


BIOGEOGRAPHY OF HANGING GARDENS OF THE COLORADO PLATEAU



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♦ INTRODUCTION

The lush plant growth of hanging gardens attracted the attention of early explorers, botanists, and pioneers of the Colorado Plateau, a region dominated by bare rock and xeric vegetation. Hanging gardens are small, hydrophytic, herbaceous plant communities (Malanson 1980, Welsh and Toft 1975, Tuhy and MacMahon 1988, Welsh 1989a, Heil et al. 1991) on canyon walls in the entrenched drainage system of the Colorado Plateau. The microclimate of larger hanging gardens contrasts sharply with the surrounding high desert: water is abundant, soils are moist, and canyon walls offer periodic shade.

This study was conducted to expand our current knowledge of hanging gardens with baseline data from a comparative ecological approach. Hanging gardens, in seven National Park Service units on the Colorado Plateau, were sampled for vascular plant diversity, distribution, abundance, levels of endemism, and biogeographic origin of endemic taxa. At the consumer level, insects, other arthropods, and small mammals were collected on selected hanging gardens to determine species diversity, distribution, and relative abundance.

Since the publication of MacArthur and Wilson's (1967) Theory of Island Biogeography,

many attempts have been made to use the positive correlation between island size and species richness to conserve species diversity in fragmented and natural terrestrial habitat islands (see Shafer 1990 for a review). An initial impetus for this study was the island-like appearance of hanging garden habitats. Theoretical work on the species richness-area relationship have prompted many empirical studies testing support for one of three alternate hypotheses: (1) MacArthur and Wilson's (1963, 1967) equilibrium hypothesis, (2) Williams' (1943) (and later Connor and McCoy 1979) habitat diversity hypothesis, and (3) Arrhenius' (1921) passive sampling hypothesis. This study describes the hanging-garden vascular plant species-area relationship and tests support for these alternate hypotheses.

The immigration and extinction curves that MacArthur and Wilson (1967) incorporated into their equilibrium hypothesis were recently put into a spatially structured, multispecies metapopulation model (Gotelli 1991) as an alternative to an original metapopulation model and Hanski's (1982) core-satellite species metapopulation model. Gotelli (1991) then introduced a fourth metapopulation model which incorporated both propagule rain and the rescue effect. The last model, as well as the original metapopulation model, and the equilibrium hypothesis (MacArthur and Wilson 1967) based model, predict a unimodal distribution on species-

occurrence histograms (Gotelli 1991). The core-satellite model predicts a bimodal distribution on species-occurrence histograms. This study was primarily designed to collect distribution and abundance data for hanging-garden plant and bee species as a test of the core-satellite prediction.

◆ STUDY AREA AND METHODS

Field work was conducted on hanging gardens in the following National Park Service units during the summers of 1991-1993: Arches National Park, Canyonlands National Park, Capitol Reef National Park, Dinosaur National Monument, Glen Canyon National Recreation Area, Natural Bridges National Monument, and Zion National Park. Hanging gardens sampled were chosen in consultation with NPS personnel. Work centered on the larger hanging gardens which Welsh (1984, 1989a,b), Tuhy and MacMahon (1988), and Naumann (1990) had previously surveyed for plant species.

Hanging gardens are defined by the predominance of mesophytic and hydrophytic herbaceous vegetation (Tuhy and MacMahon, 1988) growing on wet rock walls and/or wet, subirrigated colluvial soils. The abundance of water separates hanging gardens from the surrounding slickrock and xeric vegetation. Each hanging garden was visually separated into the following microhabitats: wet walls, ledges, ledge-soil complexes, and seep lines.

Vegetation was systematically sampled (Krebs 1989, Manly 1989, unpublished manuscript, L. MacDonald, personal communication) by Daubenmire (1959) frames to estimate herbaceous canopy cover by species. The total number of vascular plants species present, species richness (McIntosh 1967), was determined by visual searching (approximately one hour per garden) and systematic community sampling to collect voucher specimens from each hanging garden.

For the largest hanging gardens insects were sampled with pitfall traps, malaise traps, and general sweep netting of the vegetation. Floral visitors were also netted on each hanging garden for 1-3 hours at midday when bees were most active.

Small mammals were sampled using eight No. 11 Havahart and two larger wire mesh live traps

baited with "lab chow" pellets dotted with anise oil. Trapping periods were one site per night with four Havaharts and one larger wire mesh live trap on and off each hanging garden site. Larger sample sizes were impractical due to the small size of the habitat.

◆ RESULTS

Several sandstone aquifers provide water flow to the hanging gardens sampled in this study and in concurrent geomorphological research (May et al. 1995). Hanging gardens in Arches NP are located along geologic faults in the Entrada sandstone on Winter Camp ridge near Freshwater Canyon. Canyonlands NP hanging gardens are located up slope of the Neck Springs Trail (Island-in-the-Sky District) at the contact of the Navajo sandstone and Kayenta formation. The small, almost riparian hanging gardens in Capitol Reef NP are located along the Halls Creek Narrows in Navajo sandstone. In Dinosaur National Monument (NM), the Weber sandstone along the Yampa River Canyon has numerous small hanging gardens, while a much larger hanging garden was located in Humbug sandstone along a side canyon of Lodore Canyon. Glen Canyon NRA hanging gardens were chosen from three main areas of Lake Powell: near the mouth of the Escalante River arm, near the mouth of the San Juan River arm, and the Great Bend area of the San Juan River arm. Most of the sampled hanging gardens in Natural Bridges NM were along White Canyon in Cedar Mesa sandstone. The hanging gardens sampled in Zion NP were mainly located in the Navajo sandstone or at its contact with the Kayenta formation within Zion Canyon.

Two hundred and one vascular plant species from 56 families were identified from 84 hanging gardens. Further taxonomic work is needed on 2 additional taxa: one specimen of *Erigeron* (daisy) from Capitol Reef NP, and four specimens of *Carex* (sedge) from Dinosaur NM.

Hanging-garden vascular-plant diversity was measured in two components: species richness and community dominance. Richness ranged from a low of two at Guano Hanging Garden (HG) in Capitol Reef NP to a high of 33 at Upper Emerald HG in Zion NP with most hanging gardens ranging between 7-19 species. Species richness was significantly different among the seven parks (ANOVA $F = 7.144$, $P = 0.000$, $df = 6,77$).

Capitol Reef NP, with an average of 6 species/hanging garden, had significantly fewer species per hanging garden than Arches NP, Canyonlands NP, Dinosaur NM, Glen Canyon NRA, and Zion NP with averages of 15, 14, 16, 16, and 20 species/hanging garden respectively. Species richness in Natural Bridges NM was intermediate with an average of 10 species/hanging garden. Dominance values ranged from 0.99 to 0.20 with a mode at 0.44 - 0.47. Hanging garden dominance by a single species was negatively correlated with species richness ($r = -0.499$, 95% CI = -0.305 to -0.653, $P = 0.000$).

Bees (Superfamily Apoidea) were collected from pitfall or malaise traps or as floral visitors on 49 hanging gardens. Twenty-five species in four families (Anthophoridae, Apidae, Halictidae, and Megachilidae) have been identified. Zion NP and Glen Canyon NRA were more species rich (12 and 13 respectively) than Dinosaur NM, Canyonlands NP, Natural Bridges, and Arches NP (4, 3, 2, and 1 respectively). Within Family Apidae (7 species collected), Zion NP was the most species rich with five; but, by excluding the exotic *Apis mellifera* (honey bee), Dinosaur NM and Zion have equal *Bombus* (bumblebee) species richness. Apoid bees were more abundant on hanging gardens than off (25:1 ratio for malaise trapped specimens). The most polylectic bee species collected, *B. morrisoni* and *B. occidentalis*, were collected from five vascular plant species. *Bombus morrisoni* was the predominant bee floral visitor for the hanging-garden endemic plant *Cirsium rydbergii* (Rydberg's thistle) in Arches NP, Canyonlands NP, and Glen Canyon NRA and for *Swertia radiata* (elkweed) in Natural Bridges NM. A total of eight species of bee floral visitors was collected on both *C. rydbergii* and *Aralia racemosa* (American spikenard).

Four species of small mammals were trapped on hanging gardens: *Peromyscus crinitus* (canyon mouse), *P. maniculatus* (deer mouse), *Dipodomys ordi* (Ord's kangaroo rat), and *Neotoma lepida* (desert packrat). Small mammal trapping success did not differ between on and off garden sites (paired sample t-test, $T = 1.430$, $df = 15$, $P = 0.173$).

Most hanging gardens were less than 100 m² in size with a few of the larger ones over 1000 m². Hanging garden size differed significantly among the seven parks (ANOVA $F = 6.078$, $P = 0.000$). Similar to the pattern in species richness,

Capitol Reef NP hanging gardens were significantly smaller in size than those in Arches NP, Canyonlands NP, Dinosaur NM, Glen Canyon NRA, and Zion NP but not significantly smaller in size than those in Natural Bridges NM.

The data for hanging-garden plant species richness and size were fitted by linear regression (SYSTAT 1992) to the log form of the power function $S = cA^z$ (Preston 1960, MacArthur and Wilson 1967), with S = species richness, and A = hanging garden size. Plant species-area relationships were not significantly different among the parks. The total linear regression for the species-area relationship for all 84 hanging gardens in seven parks was $S = 3.955(A)^{0.256}$ with area explaining 44% of the variance in richness ($r^2 = 0.436$). The slope ($z = 0.256$) of the total regression line was significantly different from zero ($F = 63.472$, $P = 0.000$, $df = 1, 82$) and indicative of isolated communities (Preston 1960, 1962a, b, MacArthur and Wilson 1967).

To test the core-satellite bimodal frequency of occupation prediction (Hanski 1982), a species-occupancy histogram was constructed to show the number of sites occupied by plant species in hanging gardens of the Colorado Plateau. Most species were found on only a few sites: e.g., 71 species were found only on one hanging garden and 32 species were found on only two hanging gardens. At the other extreme, *A. capillus-veneris* (maidenhair fern) and *C. scopulorum* (Jones' reedgrass) were found in 56 and 55 hanging gardens respectively. The species-occupancy histogram fits a logarithmic series distribution ($\chi^2 = 24.277$, $df = 200$, $P = 1.000$) and did not appear to fit the bimodal prediction. The comparable apoid bee species-occupancy histogram also fits a log series distribution ($\chi^2 = 6.991$, $df = 24$, $P = 1.000$) and did not appear to be bimodal.

Of the 201 vascular plant species found on 84 hanging gardens, 12 were taxa endemic to the Colorado Plateau and seven of these were taxa endemic to hanging gardens. The level of endemism differed significantly among the seven parks. Arches NP hanging gardens were richer in hanging-garden endemics per hanging garden than the other six parks (ANOVA $F = 11.285$, $df = 6, 77$, $P = 0.000$). Significantly lower numbers of hanging-garden endemics per hanging garden were found in hanging gardens of four parks: Capitol

Reef NP, Dinosaur NM, Natural Bridges NM, and Zion NP. Canyonlands NP and Glen Canyon NRA hanging gardens were intermediate in hanging-garden endemic richness. Arches NP and Glen Canyon NRA had a higher total number of hanging garden endemics than the other parks: Arches NP and Glen Canyon NRA had five hanging-garden endemic species compared to four for Canyonlands NP, two for Dinosaur NM, Natural Bridges NM and Zion NP, and one for Capitol Reef NP.

The distribution of the endemic plant taxa indicated two distinct groups: Zion NP and the other six parks. Four of the Colorado Plateau endemics were found only in Zion NP, while the remaining eight were found only outside Zion NP. The two most widespread hanging-garden endemic taxa, *A. micrantha* (alcove columbine) and *Zigadenus vaginatus* (alcove death camas), were not found in Zion NP or Capitol Reef NP. The abundance of hanging-garden endemic taxa, estimated as the sum of hanging-garden endemic taxa canopy coverage within each hanging garden, was not significantly different among six parks (ANOVA $F = 2.201$, $df = 5, 66$, $P = 0.065$).

The abundance of plant species was estimated by canopy coverage techniques on 75 of the 84 hanging garden communities sampled. The hanging-garden endemic *A. micrantha* was abundant in the smaller hanging gardens from the northern and central parts of our study area. *Adiantum capillus-veneris* was abundant in smaller hanging gardens from the southern part of the study area. Simplified Morisita community-similarity indices, calculated from the species-level canopy coverage estimates, ranged from zero to 0.998: i.e., from no species in common to communities with almost identical species-level abundances.

A cluster analysis (SYSTAT 1992) of the similarity indices indicated five major types of hanging garden vegetation and a sixth group of low similarity hanging gardens which were not similar to each other or to the five major types. The Fern type was dominated by *A. capillus-veneris* at 52 - 99% of the canopy but occasionally associated with *A. micrantha*. Fern-columbine, the second type, had smaller amounts of *A. capillus-veneris* in the canopy at 16 - 28% and was always associated with *A. micrantha*. Hanging gardens of the Reedgrass type were dominated by *C. scopulorum* at 26 - 71% of the canopy. The fourth type, Columbine, was dominated by *A. micrantha* at 22 - 99% of the

canopy coverage. The last and most complex vegetation type was dominated by *C. rydbergii* and/or *A. capillus-veneris* with their sum at 21 - 82% of the canopy coverage. This Fern-thistle type also had *C. scopulorum* present 82% of the time. The remaining hanging-gardens plant communities were clustered into a dissimilar group since they did not fit into any of the five vegetation types.

◆ DISCUSSION

There was a negative correlation ($r = -0.499$) between plant species dominance and species richness. Upper Emerald HG at Zion NP had a dominance of 0.26, and three (out of a total of 33) species contributed approximately 25% each to the canopy coverage: *Dodecatheon pulchellum* var. *zionense* (Zion shootingstar), *Smilacina stellata* (stellate smilacina), and *Calamagrostis scopulorum* (Jones' reedgrass). Hanging gardens such as Upper Emerald, which had a relatively high number of plant species ($S = 33$) and low dominance proportions ($d = 0.26$), were judged to be more diverse than hanging gardens such as AM in Natural Bridges NM with a low number of species ($S = 5$) and high dominance proportions ($d = 0.99$). If species richness and species dominance are adequate measures of species diversity, then management efforts to conserve plant biodiversity should first be directed toward the largest hanging gardens.

Eastwood (1896) and Welsh and Toft (1975) listed boreal biogeographic affinities for four of seven plant taxa endemic to hanging gardens: *Carex haysii*¹ (Hays sedge), *Dodecatheon pulchellum* var. *zionense*² (Zion shootingstar), *Mimulus eastwoodiae* (Eastwood's monkeyflower), and *Primula specuicola* (cave primrose). Other hanging garden vegetation with boreal affinities were *A. capillus-veneris*, *E. gigantea*, *M. cardinalis*, and the Colorado Plateau endemics: *Carex curatorum* (Canyonlands sedge) and *Habenaria zothecina*³ (Alcove bog-orchid) (Eastwood 1896, Welsh and Toft 1975). With one exception, I agree with this assessment. Cronquist

¹Included in taxon *Carex curatorum* at that time

²Listed as *Dodecatheon pauciflorum* at that time

³Included in taxon *Habenaria sparsiflora* at that time

et al. (1986) and Paris (1993) indicated that *A. capillus-veneris* occurs in a band from southern California generally east to Georgia and the Carolinas; south to the West Indies, Venezuela and Peru; and in tropical to warm temperate regions of Eurasia and Africa. In addition, there are disjunct populations in British Columbia and South Dakota. Based on this evidence, we disagree with Welsh and Toft (1975) and conclude that the biogeographic affinity of this abundant, widespread hanging-garden species must lie in the subtropics or tropics not in the boreal region.

Paleo-endemic species are ancient, systematically isolated taxa whose present distribution is relict (Stebbins and Major 1965). By these criteria, taxa endemic to hanging gardens and to the Colorado Plateau cannot be part of a "relictual refugia" flora as suggested by Welsh and Toft (1975). A "refugia" hypothesis may be correctly applied to non-endemics such as the warm temperate to tropical *A. capillus-veneris*, to the prairie grasses *Panicum virgatum* (switchgrass) and *Schizachyrium scoparium* (little bluestem) and to *Toxicodendron rydbergii* (poison ivy), a woody eastern-deciduous species. Alternatively, these species may have dispersed into the hanging garden communities from their respective biomes. However, the relictual refugia hypothesis does not fit three taxa that are widespread and abundant on hanging gardens but also found in other regional habitats: (1) *C. scopulorum* in montane habitats, (2) *Carex aurea* (Golden sedge) in moist places at all elevations, and (3) *Epipactis gigantea* (helleborine orchid) in wet riparian zones at cliff bases.

Three other taxa that are widespread and abundant in hanging garden plant communities are endemic to that habitat: *A. micrantha*, *C. rydbergii*, and *Zigadenus vaginatus* (alcove deathcamas). We suggest that hanging-garden endemic taxa may be recently evolved: i.e., neoendemics (Stebbins and Major 1965). Shifting species distributions due to alternate cooling and warming periods during the Pleistocene may have provided the mechanism for allopatric speciation to occur on hanging gardens. This hanging-garden neoendemic hypothesis should be tested in future biogeographic research. In summary, hanging garden plant communities are a mix of species that are found in similar moist regional habitats, species that may be either relictual from southern or eastern biomes or have dispersed in from those biomes, and species that may have evolved in place (neoendemics).

A biogeographic analysis of the distribution of bumblebees (Apidae: *Bombus*) indicated that five of the six species collected are found in boreal and montane forest biomes. Michener et al. (1994) indicated that bumble bees (Apidae: *Bombus*) are more common in mesic temperate, and especially cool temperate, habitats but uncommon in deserts. This study supports this pattern since Apoid bees were more abundant on hanging gardens than off. Hanging-garden bumble bee populations may be relictual from the cooler climates of the late Pleistocene, or alternatively, may have dispersed into hanging gardens from regional montane areas such as the La Sal Mountains. *Bombus* distributions may provide a means to test the importance of vicariance versus dispersal on Colorado Plateau insect biogeography.

Bumblebees tend to be generalized floral feeders, but our records match only two previously documented bumblebee species-plant genus associations: *B. morrisoni* on *Cirsium* and *B. huntii* on *Dodecatheon*. Both species are widespread in the Great Basin. The floral visitation records for *B. centralis* on *Aralia*, *B. melanopygus* on *Dodecatheon*, and *B. occidentalis* on *Aquilegia*, *Aralia*, *Dodecatheon*, and *Mimulus* appear to be previously undocumented.

In contrast to bees, small mammal species abundance and composition on hanging gardens seem to be no different than in the surrounding xeric habitat, which agrees with a similar study in Canyonlands NP (J. Belnap, personal communication).

Hanging gardens, fynbos shrublands (Bond et al. 1988), and the vegetated soil-filled granite depressions studied by Houle (1990) and Uno and Collins (1987) are all habitats that have sharp boundaries between very different communities, have high *z* values, and are interpreted as virtual islands. These boundaries are as sharp as the land-water boundary for real (true oceanic) islands which tend to have insular *z* values of 0.20-0.35 (MacArthur and Wilson 1967). Brown (1984) noted that sharp community boundaries appear to be the result of rapid spatial changes in soil and water availability to plant roots. Reduced successful immigration from nearby habitats along these niche gradients leads to reduced species richness in real and virtual islands.

Several studies indicate that area tends to be the leading parameter in predicting species richness by multiple linear regression models. Multiple linear regression (MLGH model in SYSTAT 1992) for hanging garden physical data produced similar results. Area accounted for the largest variance in species richness data (44%) followed by number of microhabitats present (4%), and geographic position (X and Y UTM coordinates - 3% each). The lack of predictive power for the number of hanging-garden microhabitats present in this study tends to support MacArthur and Wilson's (1963, 1967) equilibrium hypothesis more than the habitat-diversity hypothesis (Williams 1943).

This research was in part designed as an empirical test of the core-satellite bimodal prediction, but vascular plant species-occupancy histograms are clearly not bimodal. A critical assumption of Hanski's (1982) model is homogeneity of habitat and species characteristics. Hanging garden habitats were chosen as a close approximation of habitat homogeneity, with the realization that at a sufficiently small scale all habitats are heterogeneous (Brown 1984). On the basis of Hutchinson's (1957) multidimensional niche theory, Brown (1984) criticized Hanski's (1982) homogeneity assumptions in that it is highly unlikely that similar sites are equally favorable for similar species. We agree since all 201 vascular plant species were probably not equally able to occupy the 84 hanging-garden study sites. Rigorous testing of the core-satellite hypothesis depends on the degree to which this assumption is met (Hanski 1982, Gaston and Lawton 1989). However, if Brown (1984) is correct in regard to multispecies distributions, strict adherence makes the hypothesis untestable. Since Hanski's (1982) core-satellite model prediction does not fit hanging garden plant metapopulation distribution patterns and since it is judged to be untestable, we should examine the three alternate models Gotelli (1991) presented. These models predict the unimodal metapopulation distribution pattern that we found in hanging gardens.

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