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The Biogeographic Significance of a Large, Deep Canyon: Grand Canyon of the Colorado River, Southwestern USA

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1. Introduction

Mountains and uplifted areas occupy more than 10% of the Earth's surface, and their associated drainages rather commonly develop as constrained, canyon-bound channels. Therefore, large deep canyons (LDCs) are relatively frequently encountered, persistent landforms, occurring either as steeply dipping, V-shaped canyons that emerge from fold, fault-block, volcanic, and dome mountains, or occurring as drainages incised into uplifted plateaus. The latter type include the world's deepest canyons, including: the 3.35 km-deep Cotahuasi Canyon of the Rio Cotahuasi, a tributary of the Rio Ocona in southwestern Peru; the 2.44 km-deep Hells Canyon of the Snake River in Idaho; the >2.1 km-deep Barranca de Cobre in Chihuahua, Mexico; and the world-renowned 2.48 km-deep Grand Canyon in northern Arizona. LDCs also occur in submarine environments at the mouths of large rivers: the Nile and the Rhône Rivers have large submarine canyons at their mouths created during repeated Pliocene desiccation of the Mediterranean basin; the Indus and Ganges Rivers form lengthy submarine deltaic canyons; the Hudson River in northeastern North America has a substantial submarine canyon; and large canyons form in other tectonically active submarine areas. Whether terrestrial or subaqueous, LDCs support or generate strong ecological gradients, and periodically or perennially provide cascading deliveries of flow, sediments, nutrients, and biota to lower elevations (e.g., Gurnell and Petts 1995; Butman et al. 2006; Canals et al. 2009), processes that may influence the distribution and evolution of life around them.

Although both terrestrial and submarine LDCs are conspicuous landforms, their regional biogeographic significance has received remarkably little scientific attention, particularly in relation to that devoted to other major landforms, such as islands, lakes, and mountain ranges (Lomolino et al. 2010). Obviously functioning as barriers throughout human history and to many biota, terrestrial LDCs form complex habitat mosaics that also function as downstream and upstream corridors through higher elevation terrain, and LDCs contain an array of refugial habitats (Fig. 1; Stevens and Polhemus 2008). Consequently, LDCs may differentially facilitate or restrict gene flow, with ecological and evolutionary impacts on regional populations and assemblages across spatial and temporal scales, and in ways different from those of other conspicuous landforms. LDCs also are preferred sites for dam

construction, and many LDCs and their associated assemblages have been altered by flow regulation throughout the world. Here I describe the biogeographical characteristics and significance of the world's most famous terrestrial LDC, Grand Canyon (GC) of the Colorado River in the American Southwest within its drainage basin, the Grand Canyon ecoregion (GCE). I compare LDC characteristics with those of other major landforms, and describe conservation issues.

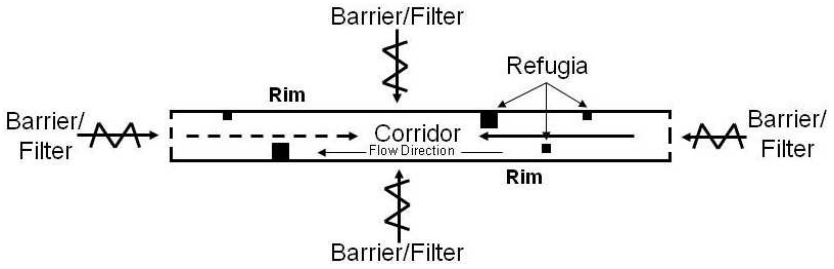


Fig. 1. Schematic diagram of the biogeographic functions of large, deep canyons.

2. Study area

The GCE includes 144,000 km² of the southern Colorado Plateau in northern Arizona, southern Utah, and western New Mexico (Fig. 2). This is a topographically complex region, ranging in elevation from 350 m AMSL on eastern Lake Mead to 3,850 m on the San Francisco Mountains near Flagstaff, Arizona, and with the highest point on the North Rim of GC at approximately 2,830 m. The climate of the GCE is continental and arid, with low elevation desert summertime high temperatures >45°C, and high elevation mountain winter low temperatures < -55°C. Precipitation is bimodal, with wintertime snowfall and rain, and mid-late summer monsoonal rains (Sellers et al. 1985). More than 90 percent of the GCE is managed by federal agencies or Indian Tribes, including: 12 National Park units, particularly including Grand Canyon National Park; 6 National Forest units; the Bureau of Land Management; and 8 Native America tribes. State lands include small tracts of state fish and wildlife management units, and private lands are few.

A major geologic province boundary divides Arizona in half, with the Basin and Range geologic province to the south and west, and the Colorado Plateau division of the Rocky Mountain geologic province to the north and east (Fig. 2). The boundary runs diagonally NW-SE through central Arizona, creating a lengthy escarpment known as the Mogollon Rim. This geologic province boundary forms a biogeographic ecotone between the Mexican-neotropical Madrean floristic region and the boreal Rocky Mountain floristic region, referred to as the Lowe-Davis line (Lomolino et al. 2010). Drainages that breach this geologic province boundary (e.g., the Virgin and Verde Rivers) are richer in species of aquatic invertebrates than are those that do not bridge the boundary (e.g., the Escalante River, the Little Colorado River, the Paria River, Kanab Creek, and Havasu Creek; Stevens and Polhemus 2008, Stevens and Bailowitz 2009).

The GCE lies at the intersection of 4 biomes, including the Madrean, Mohavean/Sonoran, intermountain, and cordilleran biomes. Low desert habitats to the south are occupied by Madrean, Sonoran, and Mohavean desert shrub vegetation, while middle elevations are

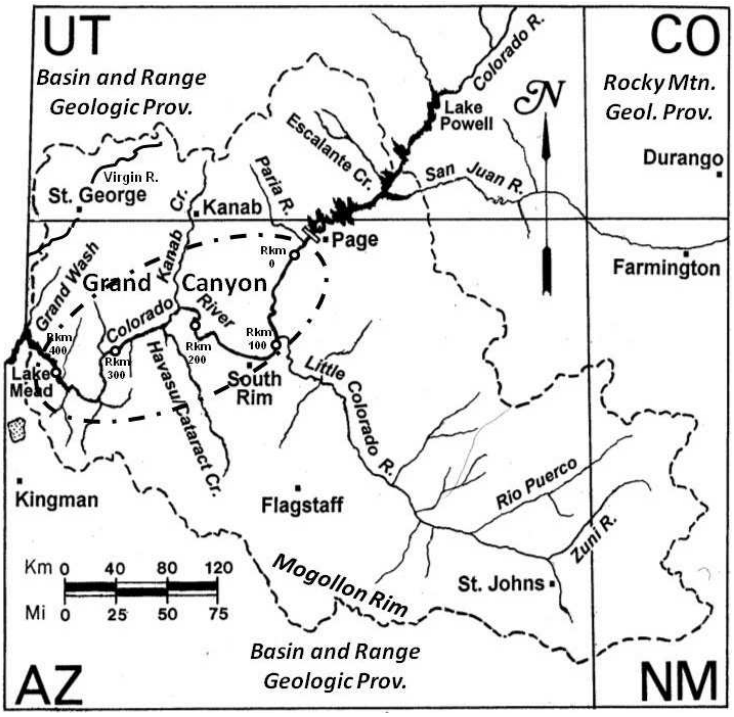


Fig. 2. Grand Canyon and the 144,000 km² Grand Canyon ecoregion (dashed line) on the southern Colorado Plateau, southwestern U.S.A.

dominated by intermountain Great Basin grasslands and pinyon-juniper woodlands. Upper elevation plateaus are occupied by cordilleran Rocky Mountain ponderosa pine (*Pinus ponderosa*) and mixed conifer forests, with large meadows, and highest elevations above 3600 m support 5 km² of Rocky Mountain alpine tundra habitat (Table 1). The GCE is strongly dominated by upland shrublands, woodlands, and ponderosa pine forests, which collectively occupy 95% of the land area, while deserts below 1000 m and montane to alpine habitats above 2800 m each occupy only about 2.5% of the land area.

The GCE is dominated by the large, deep canyons of the Colorado River and its many tributaries, and contains more than 75 ecosystems and habitats (Stevens and Nabhan 2002). Locations along the Colorado River are designated by distance from Lees Ferry, Arizona, and on the left (L) or right (R) side of the river looking downstream. Large tributaries include: the Paria River (Rkm 1.5R), the Little Colorado River (LCR; Rkm 98L), the Virgin River, Kanab Creek (Rkm 232R), Havasu/Cataract Canyon (253L), Diamond Creek/Peach Springs Wash (383L), and Grand Wash (479R; Figs. 2, 3). Hoover and Glen Canyon Dams on the Colorado River create the nation's two largest reservoirs, Lake Mead and Lake Powell, respectively, which overlap into the GCE. Not within GC, the Black, White, Eagle, and other tributaries of the upper Gila River form the southeastern drainage boundary of the GCE. Tonto Creek, a central Gila River tributary, drains the region west of the upper Gila River

Elevation Range (m)	Vegetation Zone	Characteristic Flora	Comments
<1500	Lower Sonoran	Desert shrubs, including cacti; Colorado River, springs, and reservoir riparian vegetation	GC floor and lower slopes
1100-2300	Upper Sonoran	Pinyon pine (*Pinus* spp.), *Juniperus* spp.; Great Basin shrublands; grasslands; stream and springs riparian vegetation	GC middle-upper slopes
1600-2800	Transition	Ponderosa pine (*Pinus ponderosa*), Gambel's oak (*Quercus gambelii*), Douglas fir; small streams and springs riparian vegetation	Both GC rims
2500-3300	Canadian	Mixed conifer: white fir (*Abies concolor)*, Douglas fir (*Pseudotsuga mentsezii)*, *Pinus* spp.; springs riparian vegetation	GC North Rim
3000-3600	Hudsonian	Spruce-fir forest; springs riparian vegetation	At elevations above GC in the White and San Francisco Mtns
3400-3700	Subalpine	Subalpine fir (*Abies lasiocarpa*), bristlecone pine (*Pinus aristata*), low shrubs, springs riparian vegetation	At elevations above GC in the White and San Francisco Mtns
3600-3850	Alpine	Tundra shrubs, graminoides	At elevations above GC in the San Francisco Mtns

Table 1. Merriam life zones and vegetation zonation across elevation in the GCE

basin. The Verde River basin breaches the geologic province boundary, draining the central southern portion of the GCE. The Virgin River drains southwestern Utah and northwestern Arizona, also breaching the geologic province boundary. In addition, the GCE supports thousands of caves and springs (Stevens and Meretsky 2008), and thousands of km of escarpment edges.

Embedded wholly within the southwestern Colorado Plateau, GC is naturally separated into an eastern basin, which receives the flows of the Paria and LCR drainages, and a more open western basin that connects western Grand Canyon to the Mojave and Sonoran deserts to the west and south (Fig. 3; Billingsley and Hampton 1999, Stevens and Huber 2004). The two GC basins are separated by the steep, narrow 35 km-long Muav Gorge, which creates a formidable cliff-dominated barrier to upstream and downstream dispersal of numerous southwestern plant, invertebrate, and vertebrate taxa (Miller et al. 1982; Phillips et al. 1987; Schmidt and Graf 1990; Stevens and Polhemus 2008).

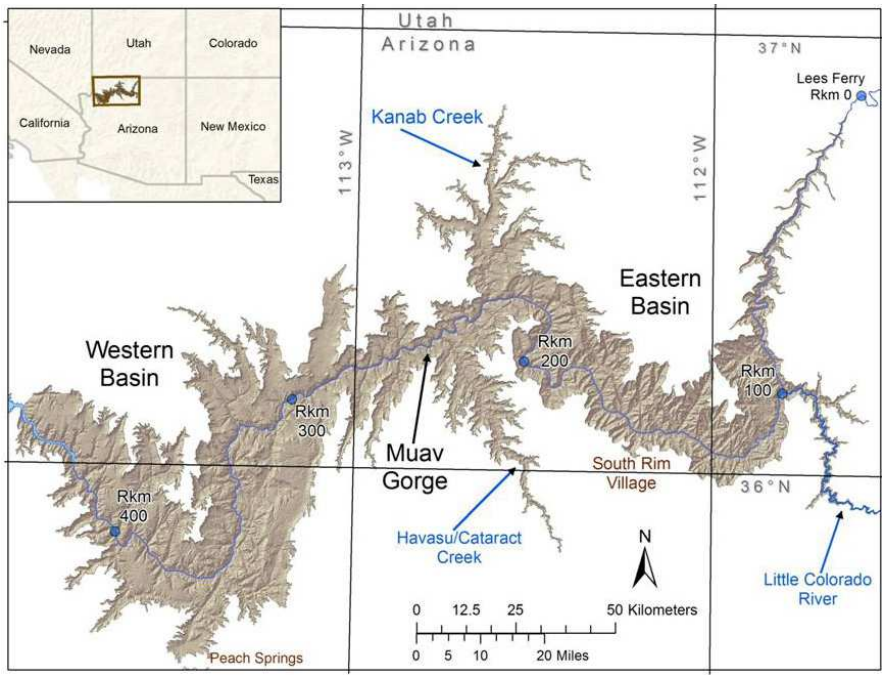


Fig. 3. Grand Canyon rim and major tributaries map, showing the eastern and western basins divided by the Muav Gorge, and distances along river from Lees Ferry (Rkm 0). Map redrawn from Billingsley and Hampton (1999), and prepared by J. D. Ledbetter.

3. Ecological gradients

3.1 Overview

LDCs create complex spatially and temporally intercorrelated environmental gradients, and ecological processes that often are stratified across elevation, strongly affecting the composition and structure of biotic assemblages. The major gradients in LDCs include: gravity, geology, regional climate, elevation, and aspect. Collectively, these affect, generate, or permit the solar radiation budget, micro- to synoptic climate, moisture availability, dip angle, pedogenesis, and natural disturbance regimes, all of which affect the development of canyon biotic assemblages over time. Here I briefly review the roles of these major physical gradients in the GCE.

3.2 Gravity

Gravity plays a profound role in species dispersal and ranges in LDCs. Passively dispersing taxa, including plants, non-flying invertebrates and vertebrates, and even some bird species more readily disperse and colonize downslope. Although the inner canyon corridor within 100 m of the river makes up less than 3 percent of the overall land area in the GC, that zone supports more than 760 plant species, more than 40% of the entire GC flora (Stevens and Ayers 2002, Busco et al. 2011). Downslope dispersal accounts for the in-canyon occurrence of many

rim-dwelling species of grasses, forbs, shrubs (e.g., *Fallugia paradoxa, Parreyella filifolia*), and trees. These upper elevation "waif" or "Gilligan" species may reach the canyon-floor desert, far from their normal habitats and, while able to become established, they may not be able to reproduce or form permanent colonies. Such species are particularly likely to occur in aspect refugia: boreal colonists often occur in the desert on north-facing slopes. Numeorus insects (e.g, *Prionus heros*, various scarabaeids, *Pandora* moths), wild turkey (*Meleagris gallopavo*), and other rim fauna also readily disperse downslope, and have been regularly detected along the river (Brown et al. 1987; LaRue et al. 2001; Stevens unpublished data).

3.3 Geology and geomorphology

Geologic context, parent rock, structure, and tectonic history play dominant roles governing the development, functioning, and characteristics of LDC ecosystems. Geology and geologic processes control: 1) elevation, a primary determinant of local climate; 2) aspect, in turn influencing solar radiation budget, microclimate, productivity, pedogenesis, habitat availability, and species distributions; 3) geomorphology, including width-depth relationships of the canyon stream channel; and 4) rock color, which may differentially affect heat loading. The subject of microtopographic ecological gradient impacts on assemblages is generally poorly studied, but topographic differences of less than 10 m can affect local microclimate and species distributions, particularly near water sources where surface heating affects humidity.

Although much debated, drainage evolution of the Colorado River in the American Southwest has occurred over the past 40 million yr through conclusion of the Laramide orogeny and the onset of Basin and Range orogenic uplift and stream capture (Hunt 1956; Dickinson 2002; review in Blakey and Ranney 2008). On-going debate over development of the Colorado River basin is divided between advocacy for an old canyon (Oligocene-Miocene origination) as opposed to a young canyon (late Miocene-Pleistocene origination), and top-down drainage integration versus integration of variably independent sub-basins. Basin and Range crustal extension caused the uplift of the Sierra Nevada Range and numerous other north-trending ranges, which block the on-shore movement of moist Pacific airflow. This geologic deformation and development of the regional rain-shadow over the past 15 million ys changed the GCE from a low-lying, mesic, savannah-dominated landscape to its present-day uplifted, arid character. Also of great biogeographic impact was the tectonic/volcanic connection between South and North America 2.7 million years ago (Wallace 1876; Webb 2006). The ensuing land bridge permitted movement of biota between continents, resulting in the Great American Biotic Interchange, resulting in the movement and extinction of numerous species. The interchange is largely responsible for the contemporary co-occurrence of 150 genera of plants and animals in South America and the American Southwest. Following integration of the Colorado River, western Grand Canyon was dammed by numerous lava flows over the past 750,000 yr, forming large Pleistocene lakes and perhaps large outburst floods (Hamblin 1994; Crow et al. 2008). Biogeographic analyses of aquatic nepomorph Hemiptera (Stevens and Polhemus 2008) demonstrate significant upstream attenuation in species richness, suggesting that such flooding reversed or retarded upriver colonization in Pleistocene time. Interestingly, the ranges of aquatic Heteroptera taxa in that study also reveal the "biological shadow" of an earlier Paleogene east- and north-flowing Nevada river system into western Grand Canyon, a river unrelated to the present-day Colorado River.

Fluvial geomorphology has been thoroughly studied in GC (e.g., Howard and Dolan 1981; Schmidt and Graf 1990; Topping et al. 2005). Rapids form at the confluence of tributary canyons when rare debris flows deliver large boulders into the Colorado River, damming the mainstream (Webb et al. 1987). Rapids create recirculation zones (eddies) that, on descending flows, deposit fine sediments in characteristic locations both upstream and downstream of the debris fans. Thus, unlike alluvial rivers, the location of sandbars in the geomorphically constrained Colorado River are fixed within 13 geomorphic reaches (Table 2). More than 550 debris fan complexes generate a distinctive suite of fluvial microhabitats, each with discrete grain sizes, soils, stage elevation relationships, inundation frequencies, and stage-zoned riparian vegetation (Turner and Karpiscak 1980; Schmidt and Graf 1990; Melis et al. 1997). Analyses of flow regulation influences at a large suite of debris fan complexes revealed that flow regulation allowed extensive development of fluvial marshes, enhancing riverine plant species richness (Stevens et al. 1995; Waring et al. in press). Clearwater releases and flood control also greatly increased aquatic productivity within the river which, coupled with riparian vegetation expansion, has led to increased waterbird biodiversity, and peregrine falcon (*Falco peregrinus anatum*) population increases and the potential for formation of novel post-dam trophic cascades (Brown et al. 1992; Stevens et al. 1997a,b; Stevens et al. 2009).

Thus, flow regulation reduced flooding disturbance and increased productivity of this naturally flood-prone river ecosystem, changing the river ecosystem energetics from allochthonous to autochthonous sources (Carothers and Brown 1991), and increasing riverine species richness and trophic complexity, in accord with the predictions of both Connell's (1978) intermediate disturbance concept and Huston's (1979) dynamic equilibrium model (Stevens and Ayers 2002). But also of scientific and stewardship interest, flow regulation differentially influenced geomorphological influences on subaqueous versus subaerial biota, colonization, and production. Flow regulation has swamped geomorphic influences on biological organization in the aquatic domain of the river, reducing differences in benthic standing stock or species among various aquatic microhabitats (Stevens et al. 1997b). In contrast, flow regulation has enhanced variation in biotic development on the various geomorphic microhabitats in debris fans in the riparian domain (Stevens et al. 1995, 1997a). Differential responses of the river ecosystem to flow regulation on the aquatic versus the riparian domains vastly complicate environmental management of focal species and habitats, creating challenging administrative tradeoffs (Stevens et al. 2001; Lovich and Melis 2007).

3.4 Elevation

Elevation strongly affects local climate, productivity, species composition, and microsite ecology. Following the model of Von Humboldt and Bonpland (1805, Jackson 2009), C.H. Merriam was the first American naturalist to quantify the influences of elevation on biotic zonation across an Arizona transect from the floor of Grand Canyon to the top of the San Francisco Peaks and out into the Painted Desert (Merriam and Steineger 1890). Merriam attributed the discrete zonation of trees across elevation primarily to temperature and latitude; however, Holdridge (1947) and others subsequently recognized the importance of seasonal and total precipitation, evapotranspiration, and other factors controlling vegetation and biome development (Olson et al. 2001).

Geomorphic Reach	Distance from Lees Ferry, AZ (km)	Dominant Bedrock Strata	Mean River Width (m)	Mean Floodplain Width (m)	Estimated Floodplain Area (ha)	% Potential Solar Energy
Glen Canyon Reach	-25 - 0	Mesozoic sandstones	85.3	---	95	65.3
Permian Reach	0-17.7	Permian-Pennsylvanian limestones, sandstone, shale	70.0	20.5	73	78.0
Supai Gorge	17.7-36.2	Pennsylvanian limestone, sandstone, shale	---	14.4	53	64.7
Redwall Gorge	36.2 - 62.8	Mississippian limestone	67.1	17.6	94	62.5
Marble Canyon	62.8-98.2	Cambrian limestones, sandstone, shale	106.7	23.9	169	66.9
Furnace Flats	98.2-123.9	Late Precambrian shales, basalts, quartzite	118.9	24.2	125	81.8
Upper Granite Gorge	123.9-189.5	Early Precambrian schist and granite	57.9	18.1	237	68.1
The Aisles Reach	189.5-202.7	Cambrian sandstone, shale	---	14.8	39	73.2
Middle Granite Gorge	202.7-225.4	Early Precambrian schist, granite	---	18.3	83	73.6
Muav Gorge	225.4-257.4	Cambrian limestones	54.9	15.3	98	54.8
Lower Canyon Reach	257.4-344.3	Cambrian limestones, sandstone, shale	94.5	17.1	297	70.3
Lower Granite Gorge	344.3 - 386.2	Early Precambrian schist, gneiss,granite	73.2	---	---	88.1
Upper Lake Mead	386.2-448.1	Early Precambrian schist, gneiss,granite; Cambrian limestone, sandstone, shale	ca. 125	---	---	---
Total	473.1	All	85.0	19.0	ca. 1800	69.5

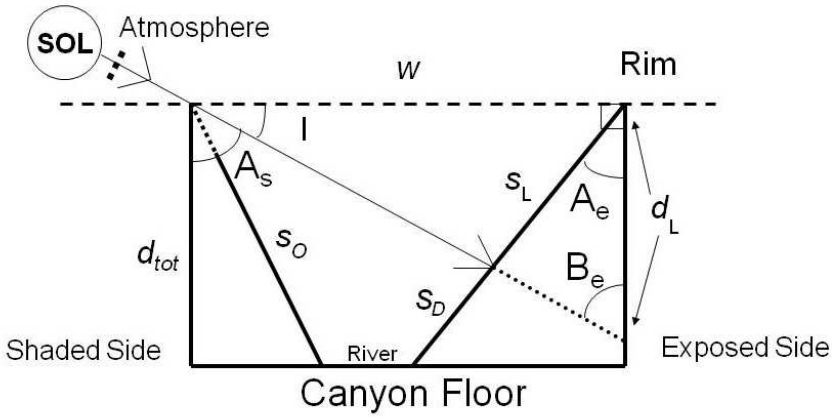
Table 2. Geomorphic reaches of the Colorado River in Grand Canyon.

Nonetheless, elevation remains an overwhelmingly important ecological state variable due to its strong negative relationship with air temperature and freeze-thaw cycle frequency, and its positive relationship to precipitation and relative humidity. The global adiabatic lapse rate is -6.49 °C/km. Analysis of paired daily minimum and maximum air temperature from 1941-2003 at Phantom Ranch (elevation 735 m) on the floor of GC with the South Rim (2100 m) produces a GC-specific lapse rate of -8.7 °C/km. The >1.3-fold steeper lapse rate in GC is likely a function not only of the dark red and black bedrock color of the inner canyon, but also to aspect. Steep, S-facing slopes in the GCE, particularly those with darker rock color, absorb and re-radiate more heat than do N-facing slopes, which often are shaded from direct sunlight, and are cooler and more humid than S-facing slopes across elevation. Overall, elevation strongly and broadly influences synoptic climate, while aspect exerts strong local control over microclimate and microsite potential evapotranspiration and therefore productivity.

3.5 Aspect and solar radiation

Solar radiation limitation is an important factor limiting ecosystem productivity of rivers and lakes (e.g., Yard et al. 2005; Karlsson et al. 2011). Depending on the latitude, depth, and cardinal orientation, LDCs also can be strongly limited by solar radiation, particularly east- or west-oriented canyons at higher latitudes (Fig. 4; Stevens et al. 1997b). During pre-dam time, the Colorado River's naturally high suspended load prevented sunlight from reaching the floor of the river (Topping et al. 2005); however, sediment retention in Lake Powell and resulting clearwater releases now allow illumination of the river floor in the upper reaches, enormously increasing benthic productivity. Yard et al (2005) measured mid-day solar radiation in the river at 25 km intervals from Glen Canyon Dam to Diamond Creek and described variation in the availability of photosynthetically active radiation (PAR) of the Colorado River aquatic domain. They reported that river surface PAR varied strongly in relation to cardinal orientation of the canyon and in relation to tributary-contributed suspended inorganic sediment load, ranging from little limitation in upstream, wide, and east-west oriented reaches to significantly reduced PAR in downstream (more turbid), narrow, north-south-oriented reaches. These results help explain the low pre-dam productivity of the pre-dam sediment-laden Colorado River, postdam stairstep decreases of benthic standing stock at the confluences of the Paria River and the LCR, and spikes in mainstream productivity at the mouths of N- or S-flowing tributary (Stevens et al. 1997b).

Yard et al. (2005) focused attention on interactions of physical solar radiation limitation on turbidity, canyon geomorphology, and aquatic productivity. To better understand potential solar radiation variation on the Colorado River floodplain in GC, I used a solar pathfinder (SPF; Solar Pathfinder 2008) to measure the percent of mean monthly potential solar radiation at riverside and at the 10-year return flood stage at each bend in the river, typically every 1-2 km between Glen Canyon Dam and Diamond Creek (Table 2). The general model for this analysis includes latitude (sun angle) and canyon configuration (width, depth, cardinal orientation), but does not account for cloud cover or atmospheric aerosol obstruction of solar radiation intensity (Fig. 4). The use of a SPF is more accurate than landscape modeling of solar reception on the river banks because the floodplain is often narrow, and minor cliff projections and large rocks strongly influence shading patterns.



Exposed Side: $s_L = [(w \sin I)/\sin(180^o-(B_e+A_e))]\sin B_e)$

$s_D = (d_{tot}/\cos A_e)-s_L$

Shaded Side: If $I > A_s$ then $s_o = d_{tot}/\cos A_s$, else $s_o = 0$

Fig. 4. A conceptual schematic of solar insolation limitation in large deep canyons. A_e- slope angle on the sun-exposed side; A_s-slope angle on the shaded side; B_e-angle of incidence on the sun-exposed side; d_L-depth of canyon on sunlit side; d_{tot}-total depth on the shaded side; I-angle of solar incidence; S_L - sunlit slope, S_D -unlit dark slope; S_O-slope length on the shaded side; w-width of the canyon. The full solar budget of a canyon is the sum of solar radiation integrated across momentary to annual time scales. This model does not illustrate or take into account atmospheric interference, which reduces the canyon's total solar energy budget.

These data demonstrate that limitation of solar radiation is substantial on the Colorado River floodplain in GC, varying by the cardinal orientation of the canyon and both local and rim cliff structure (Fig. 5). The overall average percent of potential sunlight received by the Colorado River floodplain in GC is 69.5% of that available on the rims, varying from an average low of 54.8% with virtually no direct wintertime insolation in the steep, narrow, west-flowing Muav Gorge, to 75-88.1% in the relatively wide Permian, Furnace Flats, and Lower Granite Gorge reaches. The most extreme limitations of solar limitation occur on north-facing slopes in east-west flowing segments of the canyon in the deepest portions of the Canyon. Extremely steep, narrow, deep geomorphic reaches, such as the Muav Gorge, receive no direct insolation during winter months, regardless of aspect, allowing mesic rim grasses, such as galleta-grass (*Pleuraphis* spp) to grow even on S-facing slopes. In less steep but still narrow reaches (e.g., the Aisles) galleta-grass grows only on refugial N-facing slopes, and otherwise is rare to non-existent in the lower elevations of GC.

River corridor vegetation composition varies in relation to aspect and the solar radiation budget, with greatest differences on N- versus S-facing slopes. N-facing slopes, along the river, such as those at Rkm 63-65R, 193-198L, 228-232R, and 315-318L, typically support upland and boreal Great Basin Desert plant species whose ranges are normally 600 m higher

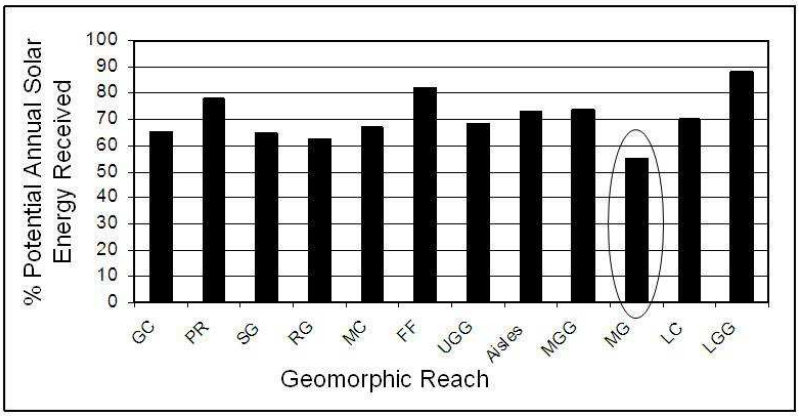


Fig. 5. Results of solar radiation budget measurements among 12 reaches on the floodplain of the Colorado River between Glen Canyon Dam and Diamond Creek in Grand Canyon. Reach abbreviations are listed in Table 2. The Muav Gorge (MG; circled) is the most deeply canyon-bound reach, receives the least solar radiation, and is a significant barrier to upriver and downriver range extensions.

in elevation, including netleaf hackberry (*Celtis laevigata* var. *reticulata),* galleta grass (*Pleuraphis* spp.), juniper (*Juniperus* spp.), buffalo berry (*Shepherdia rotundifolia*), and other perennial grasses, shrubs, and woodland taxa. In contrast and with little compositional overlap, S-facing slopes in those segments support Sonoran Desert vegetation, including several cacti taxa, brittlebush (*Encelia farinosa*), and upper riparian zone western honey mesquite (*Prosopis glandulosa* var. *torreyana*), but little desert grass cover. Analysis of the aspect of all stands of western honey mesquite and netleaf hackberry reveal strong, opposite affinity for S- and N-facing slopes, respectively. E-and W-facing slopes support a mix of N-facing slope boreal and S-facing slope desert taxa, and thus have roughly twice the species density as N- or S-facing slopes. Additional study is needed to distinguish plant compositional differences between E-facing slopes that receive early warming sunlight, from W-facing slopes, which receive hotter, late afternoon radiation. Aspect similarly influences small desert mammal composition, with N-facing slopes supporting a mixture of canyon deer mice (*Peromyscus crinitus*), woodrats *(Neotoma* spp.), and seed-feeding *Chaetodipus* spp. pocket mice, while S-facing slopes primarily support a lower diversity of weedy rodent species, dominated by western cactus deer mouse (*Peromyscus eremicus*) and less common white-tailed antelope squirrel (*Ammospermophilus leucurus*).

Elevation and aspect interactively affect solar radiation, which affects vegetation at at springs throughout the GCE. Cliff Spring near Cape Royal on the North Rim of Grand Canyon is a hanging garden (a contact spring on a cliff face; Fig. 6A). It is a high-elevation, E-facing site that receives direct insolation during winter, allowing it to thaw and warm quickly after cold winter nights. But due to the overhanging cliff, it is protected from direct insolation during the summer months. This configuration moderates the springs' summertime microclimate, allowing the highest elevation population of *Primula specuicola* wall plants to persist there. In comparison, Vaseys Paradise is a gushet spring along the Colorado River at Rkm 51R (Fig. 6B). Also E-facing, its depth in the canyon precludes direct

insolation during the winter, but its relatively warm (16°C) water and rapid warming in the morning hours, coupled with early shade, allows the endangered Kanab ambersnail (*Oxyloma haydeni kanabensis*) to persist there, one of only three naturally occurring *Oxyloma* populations in Arizona (Meretsky and Stevens 2000). More detailed modeling of elevation-aspect relationships will be productive for predicting potential climate change impacts on springs and regional vegetation.

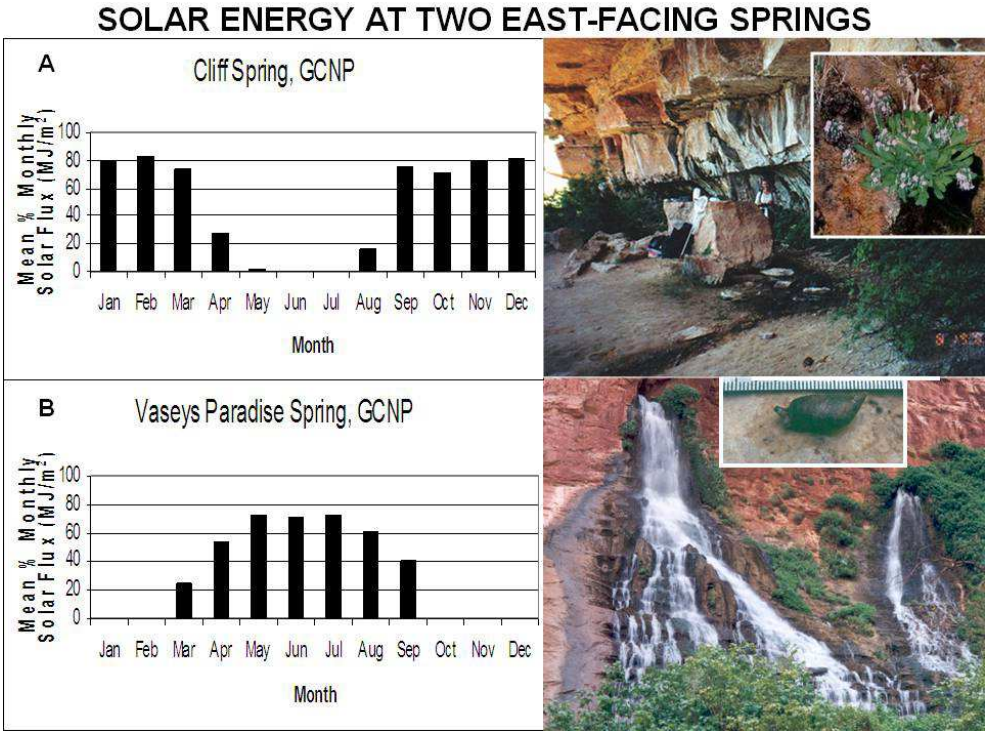


Fig. 6. Solar radiation budgets at two east-facing springs in GC: A – Cliff Spring is a hanging garden with direct insolation in winter, but is shaded by the overhanging cliff during summer, permitting persistence of a small population of *Primula specuicola* (inset); B – Vaseys Paradise is a gushet spring that received morning light throughout the year, but is shaded in early afternoon during the hot summer months, factors that allow endangered Kanab ambersnail (*Oxyloma haydeni kanabenss*; inset) to persist.

These observations, models, results, and studies demonstrate strong, pervasive, and controlling impacts of solar radiation limitation on LDC ecosystem ecology. The extent and patterns of solar radiation limitation created by cliffs in the GCE indicate that, depending on LDC width and depth, solar radiation limitations are most influential in deep E-W oriented canyons, impacts that increase with latitude and canyon depth. Solar limitation in LDCs also may exert impacts on canyon geomorphology. At the latitude of GC (35° N), N-facing slopes freeze in winter and may remain frozen for prolonged periods, while S-facing slopes generally receive direct solar radiation every day and thus undergo daily freeze-thaw cycles.

Can such aspect differences lead to faster erosion rates and cliff retreat of S-facing slopes as compared to N-facing slopes? This question has yet to be studied in detail, but may help account for the order-of-magnitude greater width of the canyon from river to rim of the S-facing North Rim of GC, as compared to that of the N-facing South Rim (Fig. 3).

4. LDC biogeography

4.1 Biodiversity

GC likely supports more than 10,000 species of (non-microbial) macrobiota, while the GCE may support 15,000 or more taxa (Table 3; estimated from Carothers and Aitchison 1976; Suttkus et al. 1978; Hoffmeister 1986; Harper et al. 1994; Busco et al. 2011; Stevens unpublished data). Plants and vertebrates have garnered most inventory attention, and recent and on-going advances in invertebrate biodiversity research are expanding understanding of the biogeographic and evolutionary significance of GC as an LDC.

Taxon	Estimated Total No. Spp in GCE	Relative Species Richness	Overall Taxon Vagility	Biogeographic Effects				References
				Corridor	Barrier	Refuge	Null	
Plants	2200	High	Low	Strong	Strong	Weak	Strong	Phillips et al. 1987
Mollusca	59	High	Low	Weak	Strong	Moderate	Weak	Spamer and Bogan 1994
Odonata	89	High	High	Strong	Weak	Weak	Strong	Stevens and Bailowitz 2009
Aquatic Hemiptera	89	High	Low	Strong	Moderate	Moderate	Moderate	Stevens and Polhemus 2008
Butterflies	140	High	High	Strong	Moderate	Moderate	Strong	Garth 1950
Tiger Beetles	44	Low	Low	Strong	Strong	Strong	Weak	Stevens and Huber 2004
Mosquitoes	18	Low	Low?	Weak	Strong	Weak	Weak	Stevens et al. 2009
Bees	500+	High	High	Strong	Strong	Strong	Strong	Stevens et al. 2007
Other Arthropoda	10000	Moderate	Variable	Strong	Strong	Moderate	Moderate	Stevens, unpublished
Fish	24	Low	High	Strong	Weak	Weak	Moderate	Minckley 1991
Herpeto-fauna	60	High	Moderate	Strong	Strong	Weak	Weak	Miller et al. 1982; Stevens 1990
Birds	340	High	High	Strong	Weak	Weak	Strong	Brown et al. 1987; LaRue et al. 2001
Mammals	104	High	Variable	Moderate	Strong	Weak	Strong	Hoffmeister 1987; Stevens 1990; Frey 2005

Table 3. Summary of selected GCE taxa, relative species richness, overall taxon vagility, biogeographical responses to GC as a LDC.

4.2 LDC landform effects

As a landform, GC influences species ranges and gene flow processes in four primary ways, each with complex subprocesses: 1) a partial or full corridor of low elevation riverine and desert habitats through the uplifted Colorado Plateau; 2) a partial or full barrier across the Plateau or in an upstream-downstream fashion; 3) a refuge, particularly for species requiring rare microhabitats, such as springs, caves, and rim edges; and 4) a null effect, not limiting gene flow across or within the landscape (Stevens and Polhemus 2008; Table 3). Below I elaborate on each of these types of landform influences using GCE biodiversity data and I discuss biogeographic anomalies in GC and the GCE.

Corridor Effects: Several biogeographic corridor functions exist in GC, including range, movement, and migration corridor effects.

Full upriver range corridor: The Colorado River corridor provides a swath of low elevation desert habitat and numerous Sonoran and Mohave Desert terrestrial biota extend their ranges upstream into the Colorado Plateau through GC, including cacti (e.g., *Echinocactus polycephalos*, various *Platyopuntia, Mammillaria*), buckwheats (e.g., *Eriogonum inflatum*), amphibians (e.g., *Bufo* spp.), reptiles (e.g., *Coleonyx variegatus*, *Sauromalus ater*), and numerous desert mammals (e.g., aquatic mammals, and *Peromyscus eremicus* cactus deer mouse, *Neotoma lepida* pack rat, *Chaetodipus intermedius* pocketmouse), and other taxa.

Partial upriver range corridor: Although also considered a partial barrier/filter effect, many species ranges extend part way up the Colorado River corridor in GC, with the Muav Gorge serving as a barrier to upstream dispersal of numerous desert plants (e.g., *Yucca whipplei* yucca, *Phoradendron californicum* mistletoe, *Larrea tridentata* creosote-bush, *Fouquieria splendens* ocotillo), invertebrates (e.g., *Brechmorhoga mendax* clubskimmer dragonfly, *Hetaerina americana* damselfy, *Abedus h. herberti* waterbug), reptiles (e.g., five *Crotalus* rattlesenake species, *Heloderma suspectum* Gila monster, *Leptotyphlops humilis* blind snake), and other taxa (Stevens and Polhemus 2008). Further upstream, the Redwall Gorge serves as a second range limit for common Sonoran Desert plant species (e.g., *Prosopis glandulosa* var. *torreyana* mesquite, *Acacia greggii* catclaw, *Encelia farinosa* brittlebush; Waring et al. in press).

Full downriver range corridor: the Colorado River also serves as a corridor for dispersal of Colorado Plateau taxa from Utah and the upper Colorado River basin downstream through GC into the lower Colorado River basin (e.g., *Corispermum americanum* nonnative goosefoot, *Salix exigua* coyote willow, and *Baccharis salicina* seep willow).

Partial downriver range corridor: Some Utah and upper Colorado River basin species ranges descend part way through GC, including: *Pariella filifolia* (Fabaceae), *Falugia paradoxa* Apache plume, *Symphoricarpos oreophilus* snowberry, *Quercus turbinella* scrub oak and *Q. gambellii* Gambel's oak, *Boehmeria cylindrica* at Rkm 55.5R Spring, *Carex specuicola*, *Oxyloma* ambersnails, and *Rana pipiens* northern leopard frog). The larger faults of Grand Canyon also provide access down from the rims, and are actively used by ungulates, terrestrial predators, humans, and passively wind-dispersing "aerial plankton".

Annual migratory corridor: Prior to impoundment the canyon served as a long-linear migratory corridor for several native fish (e.g., *Xyrauchen texanus* razorback sucker and *Ptychochelius lucius* pikeminnow; Minckley 1973, 1991) and still provides that function for numerous migratory waterbirds (Stevens et al. 1997a), and probably bats and monarch

butterflies (Garth 1950). An autumn migration route along the east side of the East Kaibab Monocline brings high densities of raptors across Grand Canyon from the north, and those birds use rising thermal air currents to ascend out of Grand Canyon on the South Rim at Lipan and Yaqui Points (Hoffman et al. 2002; Smith et al. 2008). Another hawk flyway likely exists along the Grand Wash and Hurricane Cliffs, but has not been studied.

Through-canyon movement corridor: The Colorado River provides a movement corridor for numerous aquatic species, including: 8 native fish species (4 of which have been extirpated since 1963) and 19 non-native fish species, which transport at least 17 non-native fish parasites (Minckley 1991; Choudhury et al. 2004); summer breeding waterbirds (e.g., *Anas playtrhynchos* mallard, *Ardea herodias* great blue heron); and aquatic mammals (e.g., *Castor canadensis* beaver, *Ondatra zibitheca* muskrat, and the now likely extinct *Lontra canadensis sonora* river otter; Hoffmeister 1986).

Short-term lateral migration/movement corridor: Several taxa undergo temporal movements into or out of GC. Rabe et al. (1998) documented summertime daytime roosting of spotted bat (*Euderma maculatum*) along the river in central GC, with nocturnal forays of more than 38 km/night to North Rim meadows, likely to forage on abundant coniferous forest meadow moths and beetles. On a seasonal time scale, numerous taxa move into GC from the rims in autumn and winter, including rim- and montane-dwelling taxa as diverse as *Culiseta incidens* mosquitoes, American crow and common raven (*Corvus brachyrhynchos* and *C. corax*, respectively), desert mule deer (*Odocoileus hemionus*) and mountain lion (*Puma concolor kaibabensis*; Stevens et al. 2008a; Brown et al. 1987; Stevens unpublished observations). Thus, the biogeographic corridor effect operates in numerous, complex ways, affecting a great array of taxa in this LDC.

Barrier/Filter Effects: The evolutionary consequences of GC as a barrier are well known through studies of the divided distribution of Abert's tassel-eared squirrel (*Sciurus aberti aberti*) from Kaibab squirrels (*S. a. kaibabensis*; Lamb et al. 1997). These two taxa were divided by the Pleistocene-Holocene climate transition, which eliminated suitable habitat within GC, isolating *S.a. kaibabensis* on the North Rim. The color shift between these two taxa involves a minor genetic change, and black *S.a. aberti* individuals have been reported south of GC (e.g., Allred 1995). Numerous other, but less well known examples of taxa with ranges divided by GC exist, and cryptic speciation may be commonplace. Taxa occurring north, but not south of GC include the landsnail family Oreohelicidae with the large genus *Oreohelix* (Bequaert and Miller 1973), *Satyrium behrii* hairstreak butterfly (Garth 1950), *Plestiodon skiltonianus* skink and *Pituophis catenifer deserticola* Great Basin gopher snake (Miller et al. 1982), and *Thomomys bottae planirostris* and *T. talpoides kaibabensis* pocket gophers (Hoffmeister 1986). Examples of taxa occurring on the South Rim but not the North Rim include the landsnail family Helminthoglyptidae with the large genus *Sonorella* (Bequaert and Miller 1973), *Coenomorpha tullia furcae* ringlet butterfly (Garth 1950), *Plestiodon gilberti* in Peach Springs Wash (L.E. Stevens personal observation) and *P. multivirgatus* skinks, *Pituophis catenifer affinis* Sonoran gopher snake (Miller et al. 1982), the oddly disjunct population of *Tantilla hobartsmithi* lyre snake between Lees Ferry and the LCR (Brennon and Holycross 2006), (from NE to SW) *Thomomys bottae alexandrae, T.b. aureus, T.b. fulvus, and T.b. desertorum* pocket gophers, and extirpated *Panthera onca* jaguar (Hoffmeister 1986).

The Colorado River corridor itself presents a barrier to the downstream distribution of *Phrynosoma platyrhinos* horned lizard and other species from southern Utah, and similar

upstream exclusion of common Sonoran and Mohave Desert plant species from Lake Mead, such as *Yucca brevifolia* Joshua tree and *Y. mohavensis* Mohave yucca, *Parkinsonia* spp., and *Psorothamnus spinosus* desert shrubs, which probably have been excluded by the lack of suitable low-gradient bajada habitat within the walls of GC.

Refugia: The two basins of GC generally support discrete endemic assemblages, with relatively few endemic species occurring in both. However, *Camissonia specuicola hesperia* Kaibab suncup and *Polistes kaibabensis* Kaibab paper wasp occur relatively widely through GC, and *Rosa stellata abyssa* wildrose occurs on the rims, bridging both basins.

The Eastern Basin: The eastern basin of GC supports several endemic plant species, including: *Agave phillipsiana* in Deer, Tapeats, and Phantom Creeks; *Agave utahensis* var. *kaibabensis* on calcareous or sandstone outcrops; *Euphorbia aaron-rossii* across elevation from river level in the Permian-Redwall Gorges up to 2,000 m at Cane Springs in House Rock Valley; *Argemone arizonica* in Bright Angel Creek (Arizona Rare Plants Committee 2001); *Scutellaria potosina* var. *kaibabensis* mint along the East Rim of the Kaibab uplift (Rhodes and Ayers 2010); *Cirsium rydbergii* in the Paria River gorge and downstream to Saddle Canyon; and *Silene rectiramea* in the shaded N-facing upper elevations of Red, Garden Creek, and Hermit Canyons on the south side. Endemic invertebrates in the eastern basin, include: an undescribed stonefly at Thunder River; 1-2 other new stoneflies in North Canyon; *Brechmorhoga pertinax* masked clubskimmer dragonfly; 3 *Nebria* ground beetle species; the recently described *Schinia immaculata* noctuid moth; *Cicindela hemorrhagica arizonae* tiger beetle; and *Eschatomoxys tanneri* cave darkling beetle, among others. Among the herpetofaunae, the endemic *Crotalus oregonus abyssus* Grand Canyon pink rattlesnake is virtually the only rattlesnake in the eastern basin of GC, detected thus far river to rim from Rkm 27.5 to 262 (however, a single *Crotalus viridis nuntius* Hopi western rattlesnake was photographed in Bright Angel Canyon). *C. o. abyssus* is fully replaced downstream from the Muav Gorge by at least 5 other crotalids, including: *C. atrox* western diamondback rattlesnake, *C. mitchelli* speckled rattlesnake, *C. mollosus* blacktailed rattlesnake, *C. oregonus lutosus* Great Basin rattlesnake, and *C. scutulatus* Mohave rattlesnake (Miller et al. 1982; Brennon and Holycross 2006). Lack of access through the cliff-bound Muav Gorge likely protects *C. o. abyssus* from upriver movement of these five western GC basin rattlesnake taxa into the eastern basin.

The Western Basin: Plant species endemic to the western GC basin include: *Camissonia exilis* suncup (Onagraceae) in NW Arizona and *Camissonia specuicola hesperia* in dry, gravelly washes and Colorado River sandbars; *Penstemon distans* beardtongue in Whitmore, Parashant, and Andrus Canyons; and *Astragalus lentiginosus* var. *trumbullensis* locoweed (Fabaceae) on Mt. Trumbull. Spence (2008) noted a similar pattern among endemic springs plants from Glen Canyon through Grand Canyon and into Zion Canyon. Among the endemic western basin invertebrates are the likely new waterbug *Belostoma* nr. *flumineum* in Vulcans Well Spring (289L), several cave invertebrates (see below). Among western basin herpetofaunae, Oláh-Hemmings et al. (2009) analyzed mitochondrial DNA, reporting that the highly isolated population of *Rana* near *yavapaiensis* lowland leopard frog in Surprise Canyon (Rkm 399R) is the result of a middle Pleistocene separation from the main *R. yavapaiensis* clade.

Caves: Several specific refugial habitats in GC support numerous restricted, rare, or endemic taxa. Caves are abundant in the 120-200 m-thick Redwall limestone, and evince ancient and some still-active groundwater channels. GC caves support: many of the Canyon's 22 known

bat species and their parasites; the endemic Grand Canyon cave larcid pseudoscorpion *Archeolarca cavicola* – known only from Cave of the Domes in central GC); an undescribed genus of sphaeropsocid bark louse (Psocoptera) and *Loxosceles kaiba* recluse spider, the primary prey of which are the endemic cave darkling beetles *Eschatomoxys pholitor* and *E. tanneri*. Recent exploration of GC caves by J.J. Wynn (U.S. Geological Survey, Flagstaff) and K. Voyles (U.S. Bureau of Land Management, St. George) have revealed additional new invertebrate species, including another unique spider, two new millipede species, an undescribed rhaphidophorid cave cricket genus, and at least one new coleopteran species. Although GC caves are numerous, they appear to support highly individualistic assemblages, with relatively low similarity among caves, and with endemic taxa often restricted to one or a few closely-related caves.

Springs: Springs are well known as refugial habitats in arid regions (Stevens and Meretsky 2008). In the GCE springs habitat makes up <0.001 % of the overall landscape, but springs support numerous springs-specialist plant species: at least 9.5% of the regional flora are springs-specialist taxa. Several groups of these springs-specialist plants occur in the GCE: 1) facultative springs plants, such as cardinal monkeyflower (Scrophulariaceae: *Mimulus cardinalis*) also occur in protected habitats along perennial streams. 2) obligate springs species may either be widespread across the GCE, such as *Epipactis gigantea* heleborine orchid, *Primula specuicola* cave primrose, and *Cirsium rydbergii* thistle, or 3) species very narrowly restricted to one or a few springs (e.g., Asteraceae: *Flaveria mcdougallii* ragweed along the Colorado River between Rkm 218-285; *Ranunculus uncinatus* buttercup at North Rim springs). Some plant species may be relatively common nationally, but only have been detected in GCE at springs, such as *Persicaria amphibia* water knotweed at Rkm -14.4L and *Boehmeria cylindrica* false nettle at 55.5R.

GCE springs also support rare and some endemic invertebrates, and springs assemblages are often highly individualistic. Stevens and Polhemus (2008) reported that 53% of the 89 aquatic Hemiptera taxa in the GCE were restricted to 3 or fewer of 444 localities (primarily springs) at which aquatic Hemiptera were detected. For example: *Ochterus rotundus (*Ochteridae*)* only occurred at GC springs, far outside of its range in south-central Mexico (Polhemus and Polhemus 1976). *Belostoma* nr. *flumineum* (Belostomatidae: likely a new taxon based on its year-round reproductive behavior) occurs only at Vulcans Well Spring (Rkm 289L); *Abedus breviceps* (Belostomatidae) occurs only at Boucher Spring and Creek (Rkm 154.5L); and *Abedus herberti utahensis* occurs only at a springs complex in the lower Virgin River drainage. While high levels of endemism among low-vagility Nepomorpha waterbugs might not be surprising, Stevens and Bailowitz (2009) reported a similar, although weaker pattern, among the far more dispersive Odonata of the GCE: 15 (16.9%) of Odonata species were rare and restricted to 3 or fewer localities, and 4 (4.5%) species were detected at only a single locality. Like *Ochterus rotundus*, the masked clubskimmer dragonfly occurs along several springfed desert streams, far from its range in Central America. In addition, at least one endangered fish species, *Gila cypha* humpback chub reproduce successfully only in the outflow of springs in the lower LCR, at one subaqueous springs complex on the floor of the Colorado River at Rkm 48.3, and in the lower, springfed reaches of Kanab and Havasu Creeks.

Plateau Refugia: The plateau lands around GC support numerous endemic species, some of which only occur on the rims or at upper elevations in GC, including: five *Pediocactus* (Cactaceae) taxa, of which *P. bradeyi* principally occurs at the contact between the Mesozoic

Moenkopi Formation and the underlying Kaibab Limestone, *P. paradinei* along the east side of the Kaibab Plateau, and *P. peeblesianus* var. *fickeiseniae,* which occurs more broadly across northern and northwestern Arizona between 1310-1660 m elevation. House Rock Valley and the Paria Plateau area support endemic *Sclerocactus sileri* (Cactaceae), and the Little Colorado River Platform supports *Phacelia welshii* scorpionweed, and other xeric-adapted mid-elevation plants. *Sclerocactus parviflorus* var. *intermedius* pineapple cactus occurs on the Esplanade Platform on both sides of the Canyon in both basins. *Talinum validulum* (Portulacaceae) occurs on both sides of GC in the western basin. Between elevations of 2450 and 2800 m, the uplifted North Kaibab Plateau supports several microendemic taxa, including *Castilleja kaibabensis* paintbrush, *Lesquerella kaibabensis* (Brassicaceae), *Selaginella watsonii* spikemoss, and *Cicindela terricola kaibabensis* tiger beetle in subalpine meadows. Also, *Thelypodiopsis purpussii* mustard occurs on the Esplanade of the North Rim of western GC in the Toroweap area.

Escarpment Edges: Canyon rim edges are remarkably important refugial and ecotone habitats. Rim edges are abundant throughout the GCE, with its many steep, long escarpments. Rim edges have been poorly studied, but appear to be subject to greater climatic stresses than are other habitats, sustaining more severe temperatures from subsidence of cold air during winter and higher temperatures from rising hot air from desert canyons during the summer. In addition, such habitats are subject to strong, erratic winds during all seasons. As a consequence, many of the plant species that are restricted to rims are mat- or clump-forming or otherwise sturdy, low-growing shrubs. GC species wholly restricted to these harsh rim habitats include *Astragalus cremnophylax* var. *cremnophylax* sentry milk-vetch, an endangered legume that occurs in a few small patches primarily on the South Rim (Maschinski et al. 1997; Busco et al. 2011). Numerous other rare and restricted, but non-endemic plant species occur on canyon rims and in rim open areas, including: *Phyllodoce* near *empetriformis* heather on the South Rim; *Rosa stellata* var. *abyssus*; *Penstemon pseudoputus* and *P. rydbergii* beardtongues; and *Ostrya knowletonii* hornbeam, *Paronychia sessiflora* pink, *Phacelia filiformis* scorpionweed, *Pteryxia petraea* rock wing parsley on both rims. In addition, two butterfly species also are rim-edge specialists: the canyon ringlet (Nymphalidae: *Coenomorpha tullia furcae*) on the South Rim, and the indra swallowtail (Papilionidae: *Papilio indra kaibabensis*) on the North Rim and to Cameron, Arizona.

Specific Drainages as Refugia: Specific drainages within GC and the GCE are particularly rich in rare or endemic species. a) In the overall GCE, the Virgin River, the White Mountains of Arizona, and the Verde River all support high levels of endemic and rare invertebrates and fish. b) At least 6 regionally endemic species occur in the 10 km² North Canyon on the North Rim, including: *Cimicifuga arizonica* (Ranunculaceae - Arizona bugbane), *Speyeria atlantis schellbachi* fritillary butterfly, *Nebria* n.sp. ground beetle, two undescribed species of Plecoptera, the inocellid *Negha inflata* snakefly (the only occurrence of this family, genus, and species in Arizona), and an early-translocated population of Apache trout (Salmonidae: *Oncorhynchus gilae apache*). In addition, the forest floor there supports abundant *Formica rufa* complex (Formicidae) ants, which also may be unique and are ecologically dominant (G. Alpert, Global Ant Coordinator, personal communication). c) Deer Creek (Rkm 219 R) supports 1-2 endemic *Nebria* groundbeetles and the only known population of the large spirobolid millepede *Tylobolus utahensis* in Arizona (Shelley and Stevens 2004). d) Another canyon of note is Peach Springs Wash (Rkm 363L), which supports several herpetofauna not detected elsewhere in GC, including Gila monster, desert horned lizard, zebra-tailed lizard, western Gilbert's skink, and western diamondback rattlesnake (L. Stevens unpublished

data). These taxa reflect the connection of Peach Springs Wash across the southwestern corner of the Colorado Plateau into the Basin and Range geologic province. e) At a finer spatial scale, Montezuma Well is a large travertine mound limnocrene springs pool in the Verde River basin on the edge of the Colorado Plateau. This springs complex supports the highest concentration of endemic species (8 taxa) of any point in North America to my knowledge (Blinn 2008).

Null Effects: The ranges of several widely-distributed animal taxa appear to be little affected by Grand Canyon as an LDC. Common raven (*Corvus corax*) are abundant across elevation in the summer months, sometimes retreating to the rims and extra-canyon habitats in winter. Desert bighorn rams (*Ovis canadensis nelsoni)* are wide-ranging herbivores, occasionally swimming the river, moving across elevation, and up onto the rims. Merriam and Steineger (1890) reported bighorn sheep on the top of Mt. Humphreys outside of Flagstaff, Arizona at an elevation of 3850 m, a habitat that no longer supports this species or the now-extinct native Merriam's elk (*Cervus canadensis merriami).* In contrast, bighorn ewes and young are generally restricted to much smaller home ranges within individual geologic strata in GC, where a matriarch guides the flock across access routes to known pastures and water sources, and where they respond negatively to the noise of sight-seeing helicopters (Stockwell et al. 1991; L.E. Stevens, personal observations). Numerous other flying organisms occur widely across elevation, both in and outside of GC, including: *Pantala hymenaea, Rhionaeschna multicolor*, and other large dragonflies (Stevens and Bailowitz 2009); *Aquaris remigis* water striders (Gerridae; Stevens and Polhemus 2008); *Culiseta incidens* mosquitoes (Culicidae; Stevens et al. 2008a); and numerous bird species. Large size and flight capability are not prerequisites for ubiquitous distribution in GC. *Litaneutria minor*, a diminutive ground-dwelling mantid, and side-blotched lizard (*Uta stansburiana)* are both commonly encountered across elevation on both sides of GC, as well as in extra-canyon habitats; however, microspeciation has not been investigated among non-volant, cursorial organisms.

For many species, too few detections have been made to understand landform impacts on their ranges in GC. For example, a total of three individuals of poison ivy (*Toxicodendron rydbergii*) exist, one each at three riverside springs (Vaseys Paradise, Lower Deer Creek Spring, and Mile 142L Spring). *Scolopendron viridis* giant centipedes have been detected twice in GC to my knowledge, once in the lower riparian zone at Rkm 49R on the north side of the Colorado River, and once at Grandview Point on the South Rim (Stevens unpublished data). A single specimen of the Amblypygi, *Paraphrynus* sp. was collected in GC at Rkm 219L. Additional inventory is needed to clarify the role of GC on these distributions, if any.

Biogeographic Anomalies: Several common southwestern desert taxa are conspicuously missing from the Colorado River corridor in GC, and their absence highlights otherwise difficult-to-discern LDC ecological processes. Among the missing taxa are: horned lizards (*Phrynosoma* spp.), kangaroo rats (*Dipodomys* spp.), and lagomorphs (i.e., *Sylvilagus* spp. and *Lepus* spp.). All of these taxa are common on the canyon rims and around Lakes Powell and Mead, and all but the kangaroo rats are found at Lees Ferry; however, none have been detected along the Colorado River in Grand Canyon except at the Lake Mead boundary. In the case of the lagomophs, rabbits occur on both rims, and down onto the Esplanade Platform (a high-elevation platform) on the North (but not the South) Rim, and I observed a single *Sylvilagus* on the Tonto Platform at Cottonwood Creek in November 2001, the only

individual seen by me in more than 10,000 km of trekking through the inner Grand Canyon. Predation by wall-nesting and migrating raptors likely causes extinction probability to exceed colonization potential, thus preventing lagomorph populations from becoming established in the inner GC. In the cases of horned lizards and kangaroo rats, the steepness of the surrounding terrain likely limits habitat patch suitability, and despite relatively likely downriver/downslope colonization over millennia via rafting, extinction probability is apparently too high to permit establishment.

Another biogeographic anomaly is the much-reduced presence and ecological role of termites (Isoptera) in Grand Canyon. Termites are abundant desert southwestern decomposers and provide substantial food resources to a wide array of insectivores (Ueckert et al. 1976). Their relative scarcity and small colony sizes in Grand Canyon are surprising, and few species have been detected (Jones 1985). The generally steep terrain of the canyon means that fallen wood is unstable as habitat, and driftwood piles along the river were, in pre-dam time, too commonly wetted or moved by flooding to provide suitable, long-term termite habitat. Thus, like the missing vertebrate taxa, habitat size and stability probably limit termite colonization on the floor of GC. One consequence of the absence of termites is that driftwood piles in Grand Canyon contain logs that regularly exceed 1,000 yr in age (A. McCord, University of Arizona Tree Ring Laboratory, personal communication), providing a largely overlooked wealth of paleoecological information.

Lastly, many records of highly disjunct species distributions exist in GC. For example: a single, large, isolated stand of *Canotia holocantha* cruxifixion-thorn (Celastraceae) exists in a small canyon at Rkm 196L; a single specimen of *Xantusia vigilis* was collected in the middle reaches of Clear Creek (Rkm 135R; Miller et al. 1982); the damselfly *Coenagrion resolutum* occurs in a few ponds on the North Rim (Stevens and Bailowitz 2009); the termite *Incisitermes minor* (Isoptera: Kalotermitidae) was collected at Cardenas Creek (Rkm 114L) but otherwise is known only from the Pacific Coast (Jones 1985); the Surprise Canyon relict leopard frog occurs in a highly isolated population in western GC; and numerous erratic bird records exist in GC, including a scissortail flycatcher (*Tyrannus forficatus*), a painted bunting (*Passerina ciris*) and 2 records of magnificent frigatebird (*Fregata magnificens*; Brown et al. 1987; LaRue et al. 2001). A perplexing skeleton of a collared peccary (*Pecari tajacu*) was found in middle Spring Creek (Rkm 328R; Stevens unpublished data, skull housed at the National Park Service collection at Grand Canyon). Although this species is expanding its range northward from the southern deserts, it was not previously known to occur north of the Colorado River. Each of these records represents range extension of populations considerably external to GC, primarily but not exclusively from the south. Additional basic inventory is needed to better understand such apparently enigmatic range records.

4.3 LDC biogeographic hypotheses

Six questions illuminate the extent to which GC influences the distribution and evolution of biotic assemblages. Testing these questions required three critical analyses: a) a landscape analysis of land area by elevation of the GC within the larger GCE, which was accomplished using geographic information systems (GIS) analysis of 30 m digital terrain data; b) a compilation of species richness, elevation range, and rarity data for a broad array of organisms with differing dispersal capabilities within GC and the surrounding GCE, including plants, vertebrates, and selected groups of invertebrates, work that is on-going

through the Museum of Northern Arizona in Flagstaff, Arizona; and c) biogeographic affinity information for the taxa under consideration. The latter data are now available for most vascular plants and vertebrates, but only for a few of the better-known arthropod goups.

1) Do landform corridor, barrier or refuge effects differentially influence species richness over refuge and null effects? If GC is a biogeographically significant landform, then corridor, barrier/filter, and refugial effects on species ranges should greatly predominate over null effects. Among the plants, as mentioned above, nearly 46% of the flora is found in the river corridor, demonstrating a pronounced corridor effect. Instances of refuge effects and restricted distributions of unique genomes are becoming more widely recognized (e.g., Stevens and Polhemus 2008; Bryson et al. 2010). While partial corridor effects are numerous, relatively few non-endemic plant taxa are restricted to one or the other rims, suggesting that barrier effects among plants are relatively weak (Table 3).

Among invertebrates, high resolution data on Odonata and aquatic Hemiptera revealed the following patterns. For the 58 Odonata taxa found in GC (Stevens and Bailowitz 2009):

Partial or full corridor (58.6% of species) >> Refuge (19.0%) >
Barrier/filter (13.8%) > Null (10.3%).

Assuming that null and corridor effects should prevail equally (expected values of 33.3% each), and that barrier and refuge effects might be half as important for this generally vagile taxon (expected values of 16.7% each), the hypothesis was supported ($X^2_{df=3}$ = 19.33, P = 0.0002), with 89.7% of the species ranges affected by the LDC landform though corridor, barrier, or refuge effects. Somewhat similarly, among the 54 aquatic Heteroptera taxa in GC, the following pattern was detected:

Partial or full corridor (37.0%) > Barrier/filter (27.8%) >
Null (18.5%) > Refuge (16.7%).

Thus, a total of 81.5% of GC aquatic Hemiptera demonstrated range patterns related to LDC landform configuration. Differences in the strength of landform impacts between Odonata and aquatic Hemiptera may be related to vagility, with many Odonata being more capable of long-distance dispersal. Evidence from these studies also points to a more concentrated landform impact on both of these taxa in GC as compared to the general ecotonal impacts of the Mogollon Rim (Polhemus and Polhemus 1976).

Among the GC herpetofauna, the role of partial and full corridor distributions also is dominant, as mentioned above (Table 3). Several species are widespread and occur from river to rim throughout GC (e.g., the lizards *Uta stansburiana* and *Urosaurus ornatus*). Those and other lizard taxa are found throughout the river corridor, including: *Coleonyx variegatus* gecko, *Sceloporus magister* spiny lizard, *Sauromalus ater* chuckwalla; and *Aspidoscelis tigris* whiptail (Brennon and Holycross 2006). However, many lizard and snake species ranges extend partway up the river corridor, including *Heloderma suspectum* Gila monster to Rkm 325L, *Callisaurus draconoides* zebra-tailed lizard in sand dunes at the mouth of Diamond Creek (Rkm 363L, habitat from which they were recently extirpated; Stevens 2011), and *Xantusia vigilis* night lizard. We discount the report of *H. suspectum* from Clear Creek in the eastern basin of GC (Miller et al. 1982) – that observation was likely an immature *Sauromalus*

ater. Rather few reptile species ranges extend partway down the Colorado River corridor, excepting Crotaphytidae: *Crotaphytus collaris*, which gives way to *C. bicinctores* in lower GC, and *Phrynosoma platyrhinos,* which only occurs along the Colorado River downstream to Lees Ferry, and does not occur within GC except partway down Peach Springs Wash. Similarly, *Gambelia wislizenii* occurs at Lees Ferry and in upper Diamond Creek, but not in inner corridor of GC. Another distinctive example of N-S barrier effects among the herpetofauna is the range of *Pituophis catenifer* gopher snake, with *P.c. affinis* exclusively south of the Colorado River and *P. c. deserticola* only found north of the river (Brennon and Holycross 2007).

At least 178 mammal taxa have existed in the GCE in historic times, with 128 species among 67 genera in 23 families in 7 orders (Durrant 1952, Hoffmeister 1986, Flinders et al. 2005). The GCE fauna is overwhelmingly dominated by Rodentia, with 94 taxa, followed by Carnivora with 28 taxa and Chiroptera with 24 taxa. At least 113 mammal taxa exist in or on the immediate rims of Grand Canyon, with 97 species among 59 genera in 22 families. Excluding humans, 10 mammal species are non-native. Hoffmeister (1986) lists 145 recent mammal species in Arizona, a number that has changed somewhat due to further collecting and improved taxonomy. Therefore, the GCE supports at least 88% of the state's fauna, and the GC supports two thirds of the State's fauna. Hoffmeister (1986) reported 55 widely-distributed species in the GCE, with at least 14 taxa restricted to upper elevations, five species restricted to the north of the Colorado River, and 10 species restricted to south of the river. Thus, neotropical influences on the GCE mammal fauna prevail over those of the nearctic region, a pattern similar to that of other taxa.

My review of the data on 104 mammal taxa in GC for which data are available indicates the following biogeographic pattern:

Null (34.6%) = Barrier (34.6%) > Corridor/Partial Corridor (18.3%) > Refuge (12.5%).

Thus, barrier, corridor, and refuge effects collectively dominate over null effects ($X^2_{df=1}$ = 9.846, $P < 0.002$), indicating that GC is a significant biogeographic feature for mammals. Although the landform impact on GC species ranges is overwhelmingly evident, the significance of GC as an LDC requires closer analysis of the distribution and evolution of endemic taxa (see question 6, below).

2) Does biogeographic affinity influence assemblage composition in GC? Greater-than-expected species richness of GC and the GCE in general is a partial result of topographic complexity, as well as the position of the GCE as a mixing zone during late Cenozoic time. The GC and GCE support several suites of taxa. a) A distinctive Madrean biota is comprised of Central American, Mexican, and pan-tropical plant and animal taxa whose ranges likely extended into the region during warm interglacial phases, and these taxa generally occupy lower elevations (e.g., Phillips et al. 1987; Stevens and Polhemus 2008; Stevens et al. 2008a,b). Peculiar to this group are the "Guatemalan taxa": isolated GCE populations with ranges otherwise occurring in Central and northern South America. For example, masked clubskimmer dragonfly and *Ochterus rotundus* waterbug are found at GC springs and also in Central America (Stevens and Polhemus 2008; Stevens and Bailowitz 2009). b) Boreal Rocky Mountain taxa extended their ranges southward and downslope during glacial phases and still occupy refugia at upper elevations and in mesic, north-facing habitats at lower elevations. Such taxa include the coniferous forest and Great Basin shrub plants, *Coenagrion*

resolutum damselfly, various gerrid waterstriders (Hemiptera), and other taxa. c) In addition to species with exogenous biogeographic affiliations, a large suite of broadly distributed species exists that are more-or-less centered in their ranges (e.g., *Anax junius* and *Rhionaeschna multicolor* dragonflies; *Danaus plexippus* monarch and *Vanessa cardui* painted lady butterflies; and others). d) Also, in the case of Odonata, as many as 18 (20.2%) of the 89 GCE taxa have ranges that include or are centered on the Pacific Coast of North America, an intriguing pattern suggesting that some dragonfly ranges may predate the Basin and Range orogeny. The back-and-forth and elevational adjustment of assemblages during glacial advances and retreats between climate oscillations, and the stability of refugial microhabitats within GC contribute to the relatively high biodiversity of this LDC.

3) Does elevation influence species richness in a fashion analogous to the effects of latitude? Many of the GCE faunal taxa studied thus far show the well-known latitudinal diversity gradient, a pattern of declining species richness across latitude (reviewed in Lomolino et al. 2010). Exceptions to the pattern include species, such as conifers, Salicaceae and tenthridinid sawflies, and ichneumonid wasps that are derived from boreal regions. Species richness also generally declines across elevation in a fashion analogous to latitude; however, the "mid-domain effect" of elevation on species richness commonly results in a unimodal peak of species richness at intermediate elevations (Romdal et al. 2005; review in Lomolino et al. 2010). Our work on plants (Figs. 7A, B), and macroinvertebrates (Fig. 8) demonstrate that although the mid-elevation richness peak is distinctive (e.g., among plants – Fig. 7A; aquatic Hemiptera and Odonata - Stevens and Polhemus 2008 and Stevens and Bailowitz 2009, respectively; and landsnails and non-melittid bees – Stevens unpublished data), the effect is largely accounted for by the species-area relationship: the ratio of the $\log_{10}$-transformed insect species richness to the $\log_{10}$ area of the GCE within 100 m belts revealed a strong negative response across elevation (Figs. 7B, 8). The GCE flora and fauna both consist of broad mixtures of Maderan and Rocky Mountain taxa. The 1600 m elevation zone may approximate the division between those two assemblages, and the sensitivity of composition and vegetation structural responses to climate change may warrant more focused research on that zone.

4) Does vagility influence species richness (are highly mobile taxa relatively more species rich than less mobile taxa)? I used the literature and available information to conduct a qualitative analysis of landform effects for a wide array of taxa for which biogeographic data are available from within the GC and across the GCE (Table 3). This analysis indicates that taxa with low overall vagility show stronger evidence of barrier/filter effects than those with higher vagility (e.g., strongly dispersive taxa), and the data indicate that taxa with high vagility are relatively more species rich than taxa with low vagility. While somewhat intuitive, these patterns reinforce the view that GC is an isolated, relatively young geologic feature, one still undergoing colonization and assortative assemblage development by species colonizing from the surrounding region and affecting in-canyon refugia.

5) Does species richness attenuate upstream through the Colorado River corridor? Plant distribution data in the Colorado River corridor indicate some support for this pattern. The ranges of numerous conspicuous species extend part-way up into Grand Canyon, including: *Yucca whipplei* yucca, *Fouquieria splendens* ocotillo, *Prosopis glandulosa* mesquite, *Acacia greggii* catclaw, *Ferocactus cylindrica* barrelcactus, several *Cylindropuntia* cholla cacti species, *Canotia holocantha* crucifixion-thorn, and *Larrea tridentata* creosote-bush, to name a few.

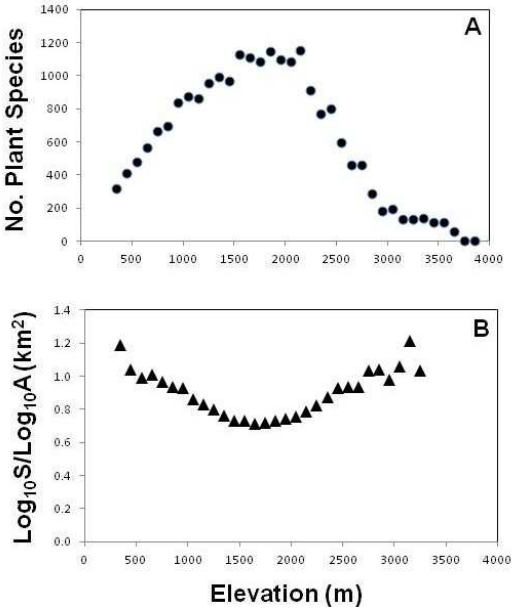


Fig. 7. Distribution of vascular plants among 100 m elevation belts in the Grand Canyon ecoregion. A – Raw plant species richness within 100 m elevation belts. B – Log_{10} plant species richness/log_{10} area (km^2) within an elevation belt, as a function of belt elevation. Modified with additional data from Stevens et al. (2007).

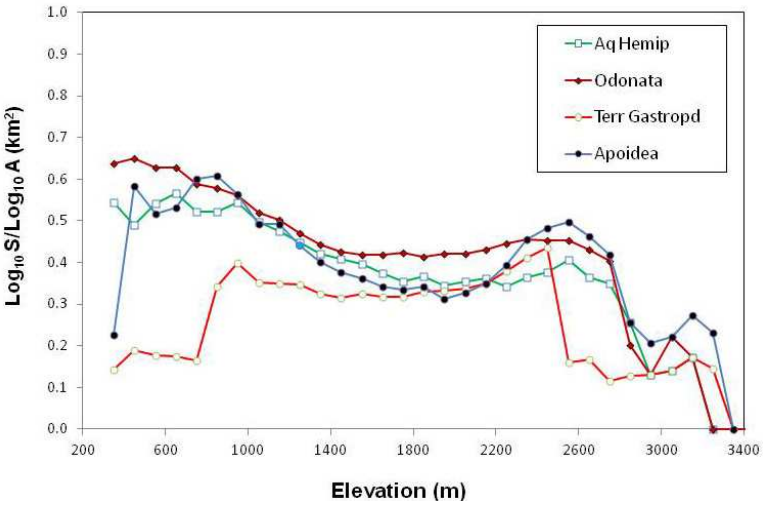


Fig. 8. Log_{10} species richness/log_{10} area (km^2) within an elevation belt, as a function of belt elevation for Grand Canyon ecoregion non-melittid bees, terrestrial gastropods, Odonata, and aquatic Hemiptera. Redrawn in part from Stevens and Polhemus (2008) and Stevens and Bailowitz (2009).

Among the insects, analysis of aquatic Hemiptera and Odonata ranges conclusively demonstrate upstream attenuation of species richness through the Colorado River corridor. Most Nepomorpha Hemiptera are found in the lower reaches of the Colorado River drainage, with only a few species of Corixidae, Notonectidae, one Gerridae, one Gelastocoridae, and two Veliidae common in the upper reaches of GC (Polhemus and Polhemus 1976; Stevens and Polhemus 2008). Even though they are generally far more vagile, Odonata diversity declines with distance upstream as well. Several provocative examples of exclusion exist: *Brechmorhoga pertinax* and *Hetaerina vulnerata* both replace widespread and common congeners in western basin of GC. These two species exist in the eastern basin of GC only along perennial springfed tributaries (Stevens and Bailowitz 2005, 2009). Whether exclusion of the more widespread Odonata congeners is the result of competitive superiority or other factors remains to be determined.

Among the herpetofauna, upstream species attenuation also is apparent, as described above (Fig. 9). Species richness on the rims is equivocal from the upper to the lower Canyon, with greater species richness on the North Rim likely attributable to the greater range of elevations there. However, both in the inner canyon and on the canyon floor, herpetofaunal species richness attenuates upstream markedly, with at least 7 taxa (24%) in the lower Canyon missing from the upper Canyon. Species-area influences may account for some of this attenuation, as the upper Canyon is narrower; however, habitat area is yet to be determined for most of these herpetofaunal taxa. Range restrictions are not clear for other terrestrial vertebrates.

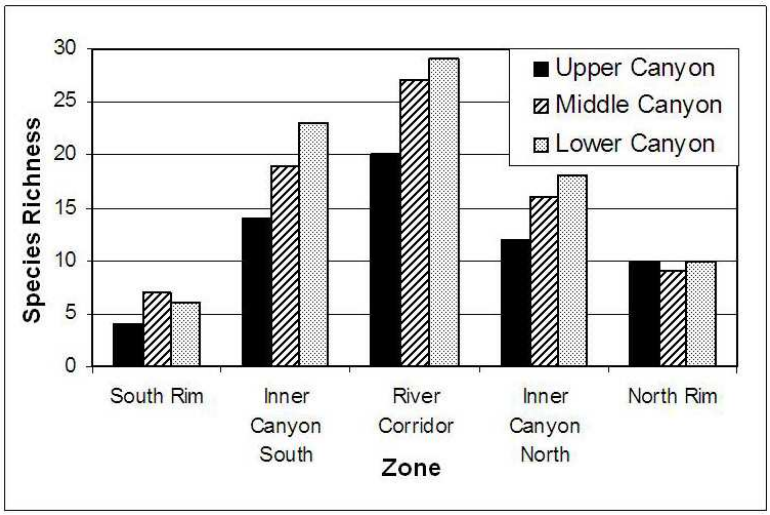


Fig. 9. Grand Canyon herpetofaunal species richness on the South Rim, the south side Inner Canyon, the Colorado River corridor, the north side Inner Canyon, and the North Rim, from the upper (eastern) to the lower (western) Grand Canyon.

6) Are levels of endemism and rarity consistent with the geologic developmental history of GC? Most endemic taxa in GC and the GCE are restricted to harsh, constant environments (e.g., high-conductivity limnocrene springs, south-facing desert slopes, rim edges, caves,

alpine habitats). Based on aquatic Hemiptera data, levels of endemism and rarity previously were regarded as being low in GC, a phenomenon attributed to the youth of GC as a landform (Polhemus and Polhemus 1976), and supported by the greater frequency of subspecific or varietal-level endemism as compared to species-level endemism. Varietal level endemics in GC are numerous, including: plants, such as *Aletes m. macdougalii*, *Arabis g. gracilipes* (found elsewhere in the GCE), and an undescribed *Arctomecon californica* variety in western GC (Phillips et al. 1987; Brian 2000; Arizona Rare Plants Committee 2001).

Numerous endemic invertebrates exist in GC and the GCE (Table 4). Many butterfly taxa that occur at lower elevations in GC appear slightly different from other populations in the Southwest, and at least 4 endemic butterfly and skipper subspecies are known from GC: *Papilio indra kaibabensis*, *Speyeria atlantis schellbachi*, *Coenomorpha tullia furcae,* and *Agathymus alliae paiute* (Garth 1950; Stevens unpublished data). Three endemic tiger beetle subspecies are known from the GCE: *Cicindela hemorrhagica arizonae* in inner GC, *C. hirticollis coloradulae in the LCR*, and *C. terricola kaibabensis* in North Rim meadows (Stevens and Huber 2004). Other varietal-level endemics include: the likely new subspecies of Vulcans Well waterbug (*Belostoma* near *flumineum*; Stevens and Polhemus 2008), Grand Canyon rattlesnake (*Crotalus oregonus abyssus)*, North Rim *Thomomys talpoides kaibabensis*, and Kaibab squirrel (Miller et al. 1982; Hoffmeister 1986).

Taxon	No. Species	% Endemic	% Rare	References
Hirundinea	~10	20	20	Stevens unpublished data
Mollusca	59	1	3.4	Baequaert & Miller, Spamer and Bogan 1994
Plecoptera	8	37.5	37.5	Stevens unpublished data
Odonata	89	1.1	5.6	Stevens and Bailowitz 2009
Orthoptera	90	2.2	----	Stevens unpublished data
Aq. Heteroptera	89	10.1	25.6	Stevens and Polhemus 2008
Tiger Beetles	44	11.9	9.5	Stevens and Huber 2004
Darkling Beetles	143	0.7	0.7	Stevens unpublished data
Butterflies and skippers	140	4.3	7.1	Garth 1950; Stevens and Bailowitz unpublished data
Trichoptera	109 (AZ)	---	---	Blinn and Ruiter 2006, 2009
Mosquitoes	18	0	72.2	Stevens et al. 2008
Chironomidae	38	10.5	10.5	Sublette et al. 1998
Total	745	9.7	19.2	All

Table 4. Percent of endemism and rarity among selected GCE invertebrate taxa. Rarity was evaluated as the percent of localities at which a species was detected in relation to the total number of localities at which members of that taxon were detected.

While early focus on these taxa suggested GC was not an evolutionarily significant landform, more collecting and observation in recent decades has revealed many more

endemic species-level taxa in GC, including several neotropical isolates (Table 4; Stevens and Huber 2004; Arizona Rare Plants Committee 2001; Stevens and Polhemus 2008; Spence 2008; Stevens and Bailowitz 2009; Utah Native Plant Society 2011). More than 150 endemic plant species exist in the GCE. Endemic plant species in GC include: plants such as *Agave phillipsiana, Camissonia specuicola* and *C. confertiflora, Argemone arizonica, Flaveria mcdougallii*, and *Silene rectiramea* (Phillips et al. 1987; Brian 2000; Arizona Rare Plants Committee 2001; Hodgson 2001); the above-mentioned cave endemic invertebrates; Kaibab monkey grasshopper - *Morsea kaibabensis*; at least four chironomid midge species (Sublette et al. 1998); Tapeats robber fly - *Efferia tapeats* (Scarbrough et al. in press); three unique *Nebria* ground beetles (D. Kavanaugh, California Academy of Sciences, personal communication); *Schinia immaculata* (Pogue 2004); Kaibab paper wasp - *Polistes kaibabensis* (Snelling 1974); and other species. While no species-level vertebrates are endemic to GC, 19.2% of 775 invertebrate species that have been studied in detail are rare and 9.7% of those species are endemic (Table 4). With at least 30 endemic faunal species in and on the periphery of GC, and with more than 200 varietal- and species-level endemic taxa in the surrounding GCE, GC is emerging as a far more important evolutionary landscape than previously recognized.

5. Discussion and conclusions

5.1 Comparison of LDCs with mountains and islands

As a LDC, GC clearly exerts a profound biogeographical influence on the ranges of biota in and around it, and increasing evidence points to the evolutionary importance of this landform. But how do LDC biogeographical processes compare with those of mountain range and island landscapes, landforms that are well known to affect species distribution and evolution (MacArthur and Wilson 1967; Brown 1971 - contested by Lawlor 1998; Lomolino et al. 2010)?

A comparison of the characteristics of these three types of landforms indicates that LDCs differ in biogeographic function from the other two types, but are somewhat more similar to mountain ranges than they are to islands or archipelagos (Table 5). The focal feature of LDCs are dendritic drainage networks, with directional, gravity-facilitated flow, sediment, nutrient, and species transport, usually in a downstream direction, but also upstream through Aeolian transport for some components. LDCs are more strongly characterized by connectivity and gravity-facilitated movement, with productivity, growing season length and species richness increasing towards the focal feature (the canyon floor). In contrast, the peaks and ridges that characterize mountain ranges are harsh, somewhat to extremely unproductive, difficult to access, with short growing seasons, and are generally inhospitable habitats. Although montane slopes may be used by wide-ranging terrestrial taxa and by migrating birds, mountain ranges appear to be considerably less likely to facilitate gene flow than are LDCs. Dispersal among islands is restrictive, often limiting an island's impact on gene flow to passive processes or to active habitat searching by highly vagile taxa. Rockfall and flooding are more dominant forms of natural disturbance in LDCs than in the other two landforms, and all three landforms provide various refugial habitats. The longevity of LDCs and islands is usually geologically shorter than that of mountain ranges, and the several to tens of millions of years that LDCs exist may not be sufficient to create as much genetic isolation.

Characteristic or Process	LDCs	Mountain Ranges	Islands
Extent of solar energy limitation	Large	Moderate	Variable
Effect of elevation on local climate	Large	Large	Variable
Role of latitude	Large	Large	Large
Productivity	Increases with depth and proximity to water	Usually decreases at upper elevations	Variable
Role of gravity	Positive	Negative	Neutral-negative
Ecological connectivity	Dendritic	Linear	Interrupted
Species Richness	Accumulative, but with upstream attenuation (GC); area and latitude dependent	Upslope attenuation; area and latitude dependent	Area, proximity to other islands, and latitude dependent
Common natural disturbances	Flooding, rockfall	Flooding, rockfall, fire, storms, volcanic activity;	Flooding, storms, volcanic activity
Trophic structure	Aerial predators (raptors) common; trophic cascades likely	Exclusion of bears, social carnivores; aerial predators (raptors) common; trophic cascades likely	Area and proximity to other islands regulates predator composition,influencing potential for trophic cascades
Role of cardinal orientation and aspect	Large	Moderate	Low
Nutrient cycling	Moderate-very long spirals	Short-long spirals	Short-long spirals
Ecosystem energetics	Allochthonous, accumulating downslope	Autochthonous-shedding upslope	Autochthonous-variable
Common anthropogenic disturbances	Hunting, grazing, damming, pollution, recreation, introduction of non-native species, climate change	Hunting, grazing, recreation, development, introduction of non-native species, climate change	Hunting, grazing, recreation, development, introduction of non-native species, climate change

Table 5. Comparison of biogeographic characteristics and roles of large, deep canyons in comparison with those of mountain ranges and islands.

Likely the largest difference between LDCs and mountain ranges is that the former are generally narrower than the latter, a difference that limits the extent of isolation on the rims and in refugia. The corridor functions of LDCs contribute to, and can facilitate, regional gene flow, and LDC aspect influences enhance in-canyon species retention and genetic diversity. In contrast, the corridor function of mountain ranges may be less significant, and vicariance effects stronger, filtering gene flow around the peidmont peripheries. The several *Ensatina* salamander taxa whose non-overlapping ranges encircle the Sierra Nevada Mountains in California is a well-known example (Pereira and Wake 2009). However, such processes also occur around LDCs. A ring clade of pocket gopher (*Thomomys bottae*) subspecies has been reported around GC (Hoffmeister 1986). Moving clockwise from Lees Ferry around GC are the non-overlapping ranges of *T.b. alexandrae, T.b. aureus, T.b. fulvus* and *T.b. desertorum* on the south side of GC, and *T.b. planirostris* and *T.b. fulvus* on the north side (Hoffmeister 1986). Whether or not such subspecific differentiation represents cryptic speciation or morphological noise (e.g., Rios and Álvarez-Casteñeda 2007) remains to be determined, but it does suggest a process similar to that of the *Ensatina* salamanders of California.

Overall, and depending on landform size and structure, LDCs can play a significant role in regional biogeography, affecting species dispersal and gene flow. LDCs play complex roles, broadly functioning as corridors, barriers, and refugia and affecting the majority of species in the landscape, and with potentially strong evolutionary consequences on regional diversity. Additional research on gene flow in and around LDCs is warranted to better understand biogeographic patterns and processes, and comparative studies are needed to compare species-area relationships among LDCs of different sizes, cardinal orientation, and latitude.

5.2 Landform development and biogeography

Badgley (2010) proposed that mammalian diversity is greatest in tectonically active landscapes, where ecotones are abundant, habitat diversity is greatest, and ecologically gradients are steepest. The biotic assemblages of the Mogollon Rim ecotone and, to some extent, GC support this hypothesis (e.g., Stevens and Polhemus 2008; Stevens and Bailowitz 2009), but not completely. In particular, her predictions 4 ("endemism…should reflect origination within the region rather than range reduction from larger areas") and 7 ("species originating in topographically complex regions should colonize adjacent lowlands more often than the reverse pattern") are not fully supported in GC, where relictual endemism prevails over adaptational radiation, and elevated species richness in refugia is more the result of colonization from surrounding biomes during favorable climate conditions. Nonetheless, the upriver attenuation of aquatic Heteroptera and Odonata taxa reported in our work suggests that species richness is related to proximity to geologic province boundaries and regional topographic diversity.

Landform evolution is evident not only in regional geology, but also through the distribution and genomes of present-day species. However, the role of past landscape change on contemporary biogeography is difficult to determine. Mitochondrial analysis of GC *Hyla arenicolor* treefrogs indicates a discrete episode of introgressive hybridization with *H. eximia* in the latest Miocene and recent or on-going hybridization with *H. wrightorum*

(Bryson et al. 2010). The timing of those introgressions may reflect initial opening of the Colorado River to the Gulf of Mexico, and post-Pleistocene faunal mixing, respectively. But many other examples of ancient landform change and contemporary biogeography are likely to exist. Is the range restriction of most GC nepomorph Hemiptera to westernmost GC the shadow of the ancient (Oligocene?) river drainage from what is now southern Nevada into Arizona and north into Utah (Stevens and Polhemus 2008)? Does the Pacific Coast affinity of at least 3, and perhaps as many as 18 dragonfly species reflect pre-Basin and Range orogenic connectivity? Why do more than twice as any neotropical/Mexican mammals reach their northern range limits at the Colorado River, as compared to boreal species (Hoffmeister 1986). Why are *Ochterus rotundus*, 8 other aquatic GCE Hemiptera, and masked clubskimmer dragonflies neotropical isolates, with ranges otherwise centered in central and southern Mexico? Further research, including distributional, autecological, and genetics analyses of these generally poorly known taxa, is needed to determine whether and at at what scale environmental changes influence present-day LDC biogeography in the GCE.

5.3 Conservation biogeography

Human impacts on the GCE have profoundly altered ecosystem structure, composition, and biogeography through three processes: habitat alteration, extirpation, and the introduction of non-native species. The Colorado River is one of the most regulated rivers in North America, with a dozen large dams and thousands of small impoundments throughout its catchment (Hirsch et al. 1990). Dams and irrigation systems have fundamentally altered flow, flood dynamics, sediment transport, water temperature and chemistry, and the distribution of riverine biota. The loss of 4 of the 8 native fish species from GC due to habitat changes and interruption of migration has been thoroughly described (Minckley 1991), but less recognized has been the impact of greatly diminished connectivity on plant colonization processes, and interruption of range among tiger beetles, herpetofauna, southwestern river otter (*Lontra canadensis Sonora*), and other river corridor biota (Stevens 2011). So to, the rims of GC have sustained significant human impacts from fire suppression and alteration of forest structure (Fulé et al. 2002), the loss of large predators through federal extermination programs (Rasmussen 1941), and the degradation of more than 90% of rim springs and natural ponds (Grand Canyon Wildlands Council, 2002).

GC is one of the world's great landscape parks, a vast wilderness, and a United Nations-designated World Heritage Site, so it comes as a surprise that rather many biota have been lost during its protection by the National Park Service (Table 6; Newmark 1995; Stevens 2011). At least 20 and perhaps as many as 29 native vertebrate taxa have been extirpated since 1919, including all large predators (i.e, *Canis lupus youngi*, *Ursus arctos*, *Panthera onca,* and the 1+ m-long native predatory Colorado pikeminnow - *Ptychocheilus lucius*) except mountain lion (*Puma concolor*) and black bear (*Ursus americanus*; Rasmussen 1941; Hoffmeister 1986). Loss of top carnivores has likely had large but poorly understood consequences on GC ecosystems (Ramussen 1941; e.g., Estes et al. 2011). The loss of other ecologically strongly interacting species, such as prairie dog (*Cynomys gunnisoni*) likewise has reduced habitat availability for numerous other species. In addition, the population status of many other species is unknown, particularly of insects and plants that have only rarely or singly been detected (Stevens 2011).

Taxon	Extirpated Taxa	At-Risk Taxa or Insufficient Data
Plants	Yerba santa	
Plants		Numerous cacti and other plants
Plants		Sentry milk-vetch *
Turbellaria		*Leucochloridium cyanocittae*
Gastropoda		Kanab ambersnail *
Arthropoda		Numerous rare, poorly known taxa
Fish	Colorado pikeminnow *	
Fish	Razorback sucker *	
Fish	Roundtail chub	
Fish	Bonytail chub	
Fish		Humpback chub *
Herpetofauna	Northern leopard frog	
Herpetofauna	Relict leopard frog	
Herpetofauna	Zebra-tailed lizard	
Avifauna	Burrowing owl	
Avifauna	California condor **	
Avifauna	Sage grouse	
Avifauna	Yellow-billed cuckoo	
Avifauna	Pileated woodpecker	
Avifauna	Southwestern willow flycatcher *	
Mammals	Prairie dog	
Mammals		Muskrat
Mammals	River otter	
Mammals		Hog-nosed skunk
Mammals	Black-footed ferret **	
Mammals	Badger	
Mammals	Jaguar	
Mammals	Gray wolf	
Mammals	Miriam elk	
Total	**21 species**	**9 taxa**

Table 6. Extirpated, endangered (*), extirpated-but-reintroduced (**), and at-risk taxa, including those for which insufficient information exists to evaluate conservation status.

The other important human impact on GC has been the introduction of numerous non-native species. At present, at least 194 non-native vascular plant species are known from GC National Park, 10.7% of the entire flora, and the same percent of non-native plants as exists in the United Kingdom (Stevens and Ayers 2002; Busco et al. 2011; Stevens unpublished data). As in Stohlgren et al. (1999), Stevens and Ayers (2002) reported that hotspots of native plant species richness, such as springs and riparian habitats, also support higher numbers of non-native species. They also documented numerous non-native fauna in GC. Among the non-native invertebrates: *Procambarus clarkii* crayfish and *Dreissena rostriformis bugensis* quagga mussel are encroaching from Lake Mead; *Potamopyrgus antipodarum* New Zealand

mudsnail is widespread in the upper Colorado River in GC; *Diorhabda* spp tamarisk leaf beetles have recently become abundant; *Anatis lecontei* is a common, predatory ladybird beetle; *Pieris rapae* cabbage white butterflies recently have been detected in GC; the large moth *Noctua pronuba* has recently invaded upper GC; and hybrid Africanized honey bees (*Apis mellifera scutellata*) are ubiquitous across elevation in GC and throughout the Southwest. Among fish, 20 coldwater and warmwater species have been introduced, threatening the remaining 4 native species, and among herpetofauna, *Apalone spinifera* softshell turtles occur in Lake Mead up to Rkm 389. Non-native birds include: rock dove (*Columbia livia*), starling (*Sturnus vulgaris*), and house sparrow (*Passer domesticus*) in GC; and chukar (*Alectoris chukar),* wild turkey, and blue grouse (*Dendragapus obscurus*) are regularly encountered on the rims. Eurasian collared dove (*Streptopelia decaocto*) were first detected in Havasu Canyon in 1994 (L. Stevens, unpublished data), and are now ubiquitous south of the South Rim in Arizona. Nonnative mammals include house mouse (*Mus musculus*) and Norway rat (*Rattus norvegicus*), Rocky Mountain elk (*Cervus elaphus nelsoni*), and feral horse (*Equus caballus*) on the South Rim, and cattle x *Bison bison* hybrids on the North Rim. Feral burro (*Equus asinus*) were widespread in GC from 1900-1982, but have been removed from the National Park. However, burros still occur on the Hualapai Reservation and on lands to the west of GC. Feral housecats (*Felis catus*) occasionally occur at Lees Ferry and on the rims.

Improved understanding of the levels of habitat alteration and loss, the extent and on-going threats of extirpation, and the role and impacts of non-native species on the region's ecosystems are essential to protect the native species, natural resources, and biogeographic processes of GC and the GCE. Notable successes have been made in the restoration of native species and natural ecological processes in the GCE, including restoration of riparian habitats at Lees Ferry, and restoration of springs habitats in northwestern Arizona by Grand Canyon Wildlands Council, Inc (www.grandcanyonwildlands.org). Protection of endangered sentry milkvetch from trampling at the South Rim has enhanced population viability (Maschinski et al. 1997). Population reintroduction/restoration successes in the GCE include: the reintroduction of formerly endangered peregrine falcons (Brown et al. 1992) and California condors (*Gymnogyps californianus*; California Condor Recovery Team 2007); on-going attempts to reintroduce black-footed ferret (*Mustela nigripes*); and protection and translocation of endangered Kanab ambersnail into an off-river springs complex in middle Royal Arch Creek (Meretsky and Stevens 2000). A robust non-native plant control program has been implemented by the National Park Service: several common exotic plant species have been eliminated in the Park, and riparian habitat restoration is being attempted. Selective removal of non-native rainbow trout (*Oncorhynchus mykiss*) may have contributed to increased population size of endangered humpback chub (*Gila cypha)* near the LCR (Coggins and Yard 2011). These examples demonstrate that focused conservation actions can be effective for protection and restoration of native species and natural ecosystems in this internationally recognized LDC.

6. Summary

Large deep canyons (LDCs) are relatively common landforms on Earth, but their regional biogeographic roles and significance has received little scientific attention. Here I summarize information on ecological gradients, species richness, and ecosystem structure on the world's best known LDC, Grand Canyon (GC) of the Colorado River in the context of

the surrounding GC ecoregion (GCE) on the southern Colorado Plateau. I first describe the extent and influences of major physical gradients in LDC biogeography affecting its biodiversity, including geomorphology, elevation, gravity, and climate. By virtue of its depth and narrowness, the inner canyon is naturally light-limited, receiving only 69.5% of ambient solar radiant energy. I then briefly review the ecology of the Colorado River ecosystem and the impacts of Glen Canyon Dam, reporting that nearly 50 yr of flow regulation has swamped geomorphic differences and limited assemblage composition in the aquatic domain, but had the opposite effect on the riparian domain. Next, I use regional biodiversity and range information on GC and GCE plants, invertebrates, and vertebrates to evaluate the biogeographic influences of GC on its biota. As a landform, GC influences species ranges and gene flow in four ways, as: 1) a partial or full range corridor of low elevation riverine and desert habitats through the uplifted Colorado Plateau; 2) a partial or full barrier across the Plateau; 3) a refuge, particularly in microhabitats like caves, springs, and escarpment rim edges; and 4) a null effect, not limiting gene flow across the landscape. Available data indicate that GC functions primarily as a corridor and barrier/filter, and also supports refugial functions, and the ranges of relatively few taxa are unaffected by GC as a landform. GC has greater species richness than expected because it is a mixing zone of: a) Maderan (Mexican and neotropical) taxa occupying lower elevations and south-facing slopes; b) boreal and upland taxa occupying higher elevations and north-facing slopes; and c) range-centered taxa occupying middle elevations. Aspect refugia likely acquire taxa during climate extremes and support those populations well into climate transitions. Strongly vagile (e.g., flying taxa like butterflies, dragonflies, birds, and bats) tend to be relatively more species rich than low-vagility taxa (e.g., non-volant taxa, such as land Mollusca and non-flying beetles). Endemism is not as low in the region as previously reported, with 9.7% endemism among 745 invertebrate species in 10 orders studied thus far. Factors limiting development of endemism include the relatively young age of the landform (5-17 million years old), climate changes, and damming of the river by volcanic eruptions during the past half million years. At least 20 and perhaps as many as 29 vertebrate taxa, including nearly all large, wide-ranging predators have been extirpated from GC and the GCE in the past century, and more than 200 non-native plant and animal taxa have been introduced into GC, substantially altering the trophic structure of GC ecosystems. As an LDC, GC exerts a profound effect on the biota within and around it, functioning differently and in a more complex fashion than do other kinds of landforms. Due in part to this complexity, the assemblages and ecological functions of GC are susceptible to numerous human alterations, even when the best conservation practices are adopted.

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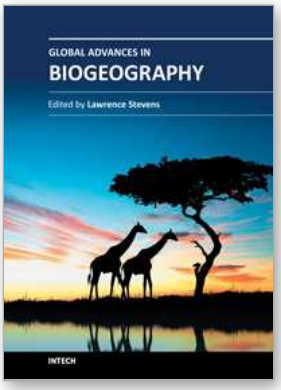

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Global Advances in Biogeography brings together the work of more than 30 scientific authorities on biogeography from around the world. The book focuses on spatial and temporal variation of biological assemblages in relation to landscape complexity and environmental change. Global Advances embraces four themes: biogeographic theory and tests of concepts, the regional biogeography of individual taxa, the biogeography of complex landscapes, and the deep-time evolutionary biogeography of macrotaxa. In addition, the book provides a trove of new information about unusual landscapes, the natural history of a wide array of poorly known plant and animal species, and global conservation issues. This book is well illustrated with numerous maps, graphics, and photographs, and contains much new basic biogeographical information that is not available elsewhere. It will serve as an invaluable reference for professionals and members of the public interested in global biogeography, evolution, taxonomy, and conservation.

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