the terrestrial zone and 2 terrestrial generalists not found in the riparian zone. There were 31 taxa that were found in to be temperature and habitat (zone) generalists; of those there were 12 taxa that were temperature generalists that were found

in both the riparian and terrestrial zones (both habitat and temperature generalists found in both temperature treatments for both zones).

When comparing the three germination groups between perennial headwater and ephemeral stream types, an average of 6.3 species per site were perennial cool germinants, 5.2 species were perennial warm germinants, and 3.0 were perennial generalists. For the ephemeral streams, the respective numbers were 6.9 (cool germinants), 6.9 (warm germinants), and 2.4 (generalists) (Fig. 7, Table 1). The statistical analysis revealed that there were some significant differences between some of the temperature germination groups between stream types (Table 2). There were no statistically significant differences between the cool and warm specialists for either the perennial headwater streams or the ephemeral washes, however the number of temperature generalists for both stream types was significantly different from the number of perennial and ephemeral cool specialists and, the ephemeral warm specialists.

Table 1 Summary statistics for the number of species per temperature dependent germination group for terrestrial versus riparian zones (data grouped two ways: all sites and only sites with both riparian and terrestrial zone samples) and ephemeral versus perennial headwater streams

Germination Group	Mean	Var	SD	SE
Ephemeral Generalists	2.43	12.29	3.51	1.32
Ephemeral Cool Specialists	6.86	5.81	2.41	0.91
Ephemeral Warm Specialists	6.86	15.81	3.98	1.50
Perennial Generalists	3.00	4.50	2.12	0.71
Perennial Cool Specialists	6.33	9.50	3.08	1.03
Perennial Warm Specialists	5.22	1.94	1.39	0.46
Terrestrial Generalists	2.53	4.55	2.13	0.55
Terrestrial Cool Specialists	4.80	5.74	2.40	0.62
Terrestrial Warm Specialists	4.20	8.03	2.83	0.73
Riparian Generalists *	2.76	6.39	2.53	0.55
Riparian Cool Specialists *	6.05	7.15	2.67	0.58
Riparian Warm Specialists *	5.76	7.39	2.72	0.59
Riparian Generalists ▲	2.56	6.93	2.63	0.66
Riparian Cool Specialists ▲	5.56	6.13	2.48	0.62
Riparian Warm Specialists ▲	6.13	8.92	2.99	0.75

* Comparison between germination groups for all sites including those without terrestrial samples.

▲ Comparison between germination groups for only sites that have both riparian and terrestrial samples.

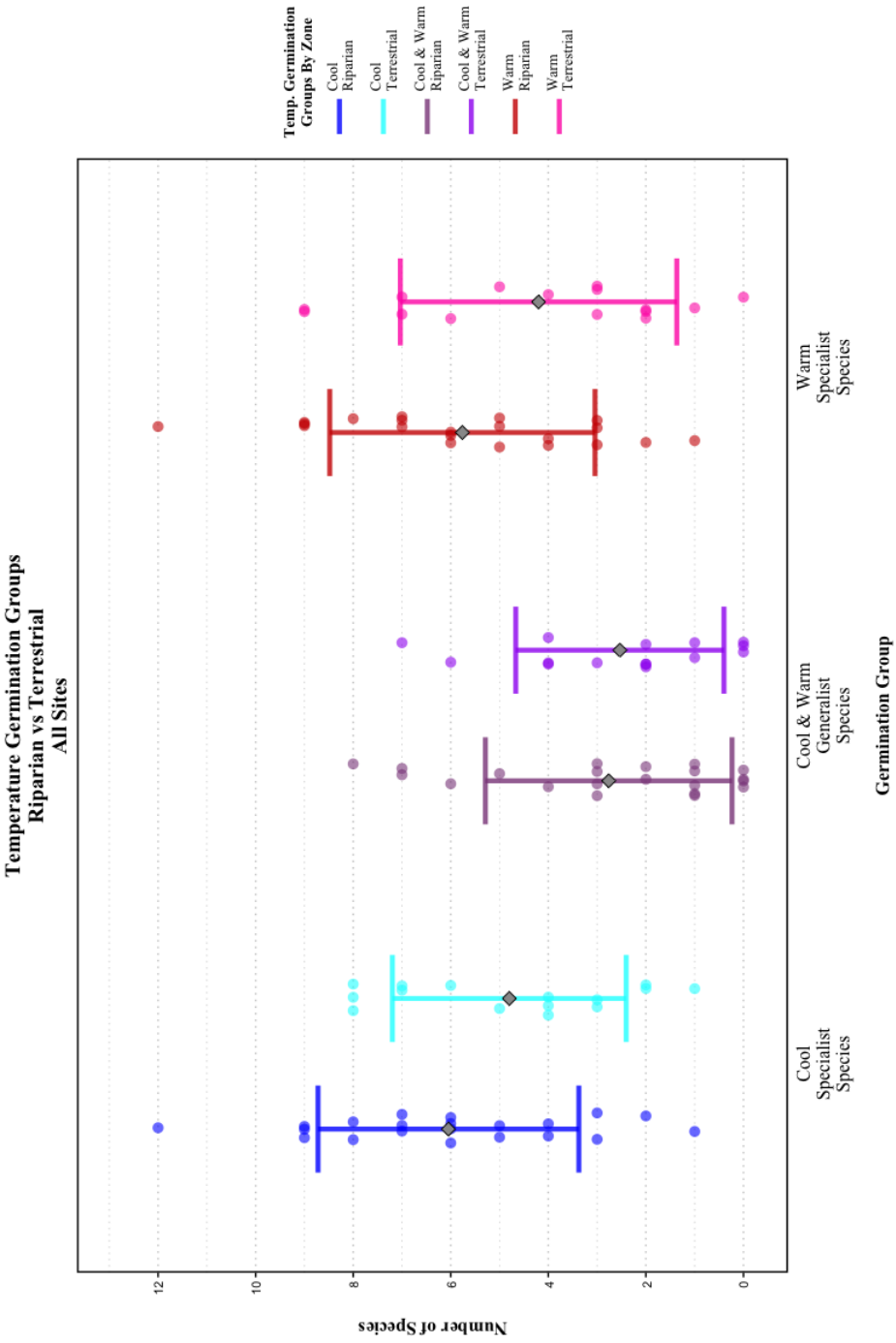


Fig. 5 Error bar plot displaying the number of species per temperature germination group within the riparian and terrestrial zones for all sites. Grey diamonds are the means; error bars are plus/minus one standard deviation

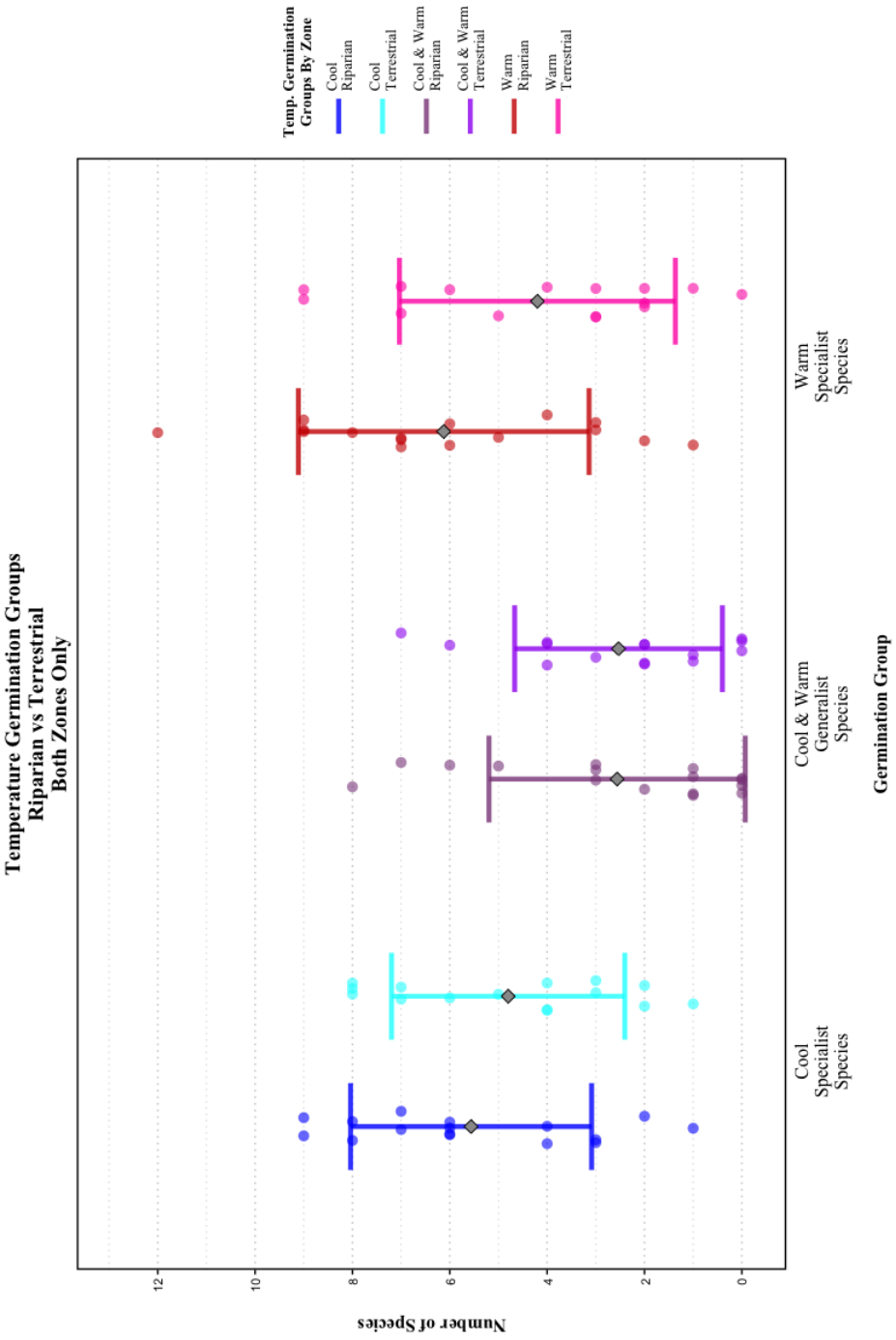


Fig. 6 Error bar plot displaying the number of species per temperature germination group within the riparian and terrestrial zones only for sites that have both riparian and terrestrial samples. Grey diamonds are the means; error bars are plus/minus one standard deviation

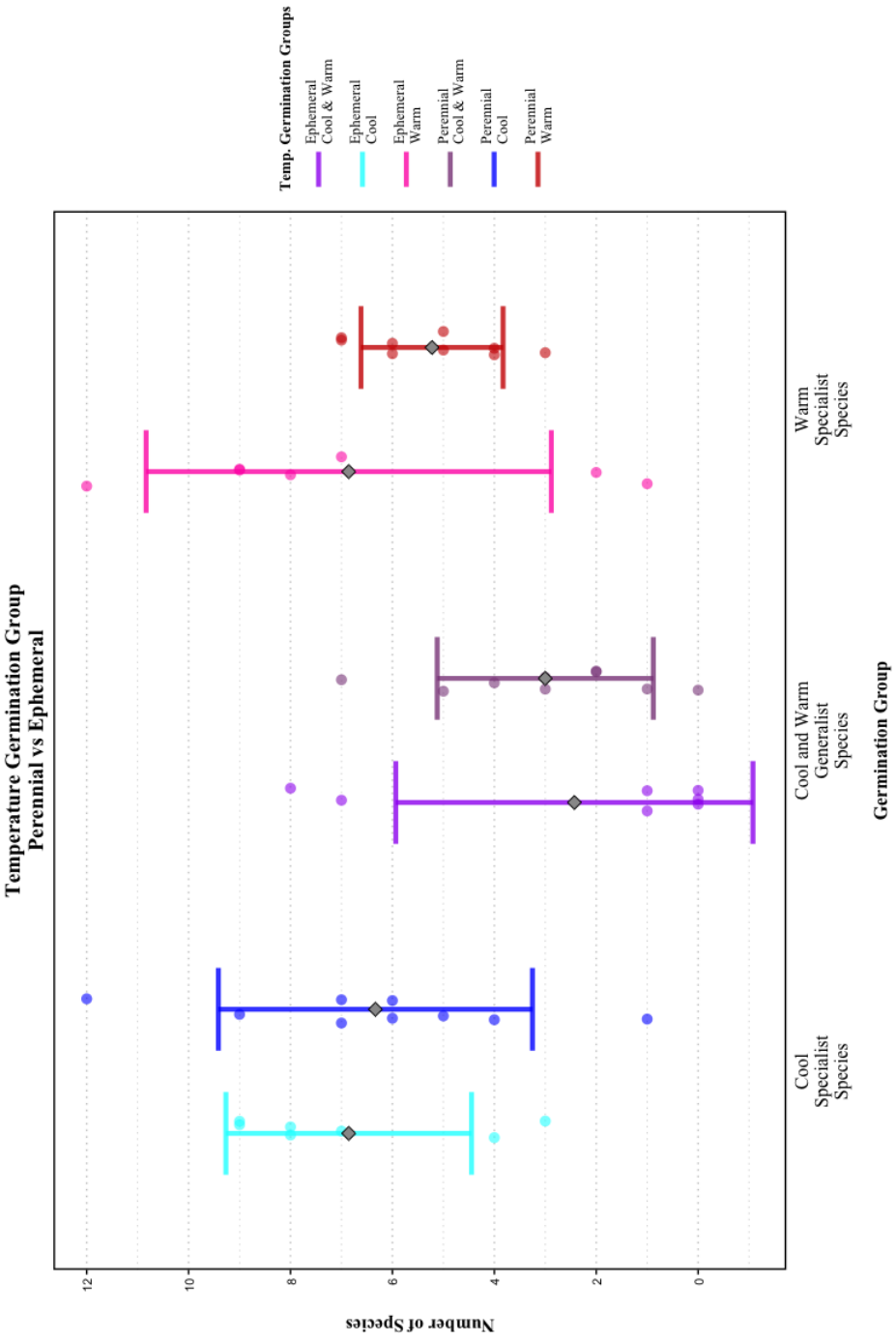


Fig. 7 Error bar plot showing number of species that germinated in the riparian zones perennial headwater and ephemeral streams. Grey diamonds are the means; error bars are plus/minus one standard deviation

Riparian vs Terrestrial (All)	Zone Germ Group	Riparian Cool	Riparian Warm	Riparian Generalists	Terrestrial Cool	Terrestrial Warm	Terrestrial Generalists
X^2 25.479	Mean Rank	71.7	68.6	36.0	59.9	52.1	33.6
p 0.000112585	avg	6.05	5.76	2.76	4.80	4.20	2.53
Df 5	std	2.67	2.72	2.53	2.40	2.83	2.13
ntr 6	Min	1	1	0	1	0	0
t 1.983	Max	12	12	8	8	9	7
α 0.05	r	21	21	21	15	15	15
	[1]Groups	a	a	b	a	ab	b
Riparian vs Terrestrial (Both)	**Zone Germ Group**	**Riparian Cool**	**Riparian Warm**	**Riparian Generalists**	**Terrestrial Cool**	**Terrestrial Warm**	**Terrestrial Generalists**
X^2 20.352	Mean Rank	57.8	60.5	29.5	51.0	44.7	29.6
p 0.001073168	avg	5.67	6.13	2.60	4.80	4.20	2.53
Df 5	std	2.53	3.09	2.72	2.40	2.83	2.13
ntr 6	Min	1	1	0	1	0	0
t 1.989	Max	9	12	8	8	9	7
α 0.05	r	15	15	15	15	15	15
	[1]Groups	a	a	b	a	ab	b
Perennial vs Ephemeral	**Stream Type Germ Group**	**Perennial Cool**	**Perennial Warm**	**Perennial Generalists**	**Ephemeral Cool**	**Ephemeral Warm**	**Ephemeral Generalists**
X^2 14.555	Mean Rank	29.2	24.6	15.2	33.4	32.4	13.5
p 0.01244254	avg	6.33	5.22	3	6.86	6.86	2.43
Df 5	std	3.08	1.39	2.12	2.41	3.98	3.51
ntr 6	Min	1	3	0	3	1	0
t 2.018	Max	12	7	7	9	12	8
α 0.05	r	9	9	9	7	7	7
	[1]Groups	a	ab	b	a	a	b

[1] Conover post-hoc procedure conducted using the Benjamini-Hochberg p-adjust method.

Table 2 Kruskal-Wallis test results for analyses conducted on the riparian and terrestrial (upland) zone temperature germination groups and the perennial headwater stream and ephemeral wash germination groups

CHAPTER 3: DIVERSITY OF SEED BANKS WITHIN EPHEMERAL, INTERMITTENT AND PERENNIAL STREAMS

INTRODUCTION

Throughout the Southwest, complex geology and physiography concomitant with climatic variability contribute to diverse hydrogeomorphologies—from perennial high-elevation montane streams to large low-elevation rivers (Baker et al 2004). In Arizona, streams with perennial flow are limited in number; ~94% are ephemeral or intermittent (Levick et al. 2008). The variable hydrologic conditions found along and amongst ephemeral and intermittent streams can have site specific effects on species richness and diversity (Bendix 1997). In ephemeral and intermittent streams germination pulses can be caused by both rain and floodwaters (Bagstad et al 2005; Levick et al 2008). Intermediate flood pulse events stimulate increased cover and species richness for mesic and xeric perennial plant species in Arizona streams (Bagstad et al 2005; Lite et al 2005).

Herbaceous plant species richness and cover often increase with intermediate flood disturbance and increased moisture availability in Arizona streams—especially for annual herbaceous plant species (Bagstad et al 2005; Lite et al 2005; Stromberg et al 2009a; Katz et al 2011). Intense flood events can decrease herbaceous species richness (Leck and Brock 2000), and can in certain cases decrease the establishment of perennial species (Leyer and Pross 2009). Reduced flood pulse frequency can decrease overall species richness because canopy shading from riparian forests can limit the germination of annual species (Stromberg et al 2010b); in contrast openings or gaps in canopy or

exposed soils increase the number of annual species in turn leading to an increase in species richness (Williams et al 2008; Leyer and Pross 2009).

Flood pulsing in streams can sometimes lead to increased homogeneity of seed banks between sites of different inundation duration and/or frequency within the same stream (Brock and Rogers 1998; Boudell and Stromberg 2008b; Williams et al 2008; Casanova 2015). In other cases the seed banks differ between hydrogeomorphic conditions within the stream (Hanlon et al 1998; Abernethy and Willby 1999; Tererai et al 2014). Ephemeral and intermittent stream seed bank composition and/or richness commonly differs from the extant flora from the same sample location in some way—by having significantly more, less, or different species (Brock and Rogers 1998; Goodson et al 2001; Boudell and Stromberg 2008b; Boudell and Stromberg 2008a; Williams et al 2008; Stromberg et al 2009b; Kehr et al 2014; Tererai et al 2014), but the seed bank and the extant flora are not always significantly different (Richter and Stromberg 2005). In some streams the differences between seed banks and plant communities can increase across a disturbance gradient (Abernethy and Willby 1999).

Plant communities that occur along ephemeral and intermittent streams are important to ecosystem functioning because they influence biogeochemical cycling, hydrogeomorphology, as well as provide habitat for both local and migrating wildlife (Baker et al 2004; Levick et al 2008; Naiman et al 2010). According to Perry et al (Perry et al 2012) climate change driven changes in streamflow can decrease the abundance of dominant natives and early successional tree species, increase herbaceous and drought tolerant and late successional woody species, and slow litter decomposition and nutrient cycling, all leading to habitat degradation. Due to the ecological importance of

ephemeral and intermittent streams and the fact that stream flow fluctuations due to climate change and other anthropogenic impacts are likely to increase it is important to understand how plant communities along these stream/reach types will change over time.

To increase our level of knowledge about the diversity of Southwestern riparian seed banks, and how they differed among streams with different flow regimes, I asked: 2) How does alpha diversity of the soil seed bank within riparian zones compare among hydrogeomorphorphic reaches (perennial, intermittent, ephemeral-phreatic, ephemeral) within/near a stream? 3) How does the alpha diversity of soil seed banks within the riparian zones differ among hydrogeomorphic reach types (perennial, intermittent, ephemeral-phreatic, ephemeral) for canyon and basin streams? 4) Does nestedness or spatial turnover contribute more to within stream beta-diversity?

METHODS

Question 2

I felt that it was important to examine alpha diversity using multiple indices as opposed to relying on a single index, as well as to look at diversity both graphically and statistically. I wanted to avoid the biases that certain indices have in favor of rare (species richness) or common/dominant (Simpson's Index) species. I also thought that there might be unobserved species in the seed bank, and I felt that the Chao Estimate would be helpful because it includes the unseen species (Chao et al 2006). I felt that using multiple methods to investigate riparian zone seed bank alpha diversity would allow for better objectivity and provide a broader perspective when considering the combined results of all of the methods.

To explore the riparian zone alpha diversity patterns of different reach types, I focused on five streams that had reaches with multiple hydrogeomorphic classifications: Ramsey Canyon (RC), Garden Canyon (GC), Huachuca Canyon (HC) (including their associated ephemeral sites), the Hassayampa River (HR), and Ciénega Creek (CC). Each canyon stream had four reaches: Canyon Perennial, Canyon Intermittent, Canyon Ephemeral-Phreatic, and the nearby Ephemeral. Each basin stream had three reaches: Basin Perennial, Basin Intermittent, and Basin Ephemeral-Phreatic. For each individual sample I calculated four alpha diversity indices based on the plant abundance data collected from the temperature controlled seed bank experiment: Species Richness (SR), Chao's Estimate (Chao), Simpson's index, and Shannon's index. I then converted both Simpson's and Shannon's indices to effective number of species (InvSimp and ExpH) for easier comparison between diversity indices (Jost 2006; Morris et al 2014). I grouped the warm and cool riparian zone samples (16 samples total) for each reach within each stream to conduct the statistical analyses on seed bank alpha diversity. The data were non-normal and had unequal variances in most cases so I conducted Kruskal-Wallis and associated post-hoc nonparametric tests to compare each of the four alpha diversity indices among the multiple hydrogeomorphic reaches and determine whether they were statistically significantly different for each of the five streams (O'Hara and Kotze 2010). I calculated cumulative alpha diversity for the same four indices for each hydrogeomorphic reach within each stream by aggregating the abundance data for the riparian zone samples (both cool and warm) and treating it as one large sample. I also conducted Rényi entropy and evenness graphical profile analyses for each hydrogeomorphic reach within each stream.

Question 3

To further explore the effect of hydrogeomorphology on riparian zone alpha diversity, I examined alpha diversity independent of each individual stream and instead analyze it based on stream type—canyon versus basin streams. I believed that looking at the canyon and basin streams separately would elucidate the role of hydrogeomorphology within each stream type and clarify the overall effect on riparian zone seed bank alpha diversity. To determine if there were differences in the alpha diversity of the riparian zones for the different hydrogeomorphic reach types within both the canyon and basin study areas, again only the data for the same five streams that had multiple hydrogeomorphic classifications were included as specified in the method for question 2. I analyzed the diversity data within the riparian zones for both the canyon and basin stream types by grouping hydrogeomorphic reach types together for each stream type. For example: the riparian zone samples (cool and warm) for the intermittent reaches of Ramsey Canyon, Garden Canyon, and Huachuca Canyon were all grouped together to create the Canyon Intermittent data set, and the ephemeral-phreatic sites for Hassayampa River and Ciénega Creek were grouped together to create the Basin Ephemeral-Phreatic data set. I conducted three different analyses with the canyon stream data to account for the fact that the Huachuca Canyon Perennial (HCPER) site had not been included in the seed bank study: All Canyon Sites, Ramsey and Garden Canyon Sites (NoHC), and All Non-Perennial Canyon Sites (NoPer). Based on the plant abundance data collected from the temperature controlled seed bank experiment I calculated the same four overall alpha diversity indices (SR, Chao, InvSimp, and ExpH) for each of these three canyon analyses as well as the basin analyses for each hydrogeomorphic reach type.

To determine if there were statistically significant differences in diversity between the hydrogeomorphic reach types for both the canyon and basin stream types I used the samples grouped in three different manners as stated above. I conducted Kruskal-Wallis and associated post-hoc nonparametric tests to determine whether there were statistically significant differences between the hydrogeomorphic reach types for the basin and canyon stream types for each of the four alpha diversity indices (O'Hara and Kotze 2010). I calculated cumulative alpha diversity for the same four indices for each hydrogeomorphic reach type for canyon and basin stream types by aggregating the abundance data for the riparian zone samples (both cool and warm) in the same manner as above and treating it as one large sample. I graphically analyzed the Rényi entropy and evenness profiles for each hydrogeomorphic reach type for both the canyon and basin stream types.

Question 4

I examined both the spatial turnover and nestedness components of within stream beta-diversity because streams with similar values for overall beta-diversity can have very different composition patterns. Spatial turnover is due to replacement of some taxa by other taxa between sites, while nestedness is due the taxa of sites with fewer taxa being subsets of the assemblages at richer sites (Baselga 2010; Baselga 2012). Turnover is due to species replacement and nestedness is due to species loss/gain. Turnover and nestedness components have contrasting spatial patterns (Baselga 2012). I chose to calculate both Sørensen and Jaccard dissimilarity indices because the species are weighted differently. The common species are more heavily weighted for the Sørensen dissimilarity index whereas all species are evenly weighted for the Jaccard dissimilarity index. I also chose to calculate both multi-site and pair-wise dissimilarities for each index because I wanted to be able to see the differences among the reaches as well as have overall values for each stream. For the comparisons with more than two reaches it was important to calculate a multi-site index to get a single value because use of average pair-wise measures can be misleading (Baselga 2012).

I calculated beta-diversity for the same five streams addressed in Question 3 but excluded the nearby ephemeral washes from the three canyon streams. I used the betapart package (Baselga and Orme 2012) to calculate both Sørensen and Jaccard multi-site dissimilarity indices and pairwise comparisons—including the nestedness and turnover components for both indices—between sites within the same stream. For one analysis I included the Perennial, Intermittent, and Ephemeral-Phreatic reaches for Ramsey Canyon, Garden Canyon, Hassayampa River, and Ciénega Creek. I wanted to examine

beta-diversity for Huachuca Canyon as well and conducted a separate analysis where I included the Intermittent and Ephemeral-Phreatic reaches for Ramsey Canyon, Garden Canyon, Huachuca Canyon, Hassayampa River, and Ciénega Creek.

RESULTS

Question 2

Ramsey Canyon

The Kruskal-Wallis and associated post-hoc tests conducted on the four alpha diversity indices within the riparian zones of the Ramsey Canyon sites showed no significant difference between the alpha diversity of the Canyon Intermittent, Canyon Ephemeral-Phreatic, or Canyon Perennial hydrogeomorphic reaches—the only reach that was significantly different for all four diversity indices was the Ephemeral (Table 3).

The aggregate alpha diversity calculations (Fig. 8) for the four alpha diversity indices graphically indicate that the Canyon Intermittent, Canyon Ephemeral-Phreatic, and Canyon Perennial reaches were approximately the same, and that the Ephemeral reach was the highest. The Rényi entropy profile indicates that the Ephemeral reach was more diverse, while Canyon Intermittent was the second most diverse. The profiles for Canyon Perennial and Canyon Ephemeral-Phreatic crossed at approximately $q = 3$, therefore it cannot be said which of these two reaches was most diverse overall based solely on the graph, however the mean ranks for the Canyon Ephemeral-Phreatic reach was higher than the mean ranks for Canyon Perennial reach. The evenness profiles for the Ramsey Canyon stream hydrogeomorphic reaches indicate that the Canyon

Ephemeral-Phreatic was the most even, followed by Canyon Intermittent, Ephemeral, and finally Canyon Perennial (Fig. 9).

Table 3 Kruskal-Wallis nonparametric and post-hoc test results for comparisons between hydrogeomorphic reaches for four alpha diversity indices for Ramsey Canyon

Ramsey Canyon			HydGeo Class	Canyon Perennial	Canyon Intermittent	Canyon Ephemeral-Phreatic	Ephemeral
			Site	*RCPER*	*RCUW*	*RCLD*	*RFD*
Species Richness	X^2	*22.968*	**Mean Rank**	23.6	28.3	27	51.1
	p	*0.000041*	**avg**	1.06	1.31	1.19	4.13
	Df	*3*	**std**	1.53	1.25	1.17	2.00
	ntr	*4*	**Min**	0	0	0	1
	t	*2.000297822*	**Max**	5	4	4	7
	α	*0.05*	**r**	16	16	16	16
			[1]Groups	b	b	b	a
Chao	X^2	*19.932*	**Mean Rank**	23.8	28.8	27.6	49.8
	p	*0.000175312*	**avg**	1.38	1.84	1.69	5.14
	Df	*3*	**std**	2.19	2.53	2.50	2.74
	ntr	*4*	**Min**	0	0	0	1
	t	*2.000297822*	**Max**	8	10	10	10.3
	α	*0.05*	**r**	16	16	16	16
			[1]Groups	b	b	b	a
InvSimp	X^2	*19.797*	**Mean Rank**	24.1	28.7	27.5	49.8
	p	*0.000187012*	**avg**	0.92	1.18	1.10	3.10
	Df	*3*	**std**	1.20	1.13	1.08	1.58
	ntr	*4*	**Min**	0	0	0	1
	t	*2.000297822*	**Max**	3.86	4	4	6.23
	α	*0.05*	**r**	16	16	16	16
			[1]Groups	b	b	b	a
ExpH	X^2	*21.4*	**Mean Rank**	25.9	28.3	26.4	49.5
	p	*0.0000883*	**avg**	1.48	1.54	1.45	3.46
	Df	*3*	**std**	0.99	0.88	0.84	1.73
	ntr	*4*	**Min**	1	1	1	1
	t	*2.000297822*	**Max**	4.33	4	4	6.61
	α	*0.05*	**r**	16	16	16	16
			[1]Groups	b	b	b	a

[1] Conover post-hoc procedure conducted using the Benjamini-Hochberg p-adjust method.

Garden Canyon

The Kruskal-Wallis and associated post-hoc tests conducted on the Garden Canyon hydrogeomorphic reaches was somewhat complex (Table 4). For SR the Ephemeral was significantly different from the Canyon Perennial and the Canyon Intermittent reaches, but not significantly different from Canyon Ephemeral-Phreatic reach. Canyon Ephemeral-Phreatic was only significantly different from Canyon Intermittent. The Canyon Perennial reach was the only reach that was significantly different from the Ephemeral reach. For Chao, InvSimp, and ExpH there were only two distinct subsets of hydrogeomorphic reaches that were significantly different from each other. The Ephemeral and Canyon Intermittent reaches were significantly different from each other. The Canyon Perennial and Canyon Ephemeral-Phreatic reaches were not significantly different from either the Ephemeral or Canyon Intermittent reaches.

This same trend was also apparent in the aggregate alpha diversity calculations where the Canyon Intermittent reach was the lowest for all alpha diversity indices compared to the other hydrogeomorphorphic reaches for Garden Canyon (Fig. 8). The Canyon Ephemeral-Phreatic and Canyon Perennial reaches were close in diversity and were both more diverse than the Canyon Intermittent reach. The Ephemeral reach was the most diverse based on mean ranks and graphical analyses—including Rényi entropy (Fig. 9). Mean ranks and the aggregate diversity calculations also indicate that the Ephemeral and Canyon Ephemeral-Phreatic reaches were more similar to each other than the Canyon Ephemeral-Phreatic and Canyon Perennial reaches were to each other. The Rényi entropy profiles also confirm the trend shown by the mean ranks: that the Canyon Intermittent reach was the least diverse of the Garden Canyon hydrogeomorphic reaches,

and the Canyon Perennial reach was close in diversity to the Canyon Intermittent reach. All of the hydrogeomorphic reaches were similar in evenness until around q = 2, where the Canyon Intermittent reach was most even, then Canyon Perennial, then Canyon Ephemeral-Phreatic, and the Ephemeral reach was the least even.

Table 4 Kruskal-Wallis nonparametric and post-hoc test results for comparisons between hydrogeomorphic reaches for four alpha diversity indices for Garden Canyon

Garden Canyon			HydGeo Class	Canyon Perennial	Canyon Intermittent	Canyon Ephemeral-Phreatic	Ephemeral
			Site	*GCPER*	*GCUW*	*GCLD*	*GFD*
Species Richness	X^2	*12.734*	**Mean Rank**	28.2	21.8	37.4	42.6
	p	*0.005248625*	**avg**	1.19	0.75	2.19	2.88
	Df	*3*	**std**	1.17	1.13	1.91	2.33
	ntr	*4*	**Min**	0	0	0	0
	t	*2.000*	**Max**	4	4	6	8
	α	*0.05*	**r**	16	16	16	16
			[1]Groups	bc	c	ab	a
Chao	X^2	*10.021*	**Mean Rank**	29.5	22.5	36.4	41.6
	p	*0.018388383*	**avg**	1.53	0.91	3.56	3.45
	Df	*3*	**std**	1.63	1.39	5.40	3.26
	ntr	*4*	**Min**	0	0	0	0
	t	*2.000*	**Max**	5.5	4.5	21	12
	α	*0.05*	**r**	16	16	16	16
			[1]Groups	ab	b	ab	a
InvSimp	X^2	*10.690*	**Mean Rank**	29.1	22.3	36.8	41.8
	p	*0.013527282*	**avg**	1.13	0.70	1.83	2.28
	Df	*3*	**std**	1.08	0.99	1.65	1.70
	ntr	*4*	**Min**	0	0	0	0
	t	*2.000*	**Max**	3.57	3.27	6	5.88
	α	*0.05*	**r**	16	16	16	16
			[1]Groups	ab	b	ab	a
ExpH	X^2	*10.367*	**Mean Rank**	29.4	23	36.1	41.5
	p	*0.01569*	**avg**	1.53	1.29	2.22	2.64
	Df	*3*	**std**	0.76	0.70	1.49	1.82
	ntr	*4*	**Min**	1	1	1	1
	t	*2.000*	**Max**	3.79	3.59	6	6.78
	α	*0.05*	**r**	16	16	16	16
			[1]Groups	ab	b	ab	a

[1] Conover post-hoc procedure conducted using the Benjamini-Hochberg p-adjust method.

Huachuca Canyon

The Kruskal-Wallis and associated post-hoc tests conducted on the four alpha diversity indices for Huachuca Canyon reaches showed no significant difference in alpha diversity between any of them (Table 5). For all four diversity indices the mean ranks were similar for all three hydrogeomorphic reaches (Canyon Intermittent, Canyon Ephemeral-Phreatic, and Ephemeral). The Canyon Ephemeral-Phreatic reach was the highest in alpha diversity for all indices except SR, for which the Ephemeral was the highest, followed by the Canyon Ephemeral-Phreatic.

The aggregate alpha diversity calculations (Fig. 8) for all four alpha diversity indices graphically displays the same trend observed in the Kruskal-Wallis mean ranks. The Rényi entropy profiles for the Huachuca Canyon reaches shows that all hydrogeomorphic reaches were similar in alpha diversity (Fig. 9). (When entropy profiles cross it is not possible to say which is overall the most diverse, it is only possible to determine which profile is more diverse at each specific value of q.) There were little differences between evenness profiles for the Canyon Intermittent and Canyon Ephemeral-Phreatic reaches, however the Ephemeral reach was the least even.

Table 5 Kruskal-Wallis nonparametric and post-hoc test results for comparisons between hydrogeomorphic reaches for four alpha diversity indices for Huachuca Canyon

Huachuca Canyon			HydGeo Class	Canyon Intermittent	Canyon Ephemeral-Phreatic	Ephemeral
			Site	*HCUW*	*HCLD*	*HFD*
Species Richness	X^2	*1.556*	**Mean Rank**	21.1	26.2	26.2
	p	*0.459437105*	**avg**	1.38	1.69	1.69
	Df	*2*	**std**	1.26	1.20	1.01
	ntr	*3*	**Min**	0	0	0
	t	*2.014*	**Max**	5	4	4
	α	*0.05*	**r**	16	16	16
			[1]Groups	a	a	a
Chao	X^2	*1.741*	**Mean Rank**	20.9	26.4	26.2
	p	*0.418812438*	**avg**	1.81	2.44	2
	Df	*2*	**std**	2.61	2.58	1.51
	ntr	*3*	**Min**	0	0	0
	t	*2.014*	**Max**	11	10	6
	α	*0.05*	**r**	16	16	16
			[1]Groups	a	a	a
InvSimp	X^2	*1.559*	**Mean Rank**	21.1	26.4	26
	p	*0.458538989*	**avg**	1.20	1.56	1.50
	Df	*2*	**std**	0.88	1.12	0.80
	ntr	*3*	**Min**	0	0	0
	t	*2.014*	**Max**	3.2	4	3.13
	α	*0.05*	**r**	16	16	16
			[1]Groups	a	a	a
ExpH	X^2	*1.937*	**Mean Rank**	21	27.13	25.38
	p	*0.379666937*	**avg**	1.46	1.80	1.63
	Df	*2*	**std**	0.85	0.91	0.77
	ntr	*3*	**Min**	1	1	1
	t	*2.014*	**Max**	4	4	3.44
	α	*0.05*	**r**	16	16	16
			[1]Groups	a	a	a

[1] Conover post-hoc procedure conducted using the Benjamini-Hochberg p-adjust method.

Hassayampa River

The Kruskal-Wallis and associated post-hoc tests conducted on the alpha diversity indices for the Hassayampa River show significant differences in the mean ranks for different subsets of diversity indices: SR/Chao vs InvSimp/ExpH (Table 6). There was a significant difference between the mean ranks for the Basin Intermittent reach and the Basin Perennial reach for SR and Chao. The mean ranks for InvSimp and ExpH for the Basin Intermittent and the Basin Ephemeral-Phreatic reaches were significantly different from each other, however the Basin Perennial reach was not significantly different from either of those. The overall trend exhibited by the mean ranks for all four of the alpha diversity indices indicate that the Basin Intermittent was the most diverse reach, then Basin Perennial, with the Basin Ephemeral-Phreatic reach the least diverse.

The aggregate alpha diversity calculations (Fig. 8) also indicate that alpha diversity was highest at the Basin Intermittent reach, lowest at the Basin Ephemeral-Phreatic reach, with the Basin Perennial reach between them. The Rényi entropy profiles (Fig. 9) for the Hassayampa River also shows the Basin Intermittent reach was consistently highest in alpha diversity, although the Basin Perennial was similar in value where $q = 1$ and $q = 2$. The evenness profile was similar across all hydrogeomorphic reaches; the Basin Perennial and Basin Intermittent reaches were similar to each other, and more even than the Basin Ephemeral-Phreatic reach. Overall the Basin Ephemeral-Phreatic reach was the lowest in alpha diversity based on Kruskal-Wallis mean ranks and both graphical analyses.

Table 6 Kruskal-Wallis nonparametric and post-hoc test results for comparisons between hydrogeomorphic reaches for four alpha diversity indices for the Hassayampa River

Hassayampa River			HydGeo Class	Basin Perennial	Basin Intermittent	Basin Ephemeral-Phreatic
			Site	*HRPER*	*HRINT*	*HREPH*
Species Richness	X^2	*12.413*	**Mean Rank**	22.3	33.8	17.3
	p	*0.002016357*	**avg**	1.38	3	1
	Df	*2*	**std**	0.96	2.07	1.03
	ntr	*3*	**Min**	0	1	0
	t	*2.014*	**Max**	3	8	3
	α	*0.05*	**r**	16	16	16
			[1]Groups	b	a	b
Chao	X^2	*9.158*	**Mean Rank**	22.7	32.6	18.3
	p	*0.010262737*	**avg**	1.63	3.5	1.438
	Df	*2*	**std**	1.5	3.03	1.965
	ntr	*3*	**Min**	0	1	0
	t	*2.014*	**Max**	6	11	6
	α	*0.05*	**r**	16	16	16
			[1]Groups	b	a	b
InvSimp	X^2	*8.001*	**Mean Rank**	22.9	32.1	18.6
	p	*0.018302706*	**avg**	1.20	1.88	1.00
	Df	*2*	**std**	0.87	0.83	1.03
	ntr	*3*	**Min**	0	1	0
	t	*2.014*	**Max**	3	3.74	3
	α	*0.05*	**r**	16	16	16
			[1]Groups	ab	a	b
ExpH	X^2	*6.750*	**Mean Rank**	23.5	31	19
	p	*0.034225954*	**avg**	1.50	2.13	1.37
	Df	*2*	**std**	0.57	1.02	0.72
	ntr	*3*	**Min**	1	1	1
	t	*2.014*	**Max**	3	4.26	3
	α	*0.05*	**r**	16	16	16
			[1]Groups	ab	a	b

[1] Conover post-hoc procedure conducted using the Benjamini-Hochberg p-adjust method.

Ciénega Creek

Kruskal-Wallis and associated post-hoc tests conducted on the alpha diversity indices for Ciénega Creek revealed no significant differences between mean ranks for the different hydrogeomorphic reaches (Table 7). The mean ranks for all four alpha diversity indices for the Basin Perennial reach were highest, then Basin Intermittent, with Basin Ephemeral-Phreatic the least diverse reach.

The aggregate alpha diversity calculations also support that same general trend (Fig. 8). Chao was the only index that did not follow that trend—the Basin Perennial was lower than the Basin Intermittent for that index. The Rényi entropy profiles for the Ciénega Creek reaches also exhibited the same overall trend found in the Kruskal-Wallis mean ranks consistently for all orders of q (Fig. 9). The Rényi evenness shows that the Basin Intermittent and that Basin Perennial reaches had approximately the same evenness. Both the Basin Intermittent and the Basin Perennial reaches were more even than the Basin Ephemeral-Phreatic reach.

Table 7 Kruskal-Wallis nonparametric and post-hoc test results for comparisons between hydrogeomorphic reaches for four alpha diversity indices for Ciénega Creek

Ciénega Creek			HydGeo Class	Basin Perennial	Basin Intermittent	Basin Ephemeral-Phreatic
			Site	*CCPER*	*CCINT*	*CCEPH*
Species Richness	X^2	*2.443*	**Mean Rank**	28.5	23.8	21.3
	p	*0.294784626*	**avg**	1.63	1	0.81
	Df	*2*	**std**	1.67	1.03	0.98
	ntr	*3*	**Min**	0	0	0
	t	*2.014*	**Max**	6	3	3
	α	*0.05*	**r**	16	16	16
			[1]Groups	a	a	a
Chao	X^2	*2.355*	**Mean Rank**	28.5	23.7	21.4
	p	*0.308034678*	**avg**	2.27	1.22	0.94
	Df	*2*	**std**	2.86	1.60	1.18
	ntr	*3*	**Min**	0	0	0
	t	*2.014*	**Max**	10	6	3
	α	*0.05*	**r**	16	16	16
			[1]Groups	a	a	a
InvSimp	X^2	*2.145*	**Mean Rank**	28.3	23.8	21.4
	p	*0.342092632*	**avg**	1.33	0.94	0.75
	Df	*2*	**std**	1.17	0.96	0.86
	ntr	*3*	**Min**	0	0	0
	t	*2.014*	**Max**	4	3	2.33
	α	*0.05*	**r**	16	16	16
			[1]Groups	a	a	a
ExpH	X^2	*1.192*	**Mean Rank**	27	23.4	23.1
	p	*0.551113953*	**avg**	1.69	1.34	1.27
	Df	*2*	**std**	1.08	0.67	0.51
	ntr	*3*	**Min**	1	1	1
	t	*2.014*	**Max**	4	3	2.60
	α	*0.05*	**r**	16	16	16
			[1]Groups	a	a	a

[1] Conover post-hoc procedure conducted using the Benjamini-Hochberg p-adjust method.

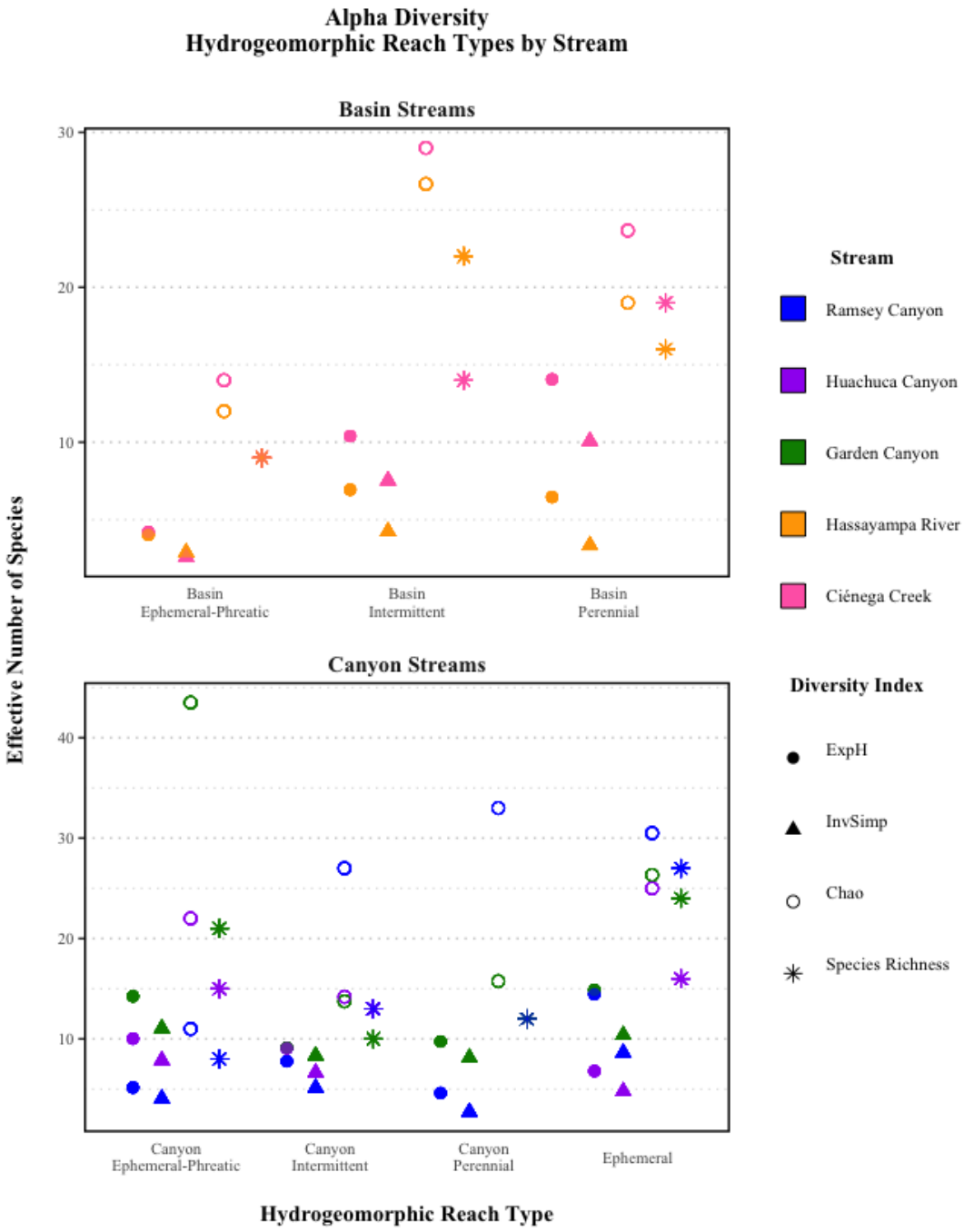


Fig. 8 Alpha diversity for four indices presented in effective number of species for hydrogeomorphic reach types for each stream/drainage with multiple hydrogeomorphic reach types

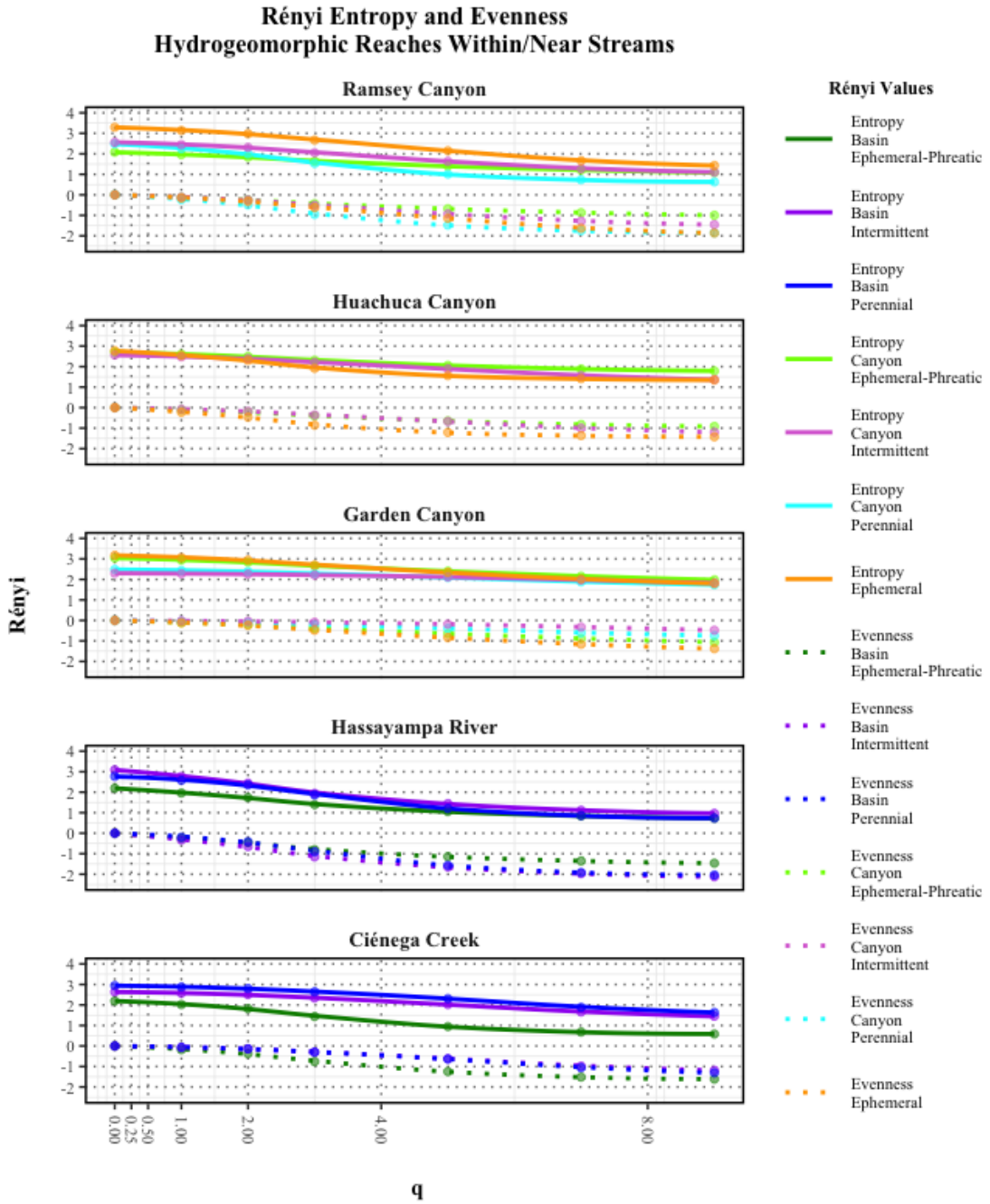


Fig. 9 Rényi entropy and evenness profiles for reach types for streams with multiple hydrogeomorphic reach types

Question 3

All Canyon Sites

Results of the Kruskal-Wallis and associated post-hoc nonparametric tests that included the riparian zones of all sites from all three canyon streams showed a significant difference in alpha diversity between the mean ranks for the Ephemeral reach type as compared to the Canyon Ephemeral-Phreatic, Canyon Intermittent, and Canyon Perennial reach types (Table 8). For all four alpha diversity indices the mean ranks of the Ephemeral reach type were the highest out of the four hydrogeomorphic classes. There were no significant differences between the mean ranks for the Canyon Ephemeral-Phreatic, Canyon Intermittent, or Canyon Perennial reach types for the four alpha diversity indices. The Canyon Intermittent reach type had the lowest mean ranks for both InvSimp and ExpH. The Canyon Perennial reach type had the lowest mean ranks for SR and Chao.

Based on the aggregate alpha diversity index calculations (Fig. 10) the Ephemeral reach type was the highest and the Canyon Ephemeral-Phreatic was second highest in diversity for all four alpha diversity indices. The Canyon Perennial reach type was the lowest in diversity for ExpH and InvSimp, and second lowest for SR and Chao. The Canyon Intermittent reach type was lowest in diversity for SR and Chao, and second lowest for ExpH and InvSimp. The Rényi entropy profile for the Ephemeral reach type was the highest, Canyon Ephemeral-Phreatic was second highest, and Canyon Intermittent was the lowest overall (Fig. 11). The Canyon Ephemeral-Phreatic and

Canyon Perennial reach types had the same evenness profile and were both more even than the Ephemeral reach type. The Canyon Intermittent reach type was the least even.

The results of the statistical analyses were consistent with the Rényi entropy profiles: for SR ($q = 0$) the profiles were close together but as q increased the Canyon Intermittent profile continued to decrease; it had the lowest mean of the ranks for ExpH and InvSimp. This result differed slightly from the aggregate alpha diversity calculations because it showed the opposite trend for SR /Chao and ExpH/InvSimp. InvSimp was lowest for Canyon Perennial instead of Canyon Intermittent for the aggregate alpha diversity calculations, however looking at the means of ranks, the difference between the Canyon Perennial and Canyon Intermittent reach types was small.

Table 8 Kruskal-Wallis nonparametric and post-hoc test results for comparisons between hydrogeomorphic reaches combined by reach type for four alpha diversity indices for all three canyon streams

Canyon			HydGeo Class	Canyon Perennial	Canyon Intermittent	Canyon Ephemeral-Phreatic	Ephemeral
Species Richness	X^2	*28.361*	**Mean Rank**	69.0	70.9	89.1	118.4
	p	*0.00000305*	**values**	1.13	1.15	1.69	2.90
	Df	*3*	**std**	1.34	1.22	1.49	2.09
	ntr	*4*	**Min**	0	0	0	0
	t	*1.974*	**Max**	5	5	6	8
	α	*0.05*	**r**	32	48	48	48
			[1]Groups	b	b	b	a
Chao	X^2	*24.354*	**Mean Rank**	71.0	71.8	89.1	116.3
	p	*0.0000211*	**values**	1.45	1.52	2.56	3.53
	Df	*3*	**std**	1.90	2.24	3.75	2.86
	ntr	*4*	**Min**	0	0	0	0
	t	*1.974*	**Max**	8	11	21	12
	α	*0.05*	**r**	32	48	48	48
			[1]Groups	b	b	b	a
InvSimp	X^2	*23.829*	**Mean Rank**	71.5	71.4	89.5	115.9
	p	*0.0000271*	**values**	1.02	1.03	1.50	2.29
	Df	*3*	**std**	1.13	1.01	1.32	1.54
	ntr	*4*	**Min**	0	0	0	0
	t	*1.974*	**Max**	3.86	4	6	6.23
	α	*0.05*	**r**	32	48	48	48
			[1]Groups	b	b	b	a
ExpH	X^2	*22.141*	**Mean Rank**	76.2	71.5	88.7	113.5
	p	*0.000061*	**values**	1.50	1.43	1.82	2.58
	Df	*3*	**std**	0.87	0.81	1.14	1.67
	ntr	*4*	**Min**	1	1	1	1
	t	*1.974*	**Max**	4.33	4	6	6.78
	α	*0.05*	**r**	32	48	48	48
			[1]Groups	b	b	b	a

[1] Conover post-hoc procedure conducted using the Benjamini-Hochberg p-adjust method.

Ramsey and Garden Canyons Only (Huachuca Canyon Excluded)

In the comparisons made between the riparian zone seed banks of the canyon streams without the Huachuca Canyon sites there were no significant differences found between the mean ranks for the Canyon Ephemeral-Phreatic, Canyon Ephemeral-Phreatic, and Canyon Perennial reach types according to the Kruskal-Wallis and associated post hoc tests results (Table 9). Again, the Ephemeral reach type differed significantly from the other hydrogeomorphic reach types. The Ephemeral reach type had the highest mean ranks for all four alpha diversity indices, Canyon Ephemeral-Phreatic the second highest, Canyon Perennial the second lowest, and Canyon Intermittent the lowest.

The aggregate alpha diversity calculations (Fig. 10) indicate that the Ephemeral reach type was the highest in alpha diversity for all four diversity indices. The Canyon Perennial reach type was the lowest for ExpH and InvSimp, and second lowest for SR and Chao. The Canyon Intermittent reach type was second lowest for all four indices. The Canyon Ephemeral-Phreatic reach type was second highest for three of the four diversity indices, but it was lowest for Chao. The Ephemeral reach type had the highest Rényi entropy profile overall (Fig. 11). The profile for the Canyon Ephemeral-Phreatic reach type was the second most diverse at $q = 0$, as q increased past 4 the Canyon Ephemeral-Phreatic profile increased until it was overlapped by the Ephemeral reach type profile. The Rényi entropy profile for the Canyon Perennial reach type was similar in profile to that of the Canyon Ephemeral-Phreatic until just past $q = 2$, where it fell further below the Canyon Ephemeral-Phreatic reach type profile. The Canyon Intermittent had the lowest Rényi entropy profile out of all of the hydrogeomorphic reach types for this

analysis. The Canyon Ephemeral-Phreatic and Canyon Perennial reach types had similar evenness profiles; Canyon Ephemeral-Phreatic was slightly more even. The Ephemeral reach type was the second least even, and the Canyon Intermittent reach type was the least even.

The overall trends for alpha diversity were consistent between the statistical analyses, the aggregate alpha diversity calculations, and the Rényi entropy profiles.

Table 9 Kruskal-Wallis nonparametric and post-hoc test results for comparisons between hydrogeomorphic reaches combined by reach types for four alpha diversity indices for Ramsey and Garden Canyon streams (Huachuca Canyon excluded)

CanyonNoHC			HydGeo Class	Canyon Perennial	Canyon Intermittent	Canyon Ephemeral-Phreatic	Ephemeral
Species Richness	X^2	*30.019*	**Mean Rank**	51.4	49.6	63.6	93.4
	p	*0.00000137*	**values**	1.13	1.03	1.69	3.50
	Df	*3*	**std**	1.34	1.20	1.64	2.23
	ntr	*4*	**Min**	0	0	0	0
	t	*1.979*	**Max**	5	4	6	8
	α	*0.05*	**r**	32	32	32	32
			[1]Groups	b	b	b	a
Chao	X^2	*25.566*	**Mean Rank**	52.7	50.7	63.3	91.3
	p	*0.0000118*	**values**	1.45	1.38	2.63	4.29
	Df	*3*	**std**	1.90	2.06	4.25	3.08
	ntr	*4*	**Min**	0	0	0	0
	t	*1.979*	**Max**	8	10	21	12
	α	*0.05*	**r**	32	32	32	32
			[1]Groups	b	b	b	a
InvSimp	X^2	*25.288*	**Mean Rank**	53.0	50.2	63.7	91.1
	p	*0.0000134*	**values**	1.02	0.94	1.47	2.69
	Df	*3*	**std**	1.13	1.07	1.42	1.67
	ntr	*4*	**Min**	0	0	0	0
	t	*1.979*	**Max**	3.86	4	6	6.23
	α	*0.05*	**r**	32	32	32	32
			[1]Groups	b	b	b	a
ExpH	X^2	*26.605*	**Mean Rank**	54.5	50.9	62.0	90.6
	p	*0.00000712*	**values**	1.50	1.41	1.84	3.05
	Df	*3*	**std**	0.87	0.79	1.25	1.80
	ntr	*4*	**Min**	1	1	1	1
	t	*1.979*	**Max**	4.33	4	6	6.78
	α	*0.05*	**r**	32	32	32	32
			[1]Groups	b	b	b	a

[1] Conover post-hoc procedure conducted using the Benjamini-Hochberg p-adjust method.

Non-Perennial Canyon Sites

The comparisons made between the riparian seed banks of the reach types for the canyon streams without the perennial sites indicated that there were no significant differences between the mean ranks for the Canyon Ephemeral-Phreatic and Canyon Intermittent reach types (Table 10). The mean ranks for the Ephemeral reach type was significantly different from both the Canyon Ephemeral-Phreatic and Canyon Intermittent reach types for all four alpha diversity indices. The results of the Kruskal-Wallis and associated post-hoc tests for all four alpha diversity indices followed the same trend: the mean ranks for the Ephemeral reach type was highest, followed by Canyon Ephemeral-Phreatic, and the Canyon Intermittent the lowest.

The aggregate alpha diversity calculations showed that the Ephemeral reach type was again the highest for all four alpha diversity indices (Fig. 10). For all four alpha diversity indices the mean ranks for the Canyon Ephemeral-Phreatic reach type were between those of the Ephemeral and the Canyon Intermittent reach types.

The Ephemeral reach type had the highest Rényi entropy profile overall for this analysis (Fig. 11). The Canyon Ephemeral-Phreatic and the Canyon Intermittent reach types were similar in profile, however the Canyon Intermittent was least diverse. The Canyon Ephemeral-Phreatic and Canyon Intermittent reach types had approximately the same evenness. The Ephemeral reach type was the least even of all of the hydrogeomorphic classes.

The results of the statistical analyses, aggregate alpha diversity calculations, and Rényi entropy profiles were all consistent with each other: the Ephemeral reach type was the most diverse, the Canyon Ephemeral-Phreatic was in the middle, and the Canyon Intermittent was the least diverse.

Table 10 Kruskal-Wallis nonparametric and post-hoc test results for comparisons between hydrogeomorphic reaches combined by reach type for four alpha diversity indices for all three canyon streams without perennial reaches

CanyonNoPer			HydGeo Class	Canyon Intermittent	Canyon Ephemeral-Phreatic	Ephemeral
Species Richness	X^2	*22.826*	**Mean Rank**	54.4	69.4	93.8
	p	*0.000011*	**values**	1.15	1.69	2.90
	Df	*2*	**std**	1.22	1.49	2.09
	ntr	*3*	**r**	48	48	48
	t	*1.977*	**Min**	0	0	0
	α	*0.05*	**Max**	5	6	8
		chao	**[1]Groups**	b	b	a
Chao	X^2	*19.912*	**Mean Rank**	55.4	69.8	92.3
	p	*0.0000474*	**values**	1.52	2.56	3.53
	Df	*2*	**std**	2.24	3.75	2.86
	ntr	*3*	**r**	48	48	48
	t	*1.977*	**Min**	0	0	0
	α	*0.05*	**Max**	11	21	12
		invsimp	**[1]Groups**	b	b	a
InvSimp	X^2	*19.897*	**Mean Rank**	55.2	70.1	92.3
	p	*0.0000478*	**values**	1.03	1.50	2.29
	Df	*2*	**std**	1.01	1.32	1.54
	ntr	*3*	**r**	48	48	48
	t	*1.977*	**Min**	0	0	0
	α	*0.05*	**Max**	4	6	6.23
		expH	**[1]Groups**	b	b	a
ExpH	X^2	*18.953*	**Mean Rank**	56.4	70.3	90.8
	p	*0.0000766*	**values**	1.43	1.82	2.58
	Df	*2*	**std**	0.81	1.14	1.67
	ntr	*3*	**r**	48	48	48
	t	*1.977*	**Min**	1	1	1
	α	*0.05*	**Max**	4	6	6.78
			[1]Groups	b	b	a

[1] Conover post-hoc procedure conducted using the Benjamini-Hochberg p-adjust method.

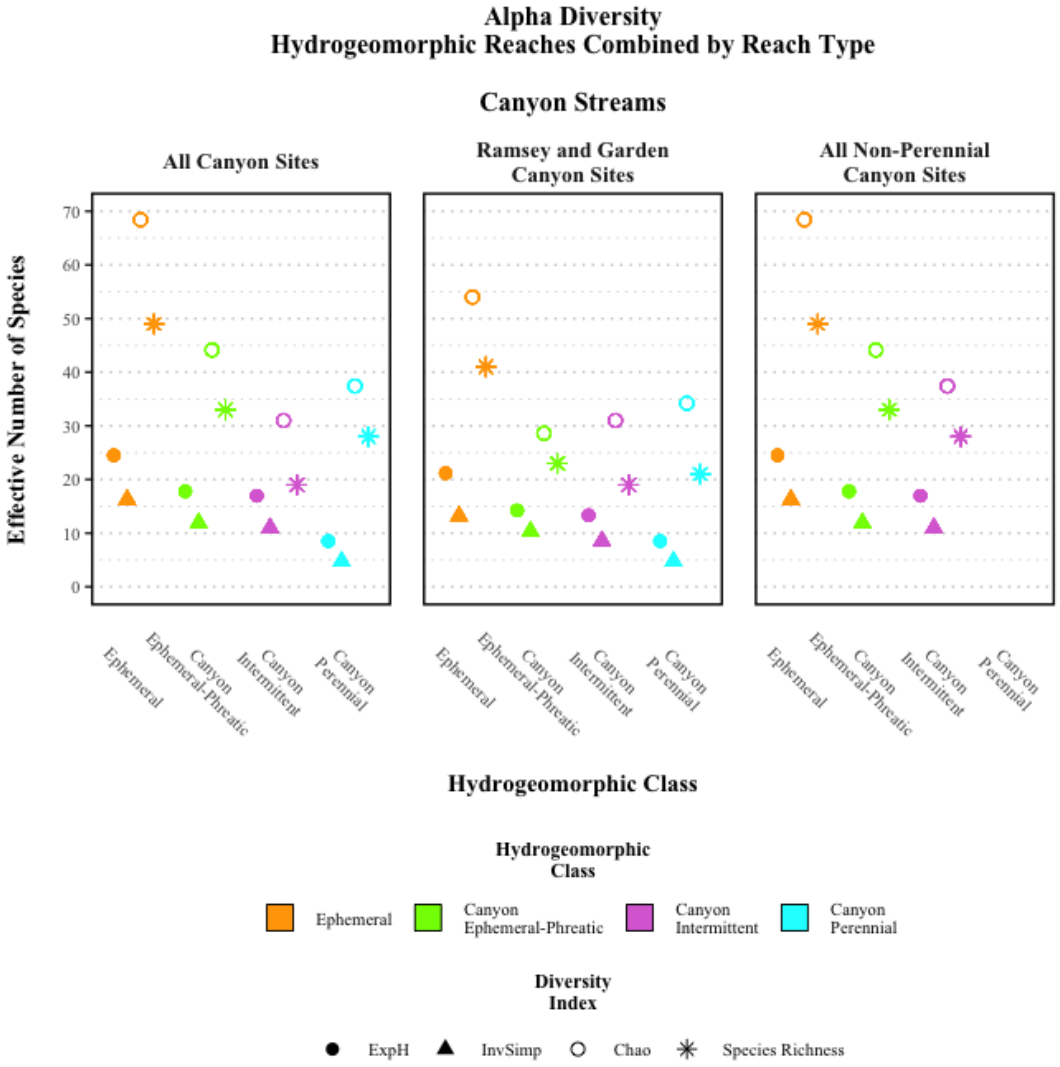


Fig. 10 Alpha diversity for four indices presented in effective number of species for canyon streams with hydrogeomorphic reaches combined by reach types

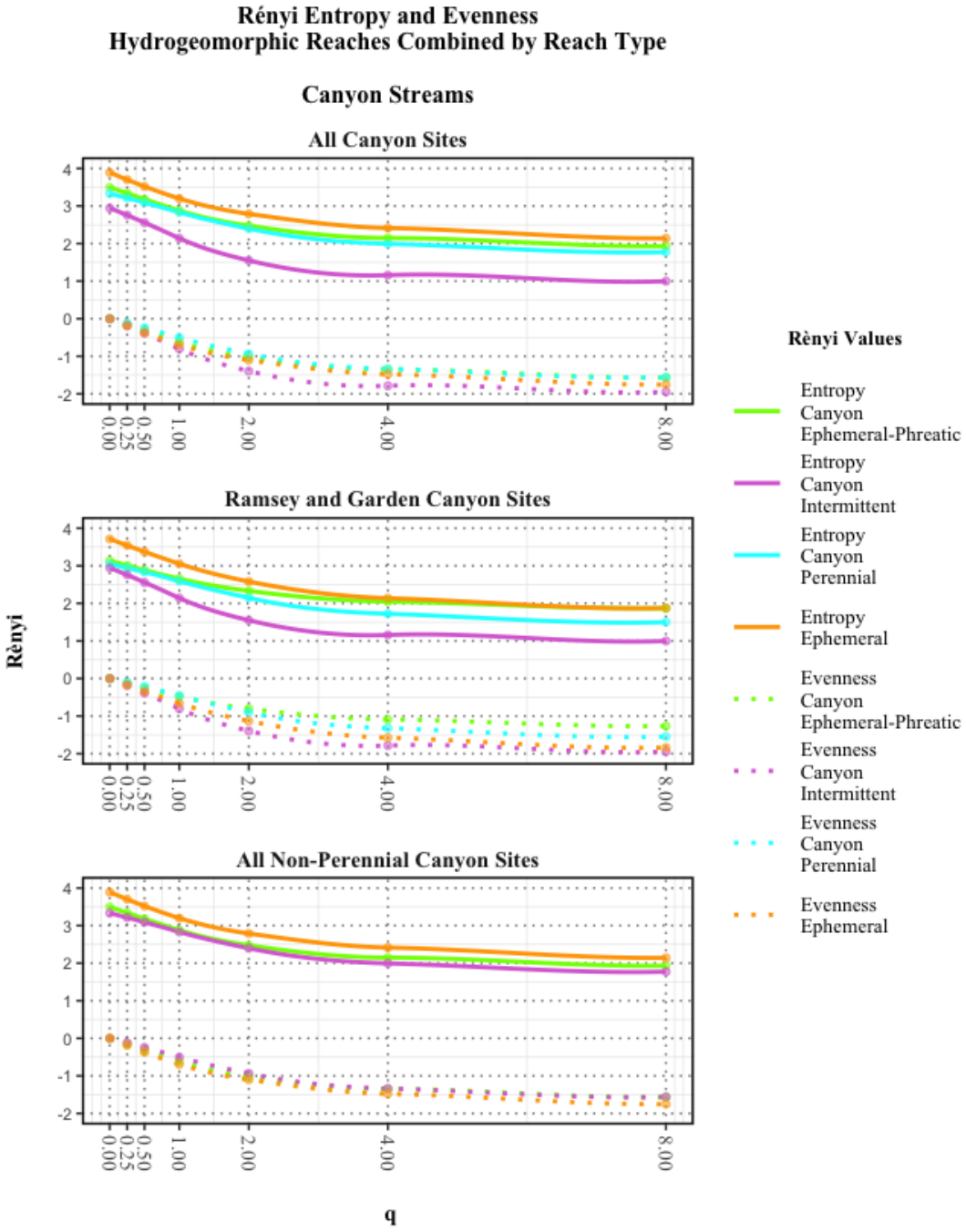


Fig. 11 Rényi entropy and evenness profiles for reaches combined by reach type for all canyon streams. Profiles were calculated based on the three different grouping described above

Basin Sites

The Kruskal-Wallis and associated post-hoc tests conducted on the four alpha diversity indices for the riparian zone seed banks of the two basin streams only showed a significant difference between the hydrogeomorphic reach types for the SR analysis (Table 11). The mean ranks for SR were significantly different between the Basin Intermittent—which was highest—and Basin Ephemeral-Phreatic, however the Basin Perennial was not significantly different from either of those reach types. The Basin Intermittent reach type had the highest mean ranks for the other three diversity indices as well, even though no significant differences were detected between reach types for those indices.

The aggregate alpha diversity calculations (Fig. 12) for the Basin streams show that for SR, Basin Intermittent and Basin Perennial were the same (tied at 31 species), and Basin Ephemeral-Phreatic was the least diverse. For Chao, the Basin Intermittent reach type was the most diverse, followed next by Basin Perennial, and Basin Ephemeral-Phreatic was the least diverse. Overall, alpha diversity values for ExpH and InvSimp were highest for the Basin Perennial reach type. The Basin Ephemeral-Phreatic reach type was lowest for ExpH, and Basin Intermittent was lowest for InvSimp.

Due to the fact that the Rényi entropy profiles for the basin hydrogeomorphic reach types cross each other it is not possible to determine which reach type is summarily more diverse based solely on the entropy profiles—it is only possible to determine which was more diverse at a specific value of q (Fig. 13). The Rényi entropy profiles for the Basin Perennial and Basin Intermittent reach types started out approximately the same.

The Basin Perennial reach type was highest until approximately q = 2, where it dropped below the profiles for both the Basin Intermittent and Basin Ephemeral-Phreatic reach types. The entropy profile for the Basin Intermittent reach type was in the middle until approximately q = 2, where the profile for the Basin Perennial reach type dropped below it. The profile for the Basin Ephemeral-Phreatic was the lowest until q = 2, where it then increased to the highest. Initially the evenness profile for the Basin Perennial reach type started out above that of the Basin Intermittent profile, however at approximately q = 2, their evenness profiles crossed, and the Basin Intermittent became more even than Basin Perennial reach type. The profiles remained fairly close in evenness as the value of q increased, with the profile of the Basin Intermittent remaining slightly higher than that of Basin Perennial reach type.

The statistical and analyses indicate that for basin streams the Basin Intermittent reach type was the most diverse, but not by a very large margin. Both graphical analyses indicate that the Basin Intermittent and Basin Perennial reach types had similar levels of diversity. They were equal with regards to SR, but the Basin Perennial reach type was more diverse for ExpH and InvSimp indices, while the Basin Intermittent reach type was most diverse for Chao. Based on all of the data it appears that the Basin Intermittent reach type might have been only slightly more diverse than the Basin Perennial reach type. The Basin Ephemeral-Phreatic reach type was the least diverse.

Table 11 Kruskal-Wallis nonparametric and post-hoc test results for comparisons between hydrogeomorphic reach types for four alpha diversity indices for basin streams

Basin			HydGeo Class	Basin Perennial	Basin Intermittent	Basin Ephemeral-Phreatic
Species Richness	X^2	*7.680*	**Mean Rank**	50.6	56.6	38.3
	p	*0.021493118*	**values**	1.50	2.00	0.91
	Df	*2*	**std**	1.34	1.90	1.00
	ntr	*3*	**Min**	0	0	0
	t	*1.986*	**Max**	6	8	3
	α	*0.05*	**r**	32	32	32
			[1]Groups	ab	a	b
Chao	X^2	*5.946*	**Mean Rank**	50.8	55.3	39.3
	p	*0.051154783*	**values**	1.95	2.36	1.19
	Df	*2*	**std**	2.27	2.65	1.62
	ntr	*3*	**Min**	0	0	0
	t	*1.986*	**Max**	10	11	6
	α	*0.05*	**r**	32	32	32
			[1]Groups	a	a	a
InvSimp	X^2	*5.424*	**Mean Rank**	50.8	55.0	39.7
	p	*0.066393844*	**values**	1.26	1.41	0.87
	Df	*2*	**std**	1.02	1.00	0.94
	ntr	*3*	**Min**	0	0	0
	t	*1.986*	**Max**	4	3.74	3
	α	*0.05*	**r**	32	32	32
			[1]Groups	a	a	a
ExpH	X^2	*4.067*	**Mean Rank**	50.6	53.4	41.5
	p	*0.130906325*	**values**	1.59	1.74	1.32
	Df	*2*	**std**	0.86	0.94	0.62
	ntr	*3*	**Min**	1	1	1
	t	*1.986*	**Max**	4	4.26	3
	α	*0.05*	**r**	32	32	32
			[1]Groups	a	a	a

[1] Conover post-hoc procedure conducted using the Benjamini-Hochberg p-adjust method.

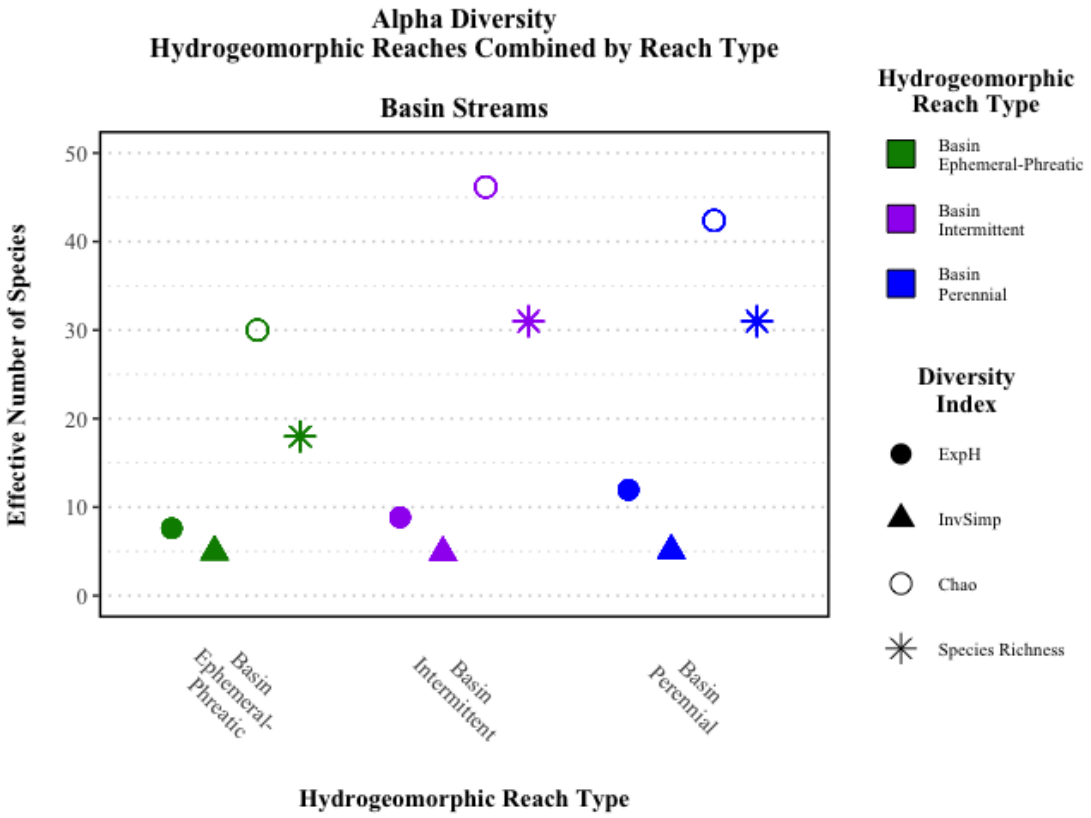


Fig. 12 Alpha diversity for four indices presented in effective number of species for hydrogeomorphic reaches combined by reach types

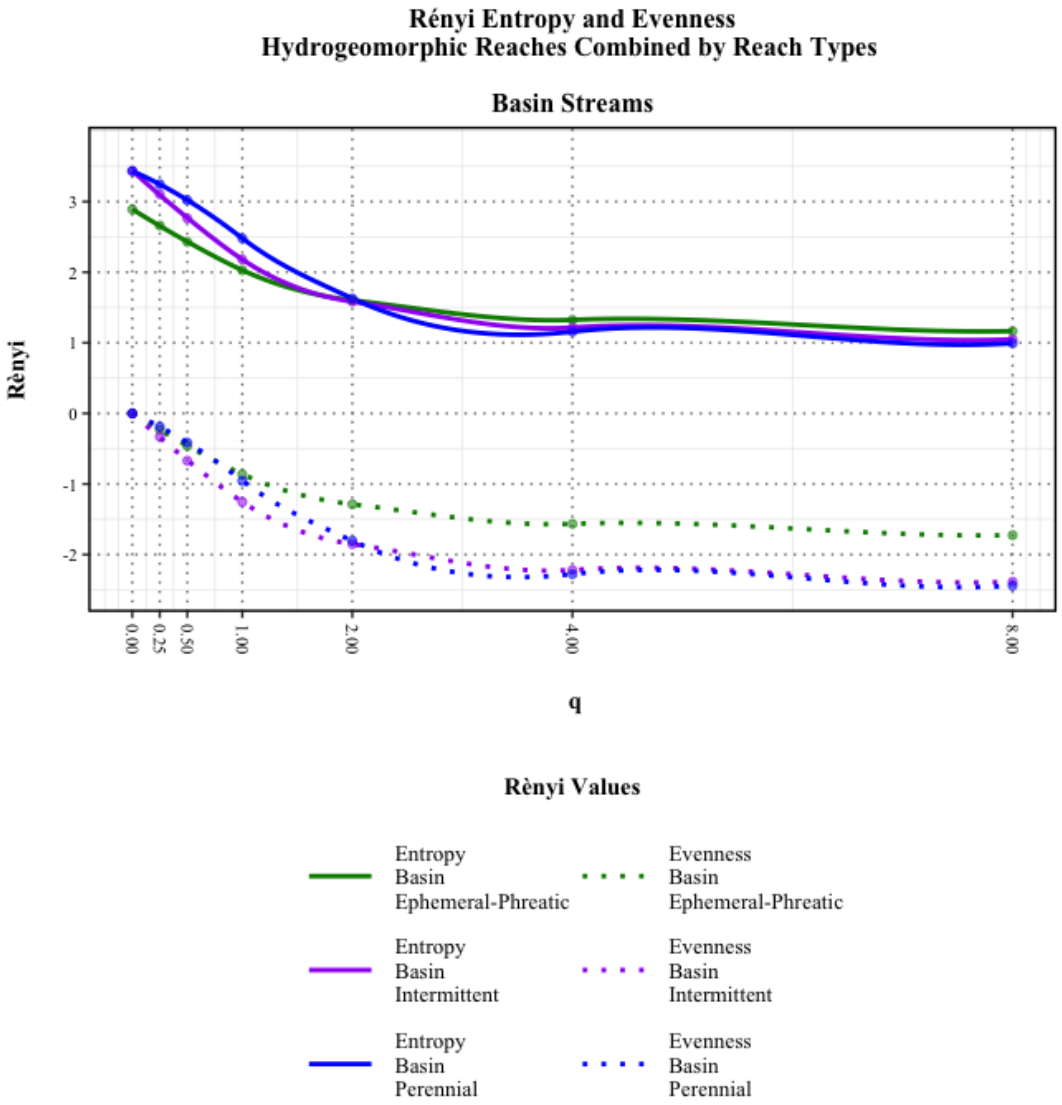


Fig. 13 Rényi entropy and evenness profiles for basin streams with hydrogeomorphic reach types combined

Question 4

I asked whether nestedness or spatial turnover contributed more to within stream beta-diversity. For the multi-site dissimilarity calculation for both analyses—Perennial reaches included and Perennial reaches excluded—the turnover component was higher than the nestedness component for both Sørensen and Jaccard indices (Fig. 14). The Hassayampa River had the highest nestedness component out of all the streams for both the Sørensen and Jaccard multi-site calculations for the analyses including and excluding the Perennial reach. For the Hassayampa River the nestedness and turnover components were most similar in value for the Sørensen multi-site calculation excluding the perennial reach. Although the turnover and nestedness components were more similar in value for this calculation than they were for the other streams, the turnover component was still higher than the nestedness component. The pair-wise and multi-site dissimilarities excluding the Perennial reaches were the same because there were only two sites (Fig. 14). The turnover components were higher than the nestedness components for all of the pair-wise dissimilarities for both dissimilarity indices including and excluding Perennial reaches. The pair-wise comparison between the Intermittent (HRINT) and Ephemeral-Phreatic (HREPH) reaches on the Hassayampa River was the only pair-wise comparison where the two components were similar in value (Table 13).

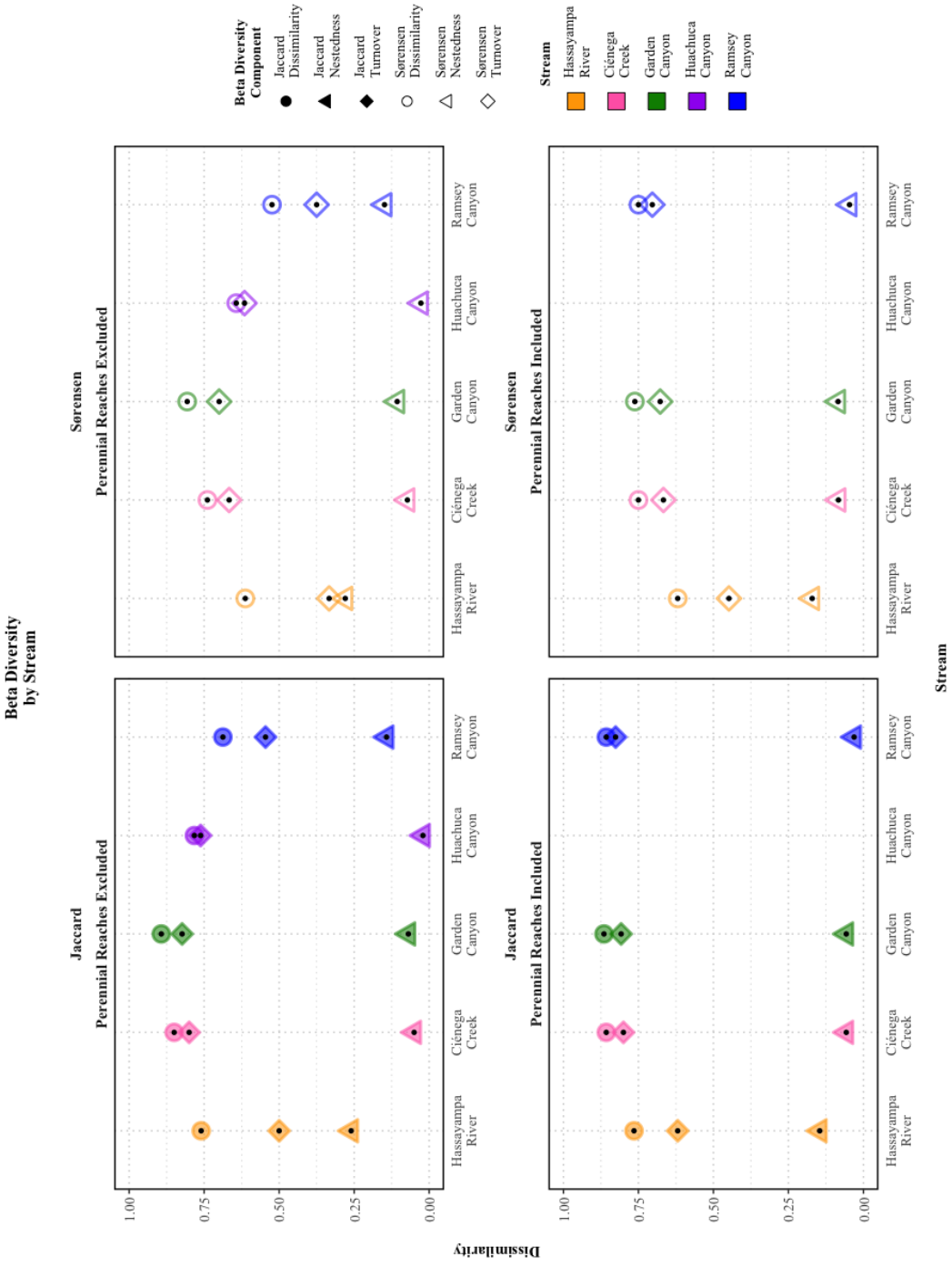


Fig. 14 Sørensen and Jaccard multi-site beta-diversity indices, including turnover and nestedness components of each, for multi-reach streams

Table 12 Sørensen and Jaccard multi-site beta-diversity indices, including turnover and nestedness components of each

Stream		Multi-Site Dissimilarity Indices		
Perennial Reaches Included		**Sørensen Dissimilarity**	**Sørensen Turnover**	**Sørensen Nestedness**
	Garden Canyon	0.7619	0.6774	0.0845
	Ciénega Creek	0.7500	0.6667	0.0833
	Ramsey Canyon	0.7500	0.7037	0.0463
	Hassayampa River	0.6190	0.4483	0.1708
		Jaccard Dissimilarity	**Jaccard Turnover**	**Jaccard Nestedness**
	Garden Canyon	0.8649	0.8077	0.0572
	Ciénega Creek	0.8571	0.8000	0.0571
	Ramsey Canyon	0.8571	0.8261	0.0311
	Hassayampa River	0.7647	0.6190	0.1457
Perennial Reaches Excluded*		**Sørensen Dissimilarity**	**Sørensen Turnover**	**Sørensen Nestedness**
	Garden Canyon	0.8065	0.7000	0.1065
	Ciénega Creek	0.7391	0.6667	0.0725
	Huachuca Canyon	0.6429	0.6154	0.0275
	Hassayampa River	0.6129	0.3333	0.2796
	Ramsey Canyon	0.5238	0.3750	0.1488
		Jaccard Dissimilarity	**Jaccard Turnover**	**Jaccard Nestedness**
	Garden Canyon	0.8929	0.8235	0.0693
	Ciénega Creek	0.8500	0.8000	0.0500
	Huachuca Canyon	0.7826	0.7619	0.0207
	Hassayampa River	0.7600	0.5000	0.2600
	Ramsey Canyon	0.6875	0.5455	0.1420

* The multi-site dissimilarities for the comparisons with the perennial reaches excluded are the same as the pair-wise calculations because only the Intermittent and Ephemeral-Phreatic reaches are used in the calculation.

Table 13 Sørensen and Jaccard pair-wise beta-diversity indices, including turnover and nestedness components of each

Pair-wise Dissimilarity Indices: Perennial Reaches Included								
Ramsey Canyon	Sørensen Dissimilarity		RCLD	RCPER	Jaccard Dissimilarity		RCLD	RCPER
		RCPER	0.9000			RCPER	0.9474	
		RCUW	0.5238	0.7600		RCUW	0.6875	0.8636
	Sørensen Turnover		RCLD	RCPER	Jaccard Turnover		RCLD	RCPER
		RCPER	0.8750			RCPER	0.9333	
		RCUW	0.3750	0.7500		RCUW	0.5455	0.8571
	Sørensen Nestedness		RCLD	RCPER	Jaccard Nestedness		RCLD	RCPER
		RCPER	0.0250			RCPER	0.0140	
		RCUW	0.1488	0.0100		RCUW	0.1420	0.0065
Garden Canyon	Sørensen Dissimilarity		GCLD	GCPER	Jaccard Dissimilarity		GCLD	GCPER
		GCPER	0.7576			GCPER	0.8621	
		GCUW	0.8065	0.6364		GCUW	0.8929	0.7778
	Sørensen Turnover		GCLD	GCPER	Jaccard Turnover		GCLD	GCPER
		GCPER	0.6667			GCPER	0.8000	
		GCUW	0.7000	0.6000		GCUW	0.8235	0.7500
	Sørensen Nestedness		GCLD	GCPER	Jaccard Nestedness		GCLD	GCPER
		GCPER	0.0909			GCPER	0.0621	
		GCUW	0.1065	0.0364		GCUW	0.0693	0.0278
Hassayampa River	Sørensen Dissimilarity		HREPH	HRINT	Jaccard Dissimilarity		HREPH	HRINT
		HRINT	0.6129			HRINT	0.7600	
		HRPER	0.6000	0.4737		HRPER	0.7500	0.6429
	Sørensen Turnover		HREPH	HRINT	Jaccard Turnover		HREPH	HRINT
		HRINT	0.3333			HRINT	0.5000	
		HRPER	0.4444	0.3750		HRPER	0.6154	0.5455
	Sørensen Nestedness		HREPH	HRINT	Jaccard Nestedness		HREPH	HRINT
		HRINT	0.2796			HRINT	0.2600	
		HRPER	0.1556	0.0987		HRPER	0.1346	0.0974
Ciénega Creek	Sørensen Dissimilarity		CCEPH	CCINT	Jaccard Dissimilarity		CCEPH	CCINT
		CCINT	0.7391			CCINT	0.8500	
		CCPER	0.7857	0.6364		CCPER	0.8800	0.7778
	Sørensen Turnover		CCEPH	CCINT	Jaccard Turnover		CCEPH	CCINT
		CCINT	0.6667			CCINT	0.8000	
		CCPER	0.6667	0.5714		CCPER	0.8000	0.7273
	Sørensen Nestedness		CCEPH	CCINT	Jaccard Nestedness		CCEPH	CCINT
		CCINT	0.0725			CCINT	0.0500	
		CCPER	0.1190	0.0649		CCPER	0.0800	0.0505

CHAPTER 4: DISCUSSION

Temperature Dependent Germination Groups

I asked the following questions about Southwestern riparian seed banks: Are there distinct suites of warm temperature and cool temperature germinating species in the soil seed banks of Southwestern streams? Does the number of temperature specialists differ between riparian and terrestrial (upland) zones? Does the number of temperature specialists differ between ephemeral streams and those with perennial headwaters?

The combined effects of seasonal temperature and moisture on the germination of many desert (terrestrial/upland) annuals is fairly well known (Went 1948; Went 1949; Baskin and Baskin 2014). Based on these previous studies I expected that there would be distinct suites of warm and cool temperature germinating species in the terrestrial(upland) zone, and indeed there were. Germination of Southwestern riparian plant species is stimulated by increased moisture availability (Bagstad et al 2005; Lite et al 2005; Stromberg et al 2009a), however the type of dormancy and thus germination temperature requirements are not known for many Southwest riparian plant species. Most Southwestern streams undergo pulses of moisture in winter and summer, but many have year-round water flows. Thus, I expected to find fewer temperature specialists and more generalist species in the riparian zone as compared to the terrestrial (upland) zone due to the increased moisture available from these flood pulses. The results of the statistical analyses showed a slightly higher number of generalist species in the riparian zones per site as compared to the terrestrial zones, but the difference was not statistically

significant, and there were on average many cool and warm temperature specialists per site. Examination of the collective seed bank composition revealed that there were large proportions of both warm and cool temperature specialists in both the riparian zone and the terrestrial zone. The riparian zone had a higher percentage of temperature generalists than did the terrestrial zone and the terrestrial zone had a higher percentage of cool temperature specialists relative to the warm temperature specialists and the generalists. The high proportion of temperature specialists in the riparian indicates that these species will be affected by changing temperatures.

Summer temperatures are increasing in the Southwest and are likely to continue to do so. Even with little change in water availability the temperature effects of climate change are likely to influence riparian zone plant community composition. The cool temperature germinating species might decrease in number, or be lost from the seed bank altogether, if winter temperatures increase above their temperature germination bands. The number of warm temperature species could also be affected because summer temperatures could increase above their temperature germination bands earlier during the spring/summer. This would decrease the amount of time available for germination for all species. An overall decrease in species richness would likely occur, with an increase in abundance of warm germinating species. Due to the importance of the timing and duration of moisture pulses on plant community composition in riparian areas (Capon 2007; Greet et al 2011; Greet et al 2012; Kehr et al 2014) an overall decrease in water availability or a change in the timing of water availability due to decreased winter precipitation or unpredictable flooding events (as previously discussed models suggest are likely to occur), it is probable that more species will be lost from the seed bank as

both temperature and moisture effects on germination compound each other. It is probable that species composition could shift toward communities dominated more by annual species and/or mesic and xeric species depending on elevation and hydrogeomorphology (Stromberg et al 2009a; Stromberg et al 2010a; Datry et al 2014).

Diversity of Riparian Zone Soil Seed Banks

Alpha Diversity: Synthesis of Questions 2 and 3

To increase our overall understanding of soil seed bank alpha diversity in Southwestern riparian areas I asked the following questions: How does alpha diversity of the soil seed bank within riparian zones compare among hydrogeomorphorphic reaches (perennial, intermittent, ephemeral-phreatic, ephemeral) within/near a stream? How does the alpha diversity of soil seed banks within the riparian zones differ among hydrogeomorphic reach types (perennial, intermittent, ephemeral-phreatic, ephemeral) for canyon and basin streams?

Based on the intermediate disturbance hypothesis (Connell 1978) and other studies on plant diversity and composition that have found higher diversity at sites with intermittent disturbance (Ellner 1987; Bagstad et al 2005; Lite et al 2005; Katz et al 2011), I expected that the intermittent sites in my study would be highest in alpha diversity. However, based on my results, this prediction did not hold true for most cases.

The within stream/drainage analyses that I conducted to answer Question 2 had varied results for riparian soil seed bank alpha diversity. The nearby Ephemeral hydrogeomorphic reaches were high in diversity for all three canyon streams; the mean ranks were highest for Species Richness at Huachuca, Garden, and Ramsey Canyons for

this hydrogeomorphic reach type. For the two basin streams the Basin Ephemeral-Phreatic hydrogeomorphic reach type was consistently lowest in alpha diversity. In general, the Intermittent hydrogeomorphic reach types for all five streams/drainages were lowest in alpha diversity for two cases, second most diverse for two cases, but only highest in alpha diversity for the Hassayampa River analyses.

The analyses of riparian zone seed bank alpha diversity within the two different stream types (Question 3) indicated for the three canyon combined stream analyses that the Ephemeral reach type was the most diverse. This was consistent with the findings from the results of Question 2. The riparian zone seed bank alpha diversity for the basin stream type (Hassayampa River and Ciénega Creek) had similar diversity values for the Basin Intermittent and Basin Perennial reach types, with the Basin Intermittent being only slightly higher. This result was consistent with the intermediate disturbance hypothesis and those of other studies on Southwestern riparian areas (Bagstad et al 2005; Lite et al 2005; Katz et al 2011), as well as my prediction.

The higher alpha diversity of the seed banks in the Ephemeral reach types was an interesting result. Similar results were found for year round species richness patterns at along an ephemeral reach of Ciénega Creek and its associated soil seed bank (Stromberg et al 2009a). These results indicate that drier reach types are important riparian zone seed bank sources. Although evidence suggests that during times when water is more limited, perennial reach types support more species (Lite et al 2005; Stromberg et al 2009a), drier reaches can also have highly diverse seed banks that contribute greatly to the diversity and composition of riparian vegetation along and surrounding Southwestern streams (Stromberg et al 2009a). It is possible that the wet/dry cycles that occur along

intermittent and ephemeral reaches might be driving the evolution of seed traits that contribute to desiccation resistance (Steward et al 2012), therefore species at these reach types might be able to adapt more quickly to the effects of climate change.

Beta-Diversity

A study conducted on the Pumphouse Wash canyon system found that the vegetation at sites within the same ephemeral drainage system were different from each other (Crawford Zimmerman et al 1999). Ephemeral-Phreatic sites on Ciénega Creek have also been found to host species not observed at perennial sites (Stromberg et al 2009a). I asked whether spatial turnover or nestedness contributed more to within stream beta-diversity for the riparian zone seed banks of the five study streams that I examined and found the majority of the dissimilarity was due to the spatial turnover component. The riparian seed banks of reaches within the same stream contain unique assemblages and only a small portion of the seed bank in each stream is a subset present at multiple sites. This is an important ecological observation highlighting the importance that each reach type has in contributing to stream-scale riparian zone seed bank diversity, and thus the diversity in the ecosystems dependent upon these streams.

Research and Conservation Implications

This study lends support to previous findings that highlight the importance of seasonal flood pulses in maintaining riparian plant diversity. It also emphasizes the concept that ephemeral and intermittent reach types can be diverse seed sources for riparian and surrounding terrestrial vegetation (Brock and Rogers 1998; Boudell and

Stromberg 2008b; Boudell and Stromberg 2008a; Williams et al 2008; White and Stromberg 2009; Tererai et al 2014). The seed banks of ephemeral and intermittent streams/reaches may be more resilient because they contain species that are adapted to the complex relationship between the temporally and spatially variable water availability and changing temperature and show a plasticity in germination allowing them to take advantage of favorable conditions (Carta et al 2013), which may be a beneficial characteristic as riparian areas are impacted by climate change and other anthropogenic perturbations. We know that regional species richness is higher due to the influence of riparian areas because they support different suites of species than the surrounding terrestrial zone (Sabo et al 2005), making conservation of riparian areas fundamental to maintaining regional biodiversity. However, as the amount of research on riparian areas increases, the ecological value and thus the need to conserve a range of hydrogeomorphic reach types—including those considered ephemeral and intermittent—is becoming more apparent (Steward et al 2012; Datry et al 2014; Acuña et al 2014).

The species identified as temperature specialists in my study can be considered only as potential temperature specialists due to the possibility that there was low detection frequency for some species. The species that were identified as potential temperature specialists for these sites warrant further species specific germination studies to determine exact germination temperature bands and dormancy breaking requirements. The storage period of the soil prior to the study also likely affected detection of many transient seeded species, most notably *Salix gooddingii* and *Populus fremontii*, which both have very short lived seeds. Herbaceous species tend to have smaller seeds that incorporate into the soil more easily than some woody species with larger seeds, therefore

these larger seeded species may have also gone undetected. Although the diurnal temperature programs for this study were created to mimic daily variation based on the local monthly temperature data there is a possibility that the germination temperatures for some species in the seed banks fell outside of these temperature bands which allowed them to go undetected in this study. The germination study was conducted for 12 weeks concurrently for both temperature treatments—only 24 weeks total out of 52 for a year—which likely decreased the detection of some species especially those that require longer warm temperature stratification. Although there were limitations involved with this study the results indicate which species are likely to be influenced by temperature changes and might benefit from further study. The lack of species specific germination data for southwestern riparian species exemplifies the need for additional research necessary to elucidate the interdependence of riparian seed banks on both moisture and temperature in combination, along with other environmental factors.

Many results from this study were consistent with previous studies on riparian seeds banks, however comparing the seed banks from the stream reaches that I investigated in this study to the extant flora from the same reaches would also help to clarify the relationship between riparian seed banks and plant community composition and diversity. I did not address the effects of water availability on riparian seed bank germination as part of this study, although I believe that this information would be quite beneficial in our efforts to understand the how ephemeral and intermittent streams function in the environment.

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APPENDIX A

NUMBER OF SPECIES PER SITE PER GERMINATION GROUP

Table 14 Species richness by temperature germination group

Site	Zone	Hydrogeomorphic Class	Perennial Headwaters	Temperature Dependent Germination Group		
				* *Cool Specialists (10-20°C)*	* *Warm Specialists (25-35°C)*	* *Cool/Warm Generalists (10-20 and 25-35°C)*
BGW	Riparian	Basin Ephemeral-Phreatic	NO	8	1	0
BGW	Terrestrial	Basin Ephemeral-Phreatic	NO	2	3	0
CCEPH	Riparian	Basin Ephemeral-Phreatic	YES	6	4	1
CCINT	Riparian	Basin Intermittent	YES	7	7	0
CCINT	Terrestrial	Basin Intermittent	YES	7	7	0
CCPER	Riparian	Basin Perennial	YES	14	7	2
GCLD	Riparian	Canyon Ephemeral-Phreatic	YES	12	15	6
GCLD	Terrestrial	Canyon Ephemeral-Phreatic	YES	11	10	3
GCPER	Riparian	Canyon Perennial	YES	8	7	3
GCUW	Riparian	Canyon Intermittent	YES	7	4	1
GCUW	Terrestrial	Canyon Intermittent	YES	10	13	4
GFD	Riparian	Ephemeral	NO	16	15	7
GFD	Terrestrial	Ephemeral	NO	4	6	2
HCLD	Riparian	Canyon Ephemeral-Phreatic	YES	9	9	3
HCLD	Terrestrial	Canyon Ephemeral-Phreatic	YES	13	15	6
HCUW	Riparian	Canyon Intermittent	YES	6	12	5
HCUW	Terrestrial	Canyon Intermittent	YES	5	10	4
HFD	Riparian	Ephemeral	NO	9	8	1
HFD	Terrestrial	Ephemeral	NO	6	4	2
HREPH	Riparian	Basin Ephemeral-Phreatic	YES	6	6	3
HREPH	Terrestrial	Basin Ephemeral-Phreatic	YES	5	3	2
HRINT	Riparian	Basin Intermittent	YES	16	13	7
HRPER	Riparian	Basin Perennial	YES	11	9	4
RCLD	Riparian	Canyon Ephemeral-Phreatic	YES	3	6	1
RCLD	Terrestrial	Canyon Ephemeral-Phreatic	YES	8	9	4
RCPER	Riparian	Canyon Perennial	YES	6	8	2
RCUW	Riparian	Canyon Intermittent	YES	9	7	3
RCUW	Terrestrial	Canyon Intermittent	YES	15	10	7
RFD	Riparian	Ephemeral	NO	15	20	8
RFD	Terrestrial	Ephemeral	NO	6	4	2
SRLW	Riparian	Basin Ephemeral	NO	10	10	1
SRLW	Terrestrial	Basin Ephemeral	NO	9	4	1
SRSW	Riparian	Basin Ephemeral	NO	4	9	0
SRSW	Terrestrial	Basin Ephemeral	NO	6	3	1
SW	Riparian	Basin Ephemeral	NO	3	2	0
SW	Terrestrial	Basin Ephemeral	NO	0	0	0

* Number of species in each temperature germination group calculated based on results of ChaoShared function from SpadeR package

All sites were included in the comparison of riparian zone to terrestrial zone

Grey rows were not included in the comparison of perennial headwater to ephemeral streams

White rows were included in the comparison of perennial headwater to ephemeral streams

APPENDIX B

SPECIES LIST WITH TEMPERATURE GERMINATION ABUNDANCE DATA

Table 15 Species list with abundance by temperature germination group

Scientific Name	Temperature Germination Group Abundance				Found in Number of Samples
	Cool Riparian	Warm Riparian	Cool Terrestrial	Warm Terrestrial	
Ageratina herbacea	13	5	10	4	18
Amaranthus fimbriatus	0	2	0	0	1
Amaranthus palmeri	9	22	0	2	13
Amaranthus powellii	0	0	3	1	2
Artemisia dracunculus	9	3	1	0	7
Artemisia ludoviciana	5	7	4	0	5
Astragalus nuttallianus	1	0	1	0	2
Atriplex elegans	1	0	0	0	1
Bidens bigelovii	3	3	1	0	3
Bidens heterosperma	0	4	0	0	1
Bidens leptocephala	2	1	4	2	7
Bidens pilosa	0	0	0	1	1
Boerhavia sp.	0	1	0	0	1
Boraginaceae sp.	0	0	2	0	2
Bothriochloa barbinodis	0	1	0	0	1
Bothriochloa laguroides	0	0	1	0	1
Bouteloua aristidoides	0	0	4	0	1
Bouteloua curtipendula	0	0	0	5	1
Bowlesia incana	4	0	0	0	1
Brassicaceae sp.	2	0	0	0	1
Bromus catharticus	2	0	0	0	1
Bromus diandrus	0	1	0	0	1
Calibrachoa parviflora	109	32	0	0	14
Carex chihuahuensis	22	17	0	0	4

Carex ultra	5	3	0	0	6
Carminatia tenuiflora	0	2	0	1	3
Chamaesyce micromera	0	1	0	0	1
Chamaesyce setiloba	0	2	0	0	1
Chamaesyce sp.	0	4	0	0	2
Chenopodium pratericola	1	0	0	0	1
Chenopodium sp.	1	0	0	0	1
Commelina dianthifolia	0	1	0	0	1
Crassula connata	2	0	21	0	4
Cryptantha angustifolia	3	0	0	0	2
Cryptantha barbigera	1	0	0	0	1
Cylindropuntia A sp.	0	0	0	1	1
Cylindropuntia B sp.	0	4	0	0	1
Cyperus fendlerianus	0	0	0	1	1
Cyperus.manimae var. asperrimus	1	0	0	0	1
Cyperus retroflexus	2	7	12	9	18
Cyperus sp.	1	1	0	1	3
Cyperus sp.	0	2	1	0	3
Descurainia pinnata	6	0	1	0	6
Desmodium rosei	0	0	0	1	1
dicot	18	16	16	10	50
Disakisperma dubium	0	1	0	9	2
Draba cuneifolia	1	0	0	0	1
Drymaria leptophylla	4	0	0	0	2
Dysphania graveolens	0	0	1	0	1
Epilobium ciliatum	1	0	0	0	1

Eragrostis cilianensis	0	5	0	3	5
Eragrostis curvula	0	1	0	0	1
Eragrostis intermedia	15	13	14	13	25
Eragrostis lehmanniana	37	21	38	12	37
Eragrostis mexicana	0	1	0	0	1
Eragrostis pectinacea	0	1	0	0	1
Eragrostis sp.	1	1	1	0	3
Eremothera chamaenerioides	1	0	0	0	1
Erigeron arisolius	0	0	1	0	1
Erigeron canadensis	11	22	13	7	28
Erigeron lobatus	1	1	0	0	2
Euphorbia heterophylla	0	0	0	1	1
Fabaceae sp.	0	1	0	0	1
Hedeoma dentata	0	0	1	0	1
Heliomeris.longifolia var. annua	27	0	14	0	12
Herniaria hirsuta	2	0	0	0	2
Heterosperma pinnatum	0	0	0	1	1
Heterotheca subaxillaris	3	1	2	0	6
Ipomoea hederacea	0	1	0	0	1
Juncus balticus	0	1	0	2	2
Juncus bufonius	55	11	2	1	18
Juncus interior	4	17	0	0	6
Juncus mexicanus	2	0	0	0	2
Juncus saximontanus	1	6	0	0	3
Juncus sp.	6	22	0	3	12
Juniperus deppeana	0	2	0	1	3

Laennecia coulteri	30	24	125	96	67
Laennecia sophiifolia	1	2	0	0	3
Lepidium thurberi	1	0	0	0	1
Logfia filaginoides	5	0	3	0	4
Lythrum californicum	1	0	0	0	1
Machaeranthera tanacetifolia	0	1	0	0	1
Mimulus cordata	0	5	0	0	1
Mimulus floribundus	20	3	4	2	12
Mimulus guttatus	8	2	0	0	7
Mimulus nasuta	14	8	0	0	11
Mimulus rubellus	1	0	2	0	3
Mimulus verbenaceus	1	4	0	1	4
Mitracarpus breviflorus	0	1	0	7	4
Mollugo verticillata	0	7	0	15	16
Monarda citriodora	0	3	0	3	3
monocot	1	0	0	0	1
Morpho sp.	1	0	0	0	1
Morpho sp.	1	0	0	0	1
Morpho sp.	0	0	1	0	1
Morpho sp.	53	25	1	1	12
Morpho sp.	1	0	0	0	1
Morpho sp.	6	0	3	1	8
Morpho sp.	0	0	6	0	1
Morpho sp.	2	0	0	0	1
Morpho sp.	0	0	1	0	1
Morpho sp.	1	0	0	0	1
Morpho sp.	7	0	0	0	1
Morpho sp.	32	0	0	0	1
Morpho sp.	0	0	1	0	1
Morpho sp.	1	0	0	0	1
Morpho sp.	4	0	0	0	1

Morpho sp.	0	0	1	0	1
Morpho sp.	0	0	0	1	1
Morpho sp.	0	0	0	1	1
Morpho sp.	1	4	0	0	2
Morpho sp.	0	1	0	1	2
Morpho sp.	0	2	0	0	2
Morpho sp.	0	1	0	0	1
Morpho sp.	0	43	1	0	5
Morpho sp.	0	1	0	0	1
Morpho sp.	0	1	0	0	1
Morpho sp.	0	2	0	0	1
Morpho sp.	0	2	0	1	2
Morpho sp.	0	0	0	4	1
Morpho sp.	0	0	3	0	2
Muhlenbergia emersleyi	0	1	0	1	2
Muhlenbergia minutissima	0	2	0	0	1
Nama demissum	0	0	5	0	4
Nasturtium officinale	8	6	14	0	7
Nemacladus glanduliferus	0	0	1	0	1
Nicotiana obtusifolia	2	0	0	0	2
Oenothera hexandra subsp. gracilis	0	2	0	0	1
Oenothera sp.	0	0	1	0	1
Onagraceae sp.	2	0	0	0	1
Oxalis sp.	1	0	1	0	2
Parietaria hespera	1	0	4	0	3
Paspalum dilatatum	1	0	0	0	1
Pectis linifolia	0	1	0	0	1
Pectocarya heterocarpa	5	0	0	0	1
Pectocarya recurvata	0	0	1	0	1
Pectocarya sp.	0	0	4	0	3
Perityle coronopifolia	0	1	0	0	1

Persicaria maculosa	0	3	0	0	1
Phaseolus acutifolius	0	0	1	1	2
Phemeranthus parviflorus	0	1	0	0	1
Physalis hederifolia	0	1	0	0	1
Piptochaetium fimbriatum	1	0	0	1	2
Plantago ovata	0	0	3	0	3
Platanus wrightii	2	1	0	1	4
Poaceae sp.	4	20	3	45	31
Polygonum sp.	2	0	0	0	2
Polypogon interruptus	2	0	0	0	1
Polypogon monspeliensis	52	4	0	0	9
Polypogon sp.	0	0	2	0	1
Polypogon viridis	6	4	1	0	7
Portulaca halimoides	0	7	0	1	2
Portulaca sp.	0	0	0	1	1
Portulaca umbraticola	0	1	0	0	1
Pseudognaphaliu m canescens	14	2	8	0	12
Pseudognaphaliu m luteoalbum	45	41	47	35	70
Quercus sp.	1	0	0	0	1
Salvia subincisa	0	2	0	0	2
Schismus barbatus	0	1	0	0	1
Schizachyrium cirratum	0	0	2	0	1
Schizachyrium sanguineum var. hirtiflorum	0	0	0	1	1
Setaria grisebachii	0	1	0	2	2
Setaria leucopila	0	3	0	0	2
Sisymbrium irio	7	19	0	0	7
Sorghum halepense	2	8	0	0	3

Sporobolus cryptandrus	0	25	1	0	4
Typha domingensis	1	1	0	0	2
Urochloa arizonica	0	3	0	0	1
Verbascum blattaria	5	1	0	1	4
Veronica anagallis-aquatica	18	0	0	0	6
Veronica peregrina	24	1	1	1	12
Xanthocephalum gymnospermoides	8	0	0	0	2
Zeltnera calycosa	1	0	0	0	1
Zuloagaea bulbosa	0	2	0	0	1

APPENDIX C

SEED BANK DESCRIPTIVE STATISTICS

SEED BANK DESCRIPTIVE STATISTICS

There were 174 total taxa including those that could only be determined to "monocot" and "dicot". There were certain species that were found in a large number of the samples: *Pseudognaphalium luteoalbum* was found in 70 samples, *Laennecia coulteri* in 67, *Eragrostis lehmanniana* in 37, *Erigeron canadensis* in 28, and *Eragrostis intermedia* in 25. The RFD site had the highest number of taxa germinate with 30, and the CCEPH and SW sites both tied with the least taxa with 9 (Table 17).

Table 16 Quantiles for abundance and species richness by sample and by pooled.ID

Quantiles	Total Abundance Pooled*	Species Richness Pooled*	Total Abundance per Sample	Species Richness per Sample
0%	0	0	0	0
25%	11	5	0	0
50%	22	7	1	1
75%	36	10	4	2
100%	237	20	76	8

*Pooled by Site, Zone, and Temperature Treatment

Table 17 Site level species richness—samples for riparian and terrestrial zones for both warm and cool samples combined.

Stream Type	Study Area	Hydrogeomorphic Classification			
		Perennial	**Intermittent**	**Ephemeral**	**NonPhreatic**
Canyon (Montane) Streams	Ramsey Canyon	RCPER 12	RCUW 25	RCLD 16	RFD 30
	Garden Canyon	GCPER 12	GCUW 26	GCLD 29	GFD 26
	Huachuca Canyon		HCUW 20	HCLD 29	HFD 20
Basin Streams	Ciénega Creek	CCPER 19	CCINT 20	CCEPH 9	
	Hassayampa River	HRPER 16	HRINT 22	HREPH 12	
	Santa Rita Exptl. Range			SRLW 28 SRSW 18	
	Barry Goldwater Air Force Range			BGW 14 SW 9	