# Odonata Biogeography in the Grand Canyon Ecoregion, Southwestern USA

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**ABSTRACT** The Odonata fauna of the Grand Canyon ecoregion (GCE) on the southern Colorado Plateau includes 89 species (35 genera, seven families), including 49 Anisoptera species (25 genera, four families) and 40 Zygoptera species (10 genera, three families), and with 58 Odonata species in Grand Canyon (GC; 24 genera, seven families). Three biogeographic hypotheses account for this relatively high regional species richness: faunal affinity (origin), elevation effects on range, and landform impacts across spatial scale. The GCE Odonata assemblage is the result of mixing of taxa from adjacent Neotropical and Nearctic regions. Allochthonous taxa include 34.8% tropical (Mexican, Caribbean, Neotropical, or Pantropical) and 21.3% boreal (Nearctic or Holarctic) species. Autochthonous species (43.8%) are range-centered in North American, neither clearly Nearctic nor Neotropical, with a strong Pacific Coast influence. Area-adjusted species richness is negatively linearly related to elevation. Tropical species have lower elevation ranges than do boreal species, whereas the elevation ranges of both allochthonous groups overlap those of autochthonous species. Odonata generally overcome landform-based range constraints at coarse spatial scales, but barrier/filter and corridor effects predominate over refuge and null biogeographic effects in GC. Anisoptera and Zygoptera biogeographic patterns are similar, except that 9-fold more Zygoptera species exist in refugia in GC compared with Anisoptera. Although no GCE Odonata previously have been considered rare or at risk, 15 (16.9%) species are restricted to three or fewer localities, four (4.5%) of species have been detected at only a single locality, and four high-elevation Nearctic species may be at risk of extirpation though climate change impacts on their habitats.

**KEY WORDS** biogeography, elevation, Grand Canyon, Odonata, species richness

Contemporary biotic assemblages are derived through geologic time-scale tectonic interactions, evolutionary radiations and extinctions, and changing environmental conditions, producing a mixture of autochthonous (endogenic) and allochthonous (exogenic) taxa. As a contribution toward an all-taxon biological inventory of the southern Colorado Plateau, we present data on the species richness and distribution of Odonata in the Grand Canyon (GC) ecoregion (GCE; Fig. 1). The vegetation of this large, deep-canyon-dominated ecoregion underwent rapid and dynamic responses to Pleistocene–Holocene desertification (Martin and Klein 1984), resulting in enhanced plant species richness through the mixing of Rocky Mountain and Maderan assemblages (Axelrod 1979, Phillips et al. 1987). Stevens and Polhemus (2008) report that GCE aquatic Heteroptera also are relatively species-rich and are composed of a mixture of boreal and Neotropical allochthonous taxa. Vegetation studies indicate dynamic dispersal and radiation responses of plant species to late Pleistocene climate changes, whereas the distribution of GCE aquatic Heteroptera apparently reflects a longer (5–50 million yr [my]) response to both environmental and landform changes. Distributional analyses of GCE Odonata can help clarify gamma (regional) diversity of this generally vagile predatory taxon and also provide insight into how biogeographic affiliation and landform impacts affect contemporary species ranges.

Vagility may play a role in species richness, particularly in topographically diverse regions, because increased gene flow is likely to limit endemism. Polhemus and Polhemus (1976, 2002) report that the desert aquatic Heteroptera assemblage in GC is depauperate, containing few endemic species. Confirming that pattern, Stevens and Polhemus (2008) also report that aquatic Heteroptera species richness attenuates in an upstream direction in the Colorado River corridor through GC. Such patterns may arise from the limited vagility of some aquatic waterbug taxa and failure to colonize the geologically youthful (5–6 my) GC (Young 2001). Odonata species previously known to occupy restricted ranges in the GCE are few and include *Cordulegaster dorsalis* Hagen in Selys (Cordulegastridae), *Ophiogomphus severus* Hagen (Gomphidae; Needham et al. 2000), *Brechmorhoga pertinax* (Hagen; Libellulidae; Stevens and Bailowitz 2005), and *Argia hinei* Kennedy (Coenagrionidae;

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**Fig. 1.** Map of the Grand Canyon ecoregion in northern Arizona, southwestern Utah, and southeastern Nevada.

Bailowitz and Stevens 2008). However, the extent of range restriction and potential endemism among other Odonata, as well as the overall role of vagility in relation to biodiversity, have not been examined in the region.

GCE Odonata distribution data allow us to test three hypotheses on the biogeographic significance of a large, deep canyon system on patterns of species richness. Specifically, we examine the importance of biogeographic affinity (origin), elevation, and landform-related constraints on Odonata species ranges and richness. These baseline data constitute the first in-depth regional biogeographic analysis of GCE Odonata diversity, areography, endemism, and rarity, and they provide insight into anthropogenic threats and conservation issues in this topographically complex and entomologically poorly studied region. We report that the GCE supports a relatively robust Odonata assemblage composed of mixed affinity, and we demonstrate that large, deep canyons, such as GC, function as biogeographically significant landscape features, even for highly mobile taxa such as Odonata.

**Hypotheses.** *Hypothesis 1: Biogeographic Affinity Strongly Influences GCE Odonata Species Richness.* Given their generally great vagility, we propose that GCE Odonata species richness should be the result of mixing of autochthonous and allochthonous species, and the region should support low levels of endemism. We describe the extent to which GCE Odonata species richness is the result of biogeographic affinity to boreal (Nearctic, Holarctic, and Palearctic), tropical (Neotropical, Mexican, Carribbean, and cosmotropical), or range-centered (North American) or cosmopolitan regions. Interpretation of the impacts of affinity on species richness requires an understanding of continental distribution patterns. The biogeographic affinity of North American Odonata species is known through the works of Westfall and May (1996), Needham et al. (2000), Förster (2001), Donnelly (2003, 2004a, 2004b), Abbott (2005), Garrison et al. (2006), and the continuing efforts of the Dragonfly Society of the Americas (Abbott 2007) and the Slater Museum of Natural History (Paulson 2008). Needham et al. (2000): fig. 561, pp. 842–843) define 13 Anisoptera biomes in North America based on aerographic analyses. In their framework, northern Sonora, Mexico, and the southern halves of Arizona and New Mexico constitute the Arizonan Anisoptera bioregion. Northern Arizona (including most the GCE) is part of their Great Basin bioregion, with the southern edge of the Colorado Plateau (the Mogollon Rim) forming the boundary between the Arizona and Great Basin biore-

gions. They also define Rocky Mountain and Californian Anisoptera bioregions to the east and west, respectively. We test the extent of GCE species affiliations among those Anisoptera biomes.

*Hypothesis 2—Elevation Effects: 2a) Elevation Strongly Influences the GCE Odonata Assemblage Structure; 2b) Odonata Species Elevation Ranges Recapitulate Their Biogeographic Affinity.* Latitude and elevation generally exert analogous, inverse impacts on species richness (Jablonski et al. 2006, but see Kouki 1999), with elevation-influenced climate proffered as a proximal cause (e.g., Colwell et al. 2008). The inverse relationship between latitude and Odonata species richness is relatively well known: Garrison et al. (2006) estimate the Neotropical region supports ≈1,650 Anisoptera species among 195 genera, four-fold more than the 464 Odonata in 83 genera documented from temperate North America (Abbott 2007). The only rigorous analysis of elevation impacts on Odonata species richness known to us is that of Louton et al. (1996), who report a total of 130 Odonata species on an elevation transect from the western Peruvian Amazon lowland forest (325 m) up to Andean montane forests (2,200 m). Their data show a 55-fold decrease in species richness across elevation along that tropical transect, broadly supporting the pattern of reduced species richness with increasing elevation.

Nonintuitively, a general review of elevation impacts on species richness reveals that species richness is often greater at intermediate elevations within landscapes (Lomolino et al. 2006). Although Stevens and Polhemus (2008) report a similar finding for GCE aquatic Heteroptera, they also find that adjustment of species richness by the land area in discrete elevation belts produces the expected linear decrease in species richness across elevation. Given the similarity of latitude and elevation impacts on species richness, and as a corollary to hypothesis 1, we predict that the GCE Odonata assemblage should be strongly organized by elevation and that elevation range should reflect biogeographic affinity: tropical taxa should have lower minimum and maximum elevation ranges than those of boreal taxa.

*Hypothesis 3: Regional Landforms Should Exert Little Impact on the Odonata Assemblage across Spatial Scale, and Therefore Biogeographic Null and Corridor Range Effects Predominate over Barrier and Refuge Constraints.* Because of their relatively great vagility, the ranges of GCE Odonata should be relatively unrestricted by landforms, such as the Mogollon Rim, or by large, deep canyon systems, such as GC. Many adult Odonata are highly mobile, and we expect little evidence of landform-related range restriction across the spatial scales studied here. Polhemus and Polhemus (1976) and Stevens and Polhemus (2008) report the Mogollon Rim to be an important range boundary for aquatic and semiaquatic Heteroptera, with the northern ranges of tropical taxa and the southern range of Nearctic taxa constrained by it. Although vagile taxa are less likely to be restricted by ecotonal boundaries, this null hypothesis clearly is a straw man. The ranges of several GCE Odonata species are recognized as being restricted, as mentioned above. At a finer (subregional) spatial scale, GC is known to function as a biogeographic corridor, a barrier/filter, and a refuge for regional cicindelid tiger beetle and aquatic waterbug assemblages (Stevens and Huber 2004 and Stevens and Polhemus 2008, respectively); however, GC does not seem to affect the ranges of some species. We compare Odonata range constraint patterns at the scale of the GCE and GC, by using the latter data to describe aerographic impacts of large, deep canyons. Overall, we expect to falsify this hypothesis, but hope to clarify the extent of landform impacts on species ranges across spatial scale.

As a corollary, we also expect little evidence of refuge effects among GCE Odonata. As a function of their often great vagility, Odonata (particularly Anisoptera) are unlikely to be restricted to fine-scale refugia, and precinctive endemism among Anisoptera is rare. Stevens and Polhemus (2008) report that at least nine low-vagility Mexican-Neotropical aquatic Heteroptera species occur as isolates in GCE refugia, representing 14.6% of the overall fauna. Among the Odonata, Stevens and Bailowitz (2005) document a highly isolated population of *B. pertinax*, a Neotropical taxon found only in a few small, spring-fed perennial streams between 600- and 1,150-m elevation in eastern GC. Nonetheless, on the basis of their generally great vagility, we predict a low incidence of highly restricted or refugial ranges among GCE Odonata.

## Methods

**Study Area.** The GCE covers 144,156 km$^2$ of the southern Colorado Plateau in northern Arizona, southern Utah, and northwestern New Mexico (Fig. 1). This geomorphologically and topographically complex region ranges in elevation from 350 m on Lake Mead to 3,850 m at the summit of the San Francisco Mountains, north of Flagstaff, AZ. The climate of the region is continental and arid, with desert summertime high temperature >45°C at low elevations, and winter mountain low temperatures < −30°C. Precipitation is bimodally distributed, with winter snowfall and rain, and summer monsoonal storms (Sellers et al. 1985). The GCE is primarily managed by federal agencies, including: more than a dozen National Park units, particularly including Grand Canyon National Park; six National Forest units; the Bureau of Land Management; and eight Native America tribes. The Arizona Game and Fish Department manages small tracts of state land and several fish hatcheries in Arizona, but overall only 9.3% of the GCE is managed as state and private land.

A geologic province boundary called the Mogollon Rim forms a lengthy SE–NW escarpment that divides Arizona in half, with the Colorado Plateau section of the Rocky Mountain geologic province to the north, and the Basin and Range geologic province to the south (Fig. 1). Biogeographically, the Mogollon Rim is the northeastern boundary of the Apachian and Mohavian biotic provinces (Dice 1943, Brown 1994), and it closely parallels the Lowe–Davis line that separates

the Mexican Madrean floristic region from the Rocky Mountain floristic region (Lomolino et al. 2006). The Mogollon Rim also serves as the border between Arizonan and Great Basin Anisoptera bioregions (Needham et al. (2000); but the abruptness of that escarpment as a range barrier for often wide-ranging Odonata has not been examined previously at a fine spatial scale.

Odonata habitats in the arid GCE are numerous and varied, ranging in size from small, isolated springs and other water bodies to large rivers and lakes. The GCE is dominated by the large, deep canyons of the Colorado River and its many tributaries, including the Paria River, Little Colorado River (LCR), Kanab Creek, Havasu Creek, Diamond Creek–Peach Springs Wash, all of which are embedded in the Colorado Plateau, and Grand Wash along the plateau's southwestern boundary (Fig. 1). In addition to the Colorado River, two other large river systems head on the Colorado Plateau and transgress the Basin and Range geologic province boundary in the GCE: the southwest-flowing Virgin River in southwestern Utah and the south-flowing Verde River in central Arizona. The Black, White, Eagle, and other tributaries of the upper Gila River form the southeastern drainage boundary of the GCE. Arizona contains the nation's greatest density of springs (Stevens and Meretsky 2008). The nation's two largest reservoirs, Lake Powell and Lake Mead, overlap into the GCE, and many small reservoirs and livestock watering ponds occur across the landscape.

Embedded wholly within the southern Colorado Plateau, GC occupies $\approx$7,000 km$^2$, of which 4,850 km$^2$ lies within Grand Canyon National Park (Fig. 1). GC is formed by the 447-km-long Colorado River corridor and is naturally divided into 12 geomorphic reaches on the basis of geologic strata (Schmidt and Graf 1990, Stevens et al. 1997). Locations along the Colorado River are designated as river miles downstream from Lees Ferry. GC is naturally separated into two basins: an eastern basin, which receives flow from the Paria and Little Colorado River drainages, and the more open, western basin that connects western Grand Canyon to the Mojave and Sonoran deserts to the west and south (Billingsley and Hampton 1999). The two GC basins are separated by the 36-km-long, steep, narrow Muav Gorge between Colorado River miles 140–160, a cliff-dominated gorge that functions as a barrier to upstream or downstream dispersal of numerous southwestern plant, invertebrate, and vertebrate taxa (Miller et al. 1982, Phillips et al. 1987, Stevens and Huber 2004, Stevens and Polhemus 2008).

**Data Sources.** Collection data from >8,900 adult Odonata specimens were compiled from 505 sampling localities throughout the GCE. Field inventories were conducted during multi-year invertebrate surveys each decade from 1974 to 2007 involving numerous river trips through GC and visits to >400 springs, tanks, natural ponds, reservoirs, and other water bodies. Collection techniques included opportunistic spot sampling, white and UV light trapping, and aquatic sampling. GCE specimen data were obtained from the following collections: the American Museum of Natural History in New York City; Arizona State University in Tempe; Brigham Young University in Provo, Utah; Colorado State University in Ft. Collins; Grand Canyon National Park at Grand Canyon, AZ; the Museum of Northern Arizona (MNA) in Flagstaff; the Smithsonian Institution's National Museum of Natural History (NMNH) in Washington DC; Northern Arizona University in Flagstaff; the University of Arizona in Tucson; and the University of New Mexico (UNM) in Albuquerque, as well as the dot-map data from the Dragonfly Society of the Americas (Abbott 2007). Observational and other data in addition to our own were provided by Douglas Danforth and Sandy Upson (Arizona), and by John Spence (Glen Canyon National Recreation Area Biologist, Page, AZ). Data on the Odonata of southern Utah were, in part, derived from Nelson and Baumann (2001), and those from northwestern New Mexico were derived from Larsen (2005), NMNH, and UNM. Arizona county data were compiled from our data and those of Johnson (2003). We follow the taxonomy of Westfall and May (1996), Needham et al. (2000), Garrison et al. (2006), and Abbott (2007). Specimens collected during this study are housed in the MNA insect collection.

**Hypothesis Tests and Other Analyses.** To test the taxon affinity (hypothesis 1), we first list the Odonata fauna in the GCE and GC, and identify the biogeographic affinity of each species, using the works of La Rivers (1938), Kondratieff et al. (1994), Westfall and May (1996), Needham et al. (2000), Förster (2001), Donnelly (2003, 2004a, 2004b), Larsen (2005), Manolis (2003), Abbott (2007), and Paulson (2008). We use Needham et al. (2000): fig. 561, pp. 842–843, and their appendix, pp. 844–854) to determine the number of North American Odonata bioregions in which each GCE Anisoptera species occurs. We use state level data from Westfall and May (1996) and Abbott (2007) to relate Zygoptera distribution to the Anisoptera bioregions. We test the null hypothesis that the GCE Odonata fauna is dominated by autochthonous species using a contingency table analysis, with the assumption that domination by endogenic species means that at least 50% of the fauna should be range-centered. We also analyze the proportional distribution of species among Anisoptera bioregions (Needham et al. 2000).

To test elevation impact hypothesis 2, we use raw specimen-based data to describe the elevation range of each GCE Odonata species, assuming that a species could occur at any elevation within the range limits determined from collection locality data. To correct for species-area effects across elevation, we use a 30-m digital elevation model of the GCE in a geographic information systems analysis to determine the surface area of the GCE in 100-m elevation increments. We present a standard $\log_{10}$-transformation of Odonata species number (S) within each 100-m elevation belt in relation to the land surface area (A, square kilometers) in that belt. We divide $\log_{10}S$ by $\log_{10}A$ in each belt and subject the data to a simple linear regression to determine the strength of association of standardized species density across elevation. To evaluate

elevation effects on assemblage composition, we present Student's *t*-test results of pairwise comparisons of minimum elevations among boreal, range-centered, and tropical species, and perform similar analyses of maximum elevations for those groups, comparing pairwise results with a Bonferroni adjustment of probability (Rice 1989). We examine assemblage composition among the low (<1,200 m), medium (1,200–2,100 m), and high (>2,100 m) elevation belts by calculating pairwise Sørensen's coefficient of community from presence-absence data on the fauna detected in the three elevation belts.

To test hypothesis 3, we evaluate landform-imposed range constraints on the fauna from the coarse scale of the Southwest, to the intermediate scale of the GCE, to the finer (subregional) scale of GC. Previous biogeographic analyses suggest that the GCE functions as a barrier, a refuge, or in a null manner, and that GC adds a corridor function to that suite of landform effects (Stevens and Huber 2004, Stevens and Polhemus 2008). According to hypothesis 3, highly vagile taxa like Odonata should exhibit a majority of null and corridor effects over barrier-filter and refuge effects. We test the overall hypothesis by categorizing each GCE Odonata species range as falling into one of three landform effect categories (null, barrier, or refuge), and group each GC species range as falling into one of four canyon landform effect (null, corridor, barrier, or refuge). We rank the importance of effect by the number of species showing each pattern, and use a contingency test with two and three df for the GCE and GC, respectively. Given the precepts of this hypothesis, we predict that approximately two thirds of GCE species could reveal null range effects, whereas the remaining third may equally demonstrate barrier and refuge effects.

We use those data to compare range constraint patterns across spatial scales, predicting that the GCE and GC should exert equivalent, strong null or corridor (GC only) impacts compared with barrier-filter or refuge impacts. We use a species-specific analysis to determine range constraints at the two spatial scales. A change from a less stringent range limitation by the Mogollon Rim to a more stringent (e.g., barrier/filter effect) constraint in GC is coded as −1, whereas no change across scale is coded as 0, and range expansion outside GC is coded as +1. Our null hypothesis assumes equal probability for the number of species showing positive, neutral, or negative biogeographic changes across scale, and we test for equivalence using a contingency table test with 2 df.

We test the overall strength of origin versus landform effects on GCE Odonata species richness by comparing the proportion of species affected by each factor. Aquatic Heteroptera in the GCE show an underlying pattern of mixed biogeographic affinity, with stronger landform-climate effects (Stevens and Polhemus 2008); however, because of greater vagility among Odonata, we predict that origin and landform effects should exert roughly equivalent impacts on the fauna, contributing to increased species richness in the GCE and GC.

For conservation analyses we use specimen-based locality data to calculate the relative distributional frequency (RDF) of each Odonata species in the GCE, where data were available. RDF is calculated as the proportion of localities at which a species was detected, and ranges in value from 0 (rare/not present) to 1.0 (ubiquitous; Stevens and Polhemus 2008). For example, *Argia vivida* Hagen has been detected at 155 of 505 Odonata collection localities, resulting in an RDF of 0.307 (Table 1). RDF is biased by species detectability and ease of observation or capture, and it is a conservative estimator of rarity because it is based on the number of sites from which adult Odonata were detected, not the many other sites at which none were detected. Nonetheless, it provides a general, relative indication of rarity, information that is otherwise unavailable.

## Results and Discussion

**Diversity and Assemblage Complexity.** We report 89 GCE Odonata species in the GCE among 35 genera in seven families, including 49 species of Anisoptera among 25 genera in four families, and 40 species of Zygoptera among 10 genera in three families (Tables 1 and 2). The GCE assemblage represents 69.5% of the 128 Odonata taxa occurring in Arizona (Johnson 2003; R.A.B. and D. Danforth, personal observation), 80.2% of that in California, 62.2% of that in New Mexico, it exceeds the Odonata species richness of Nevada, and constitutes 19.2% of the fauna of North America (Westfall and May 1996; Needham et al. 2000; Donnelly 2003, 2004a, 2004b; Larsen 2005; Abbott 2007; Table 2). Although other comparably sized regions in the United States contain as many or more Odonata species than the GCE, species richness in the GCE is remarkably high for an arid region. In addition, we report 58 Odonata species in or immediately around GC, including 24 genera in seven families (Tables 1 and 2).

*Hypothesis 1: Biogeographic Affinity Strongly Influences GCE Odonata Species Richness.* The GCE Odonata fauna is slightly dominated by allochthonous taxa, with 31 species (34.8%) species having tropical (Mexican, Caribbean, Neotropical or Pantropical) affinity and 19 (21.3%) species having boreal (Nearctic or Holarctic) affinity, whereas 39 (43.8%) species are range centered in North American, neither clearly Nearctic nor Neotropical (Table 1; Fig. 2). Two species (2.2%) considered to be range-centered are globally distributed or are found broadly across the New World. In partial support of this hypothesis, 56.2% of the GCE fauna is allochthonous, a species richness that is statistically equivalent to the number of autochthonous species ($X^2_{\nu = 1} = 1.36$, $P = 0.244$), assuming that autochthonous dominance would be inferred if it was at least greater than the proportion of allochthonous taxa. Our data also reveal a distinctive influence of the Pacific Coast of North America on the GCE fauna, with three (3.4%) species derived from the West Coast, among at least 18 GCE species ranges involving the Pacific Coastal regions. Odonata are the only GCE

**Table 1. Grand Canyon region Odonata, including family, scientific name (* in GCE but not in GC), elevation range (meters), flight dates (numbers in parentheses are extreme dates, typically from southernmost, low-elevation sites), biogeographic affinity (C.A., Central America), relative distributional frequency (RDF), and the impact of GCE and GC on range: BDD, barrier, range divided by desert; BN or PBN, GCE is a complete or partial barrier or filter creating a northern range limit; BS or PBS, GCE is a complete or partial barrier or filter creating a southern range limit; C, corridor effect (GC only); N, null effect; PDC, partial downstream corridor through GC; PUC, partial upstream corridor through GC; R, refuge effect; X, not in study area**

| Family | Scientific name | Elevation range (m) | Adult flight dates | Biogeographic affinity | RFD | Biogeographic effect of GCE, GC |
|---|---|---|---|---|---|---|
| Aeshnidae | *Aeshna interrupta interna* | 1,650–2,775 | 6 June–24 Oct. | Nearctic | 0.044 | N, BDD |
| Aeshnidae | *Aeshna palmata* | 735–2,865 | 7 June–8 Oct. | Nearctic | 0.044 | N, C |
| Aeshnidae | *Aeshna persephone* | 560–2,090 | 20 June–16 Oct. | SW to N central Mexico | 0.034 | N, C |
| Aeshnidae | *Aeshna umbrosa** | No data | No dates | Nearctic | — | BS, X |
| Aeshnidae | *Anax junius* | 365–2,600 | 10 May–3 Nov. | N America | 0.097 | N, C |
| Aeshnidae | *Anax walsinghami* | 400–2,530 | 10 May–27 Oct. | SW N America to Panama | 0.038 | N, C |
| Aeshnidae | *Oplonaeschna armata* | 675–2,380 | 7 June–23 Sept. | SW to Guatemala | 0.038 | N, N |
| Aeshnidae | *Rhionaeschna multicolor* | 365–2,865 | 25 April–15 Oct. | W N America | 0.121 | N, N |
| Gomphidae | *Erpetogomphus compositus* | 375–1,830 | 10 May–23 Oct. | W N America | 0.059 | N, PUC |
| Gomphidae | *Erpetogomphus crotalinus** | No data | No date | SW U.S. and Mexico | 0.002 | BN, X |
| Gomphidae | *Erpetogomphus lampropeltis natrix* | 1,000 to ≈2,300 | 1 July–20 Sept. | SW N America to Mexico | 0.020 | PBN, PDC |
| Gomphidae | *Ophiogomphus arizonicus* | 1,500–2,500 | 15 June–8 Oct. | SW | 0.026 | PBN, PUC |
| Gomphidae | *Ophiogomphus severus montanus** | 1,600–2,800 | 28 May–26 Aug. | AZ-Chuska Mtns, UT-GSENM | 0.032 | R, X |
| Gomphidae | *Progomphus borealis* | 480–2,100 | 30 May–13 Aug. | SW N America to Mexico | 0.030 | PBN, C |
| Gomphidae | *Stylurus intricatus** | 495–1,080 | 23 June–27 Oct. | Nearctic | 0.004 | BS, X |
| Gomphidae | *Stylurus plagiatus** | 500–1,200 | 26 Oct. | W N America | 0.006 | BS, X |
| Cordulegasteridae | *Cordulegaster diadema* | 675–2,365 | 7 July–4 Nov. | SW N America to Mexico | 0.036 | N, PDC |
| Cordulegasteridae | *Cordulegaster dorsalis** | 1,750–2,750 | 15 May–1 Aug. | W Canada & U.S. | 0.022 | R, X |
| Libellulidae: Macromiinae | *Macromia magnifica** | 1,150 | 4 June–17 July | Canada-Mexico | 0.004 | BN, X |
| Libellulidae: Corduliinae | *Somatochlora semicircularis** | 2,900–3,010 | 30 June | W-NW N America | 0.004 | BS, X |
| Libellulidae: Libellulinae | *Brechmorhoga mendax* | 400–1,265 | 9 May–27 Oct. | S N America to Mexico | 0.061 | PBN, PUC |
| Libellulidae: Libellulinae | *Brechmorhoga pertinax* | 600–1,150 | 19 July–21 Oct. | Mexico-C.A. | 0.014 | R, R |
| Libellulidae: Libellulinae | *Erythemis collocata* | 425–2,285 | 10 May–9 Oct. | N America | 0.081 | N, C |
| Libellulidae: Libellulinae | *Leucorrhina borealis** | 3,050 | 15 June 2006 | N-central N America | 0.004 | BS, X |
| Libellulidae: Libellulinae | *Libellula comanche* | 365–1,525 | 3 June–8 Oct. | U.S.-Mexico | 0.020 | PBN, PUC |
| Libellulidae: Libellulinae | *Libellula croceipennis* | 460–1,390 | 17 Aug.–27 Oct. | SW U.S. to C.A. | 0.014 | PBN, PUC |
| Libellulidae: Libellulinae | *Libellula forensis* | 365–2,105 | 27 May–26 Aug. | Western U.S. into Canada | 0.026 | PBS, BDD |
| Libellulidae: Libellulinae | *Libellula luctuosa* | 365–1,935 | 12 June–27 Sept. | Canada-Mexico | 0.028 | N, PUC |
| Libellulidae: Libellulinae | *Libellula nodisticta** | 1,600–2,285 | 9 June–27 Aug. | Western U.S.-C.A., S.A. | 0.022 | N, X |
| Libellulidae: Libellulinae | *Libellula pulchella* | 555–2,130 | 3 June–17 Oct. | Canada-U.S. | 0.032 | PBS, PUC |
| Libellulidae: Libellulinae | *Libellula quadrimaculata* | 1,735–2,800 | 24 April–5 Aug. | Panboreal | 0.050 | N, BDD |
| Libellulidae: Libellulinae | *Libellula saturata* | 395–2,550 | 20 April–28 Oct. | Western U.S.-Mexico | 0.202 | N, N |
| Libellulidae: Libellulinae | *Macrodiplax balteata** | 490 | 8 July | S U.S.-Mexico-Caribbean | 0.002 | BN, X |
| Libellulidae: Libellulinae | *Orthemis ferruginea* | 400–1,800 | 8 May–30 Sept. | S U.S.-Mexico-C.A. | 0.022 | PBN, PUC |
| Libellulidae: Libellulinae | *Pachydiplax longipennis* | 365–2,105 | 24 April–9 Sept. | Canada-Mexico-Caribbean | 0.055 | N, PUC |
| Libellulidae: Libellulinae | *Palthothemis lineatipes* | 405–2,345 | 2 May–27 Oct. | SW to S America | 0.085 | PBN, PUC |
| Libellulidae: Libellulinae | *Pantala flavescens* | 490–1,780 | 14 May–11 Sept. | N America, Asia | 0.040 | N, N |
| Libellulidae: Libellulinae | *Pantala hymenaea* | 365–2,680 | 13 June–26 Sept. | Canada-Chile | 0.038 | N, N |
| Libellulidae: Libellulinae | *Perithemis intensa* | 490–1,665 | 15 July–19 Aug. | SW to central Mexico | 0.010 | PBN, C |
| Libellulidae: Libellulinae | *Plathemis lydia* | 690–2,580 | 2 June–6 Oct. | Canada-Mexico | 0.040 | N, PDC |
| Libellulidae: Libellulinae | *Plathemis subornata** | 400–2,000 | (22 April) 27 April–1 Aug; 12 June–7 July | W Canada-central N Mexico | 0.016 | N, B |
| Libellulidae: Libellulinae | *Pseudoleon superbus** | <900 | As late as 3 Oct. | SW, Mexico, C.A. | 0.002 | BN, X |
| Libellulidae: Libellulinae | *Sympetrum corruptum* | 405–2,750 | 24 Jan.–18 Dec. | Canada-Mexico-Caribbean, Asia | 0.248 | N, N |
| Libellulidae: Libellulinae | *Sympetrum danae** | 1,685–2,400 | 29 July–24 Aug. | W N America | 0.018 | R, X |
| Libellulidae: Libellulinae | *Sympetrum obtrusum** | No data | No date | W N America | 0.006 | BS, X |
| Libellulidae: Libellulinae | *Sympetrum pallipes* | 870–2,745 | 2 June–10 Oct. | Western Canada-U.S. | 0.028 | N, BDD |
| Libellulidae: Libellulinae | *Sympetrum semicinctum fasciatum* | 850–2,410 | 16 June–6 Nov. | Canada-U.S. | 0.055 | N, PDC |
| Libellulidae: Libellulinae | *Tramea lacerata* | 380–2,285 | 11 June–15 Sept. | Canada-Mexico-Caribbean | 0.038 | N, PUC |
| Libellulidae: Libellulinae | *Tramea onusta** | 525–2,285 | 1 May–31 Aug. | N. America | 0.018 | PBN, B |
| Calopterygidae | *Hetaerina americana* | 415–1,780 | (15 Feb.) 30 Mar.–6 Nov. (16 Dec.) | No America | 0.079 | N, PUC |
| Calopterygidae | *Hetaerina vulnerata* | 550–1,800 | 3 April–21 Nov. | Mexico, C.A. | 0.113 | N, R |
| Lestidae | *Archilestes grandis* | 500–2,150 | 28 May–20 Nov. | N America | 0.121 | N, C |
| Lestidae | *Lestes alacer** | 1,200–2,130 | 11 June–9 Sept. | Mexico, C.A. | 0.020 | PBN, X |
| Lestidae | *Lestes congener** | 1,525–2,225 | 11 June–8 Sept. | Nearctic | 0.028 | N, X |
| Lestidae | *Lestes disjunctus* | 2,255–2,680 | 4 July–12 Sept. | Nearctic | 0.018 | R, R |
| Lestidae | *Lestes dryas** | 1,600–3,800 | 12 June–14 Aug. | Holarctic | 0.016 | R, X |
| Coenagrionidae | *Amphiagrion abbreviatum** | 1,500–2,310 | 30 April–14 Aug. | W N America | 0.055 | N, BDD |
| Coenagrionidae | *Argia agrioides* | 365–1,150 | 29 April–26 Oct. | W Coast N America | 0.028 | PBN, PUC |
| Coenagrionidae | *Argia alberta* | 1,780–2,315 | 12 June–25 Oct. | W central U.S. | 0.018 | R, R |
| Coenagrionidae | *Argia emma** | 1,800 | 12 May–6 July | W N America | 0.004 | BS, X |
| Coenagrionidae | *Argia fumipennis violacea* * | 900–1,800 | 29 April–31 Aug. | N America | 0.016 | N, X |
| Coenagrionidae | *Argia hinei* | 390–1,630 | 29 April–15 Oct. | SW to Mexico | 0.038 | N, C |
| Coenagrionidae | *Argia immunda** | 540–2,255 | (28 Mar.) 14 June–24 Oct. (26 Oct.) | Neotropical | 0.004 | BN, X |
| Coenagrionidae | *Argia lugens* | 365–2,135 | 31 May–26 Oct. | W Coast N America | 0.105 | N, C |
| Coenagrionidae | *Argia moesta* | 365–2,105 | (21 April) 30 May–15 Nov. | N America | 0.048 | N, C |

**Table 1. Continued**

| Family | Scientific name | Elevation range (m) | Adult flight dates | Biogeographic affinity | RFD | Biogeographic effect of GCE, GC |
|---|---|---|---|---|---|---|
| Coenagrionidae | *Argia munda** | 1950–2,255 | 14 May—18 July | SW U.S. to Mexico | 0.008 | BN, X |
| Coenagrionidae | *Argia nahuana* | 425–2,195 | (28 Mar.) 6 April–15 Oct. | W Coast N America | 0.051 | N, C |
| Coenagrionidae | *Argia oenea* | 365–1,465 | 1 May–26 Oct. | Mexico, C.A. | 0.018 | PBN, PUC |
| Coenagrionidae | *Argia pallens** | 1,095–1,495 | 31 Aug.–18 Sept. | SW N America to Guatemala | 0.004 | PBN, X |
| Coenagrionidae | *Argia plana** | 400–2,600 | 27 April–18 Oct. | SW-central U.S., C.A. | 0.071 | N, BDD |
| Coenagrionidae | *Argia sedula* | 365–1,780 | (28 Mar.) 11 June–11 Sept. (26 Oct.) | N America | 0.036 | PBN, PUC |
| Coenagrionidae | *Argia tonto** | 1,000–2,135 | 15 June–31 Aug. | Mexico | 0.030 | PBN, X |
| Coenagrionidae | *Argia translata* | 410–1,675 | 27 June–20 Oct. | N America | 0.024 | PBN, R |
| Coenagrionidae | *Argia vivida* | 365–2,420 | 22 Mar.–16 Nov. | W N America | 0.307 | N, C |
| Coenagrionidae | *Coenagrion resolutum* | 2,135–2,730 | 20 June–7 July | Nearctic | 0.006 | PBS, R |
| Coenagrionidae | *Enallagma annexum* | 1,200–2,420 | 1 June–3 Sept. | Holarctic | 0.055 | N, BDD |
| Coenagrionidae | *Enallagma basidens** | 880–950 | 26 Aug. | N America | 0.004 | PBN, X |
| Coenagrionidae | *Enallagma boreale* * | 2040–2,800 | 5 May–31 Aug. | Nearctic | 0.097 | N, BDD |
| Coenagrionidae | *Enallagma carunculatum** | 910–2,700 | 25 May–17 Oct. | N America | 0.061 | N, R |
| Coenagrionidae | *Enallagma civile* | 375–1,950 | (23 Feb.) 13 May–24 Sept. | N America | 0.067 | N, C |
| Coenagrionidae | *Enallagma praevarum* | 375–2,285 | 2 May–2 Oct. | W N America, C.A. | 0.097 | N, C |
| Coenagrionidae | *Hesperagrion heterodoxum* | 800–1,830 | 13 May–23 Oct. | Mexico | 0.038 | PBS, R |
| Coenagrionidae | *Ischnura cervula** | 400–1,495 | (22 Feb.) 28 June–14 July | W N America | 0.012 | R, X |
| Coenagrionidae | *Ischnura damula* | 850–2,600 | 29 April–31 Aug. | W N America | 0.077 | N, PUC |
| Coenagrionidae | *Ischnura demorsa* | 490–2,600 | 30 April–1 Dec. | W N. America | 0.089 | N, PUC |
| Coenagrionidae | *Ischnura denticollis* | 400–1,950 | (10 Feb.) 3 April–30 Sept. | W N America, C.A. | 0.046 | N, R |
| Coenagrionidae | *Ischnura hastata* | 400–1,500 | 11 May–6 Sept. | W N America | 0.008 | PBN, PUC |
| Coenagrionidae | *Ischnura perparva* | 560–2,100 | 12 May–30 Aug. | W Canada & U.S. | 0.030 | PBN, R |
| Coenagrionidae | *Telebasis salva* | 365–1,800 | 28 March–9 Nov. | Neotropical | 0.050 | N, R |

invertebrate taxon examined thus far that demonstrate such an influence. Patterns of Zygoptera origin are generally similar to those of Anisoptera (Tables 1 and 2; Figs. 3–5).

Comparison of our data with the Anisoptera bioregions of Needham et al. (2000): fig. 561, pp. 842–843) reveals a GCE Anisoptera assemblage strongly dominated by the (Mexican-Neotropical) Arizona bioregion, with lesser, sequentially decreasing, but approximately equal proportional contributions of California, Rocky Mountain, and Great Basin bioregions (Fig. 3). Contributions to the GCE assemblage from other Anisoptera bioregions are generally minor, attenuating over distance to the bioregion. Interestingly, the GCE is delineated by Needham et al. (2000) as falling within their Great Basin bioregion, not their Arizona bioregion. At minimum, our data indicate that the southern boundary of Arizona Anisoptera bioregion boundary of Needham et al. (2000) occurs at the northern GCE boundary (in southern Utah). Conformance of Zygoptera to the Anisoptera bioregions of Needham et al. (2000) remains untested at a continental scale, but damselfly distributions within the Needham et al. (2000) Anisoptera bioregions are generally consonant with those we report for the Anisoptera (Fig. 3).

The generally great vagility of Odonata should limit endemism in the GCE. The only highly isolated populations that may warrant investigation as potentially cryptic endemics in the GCE are *B. pertinax* and *Hetaerina vulnerata* (Hagen in Selys; Calopterygidae) in Grand Canyon; and *Coenagion resolutum* (Hagen in Selys; Coenagrionidae) on the North Rim of Grand Canyon, *Ophiogomphus severus montanus*

**Table 2. Number of species and percentage of column total species (in parentheses) of Anisoptera, Zygoptera, and overall Odonata distribution in the GC and GCE in relation to that in Arizona, other southwestern states, and North America**

| Family | GC | GCE | AZ | NM | NV | CA | N. America |
|---|---|---|---|---|---|---|---|
| Petaluridae | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 1 (0.9) | 2 (0.4) |
| Aeshnidae | 7 (12.1) | 8 (9.0) | 10 (7.8) | 14 (9.8) | 8 (9.1) | 9 (8.1) | 43 (9.3) |
| Gomphidae | 3 (5.2) | 8 (9.0) | 8 (6.2) | 18 (12.6) | 11 (12.5) | 12 (10.8) | 101 (21.8) |
| Cordulegasteridae | 1 (1.7) | 2 (2.2) | 2 (1.6) | 2 (1.4) | 0 (0) | 0 (0) | 8 (1.7) |
| Libellulidae-Macromiinae | 0 (0) | 1 (1.1) | 1 (0.8) | 1 (0.7) | 0 (0) | 0 (0) | 9 (1.9) |
| Libellulidae-Corduliinae | 0 (0) | 1 (1.1) | 0 (0) | 4 (2.8) | 0 (0) | 0 (0) | 51 (11.0) |
| Libellulidae | 20 (34.5) | 29 (32.6) | 51 (40.6) | 49 (34.3) | 37 (42.0) | 48 (43.2) | 109 (23.5) |
| Calopterygidae | 2 (3.4) | 2 (2.2) | 2 (1.6) | 4 (2.8) | 2 (2.3) | 2 (1.8) | 9 (1.9) |
| Platystictidae | 0 (0) | 0 (0) | 1 (0.8) | 0 (0) | 0 (0) | 0 (0) | 1 (0.2) |
| Lestidae | 2 (3.4) | 5 (5.6) | 6 (4.7) | 9 (6.3) | 5 (5.7) | 7 (6.3) | 19 (4.1) |
| Protoneuridae | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 3 (0.6) |
| Coenagrionidae | 23 (39.7) | 33 (37.1) | 46 (35.7) | 42 (29.4) | 25 (28.4) | 32 (28.8) | 109 (23.5) |
| Total no. Anisoptera spp. | 31 (53.4) | 49 (55.1) | 72 (56.7) | 88 (61.5) | 56 (63.6) | 70 (63.1) | 323 (69.6) |
| Total no. Zygoptera spp. | 27 (46.6) | 40 (44.9) | 55 (43.3) | 55 (38.5) | 32 (36.4) | 41 (36.9) | 141 (30.4) |
| Total no. spp. | 58 | 89 | 128 | 143 | 88 | 111 | 464 |

GC and GCE data from this study; Arizona, Nevada, and California data are from Stevens and Bailowitz (2008); New Mexico data are from Larsen (2005) in part; North American data are from Abbott (2007).

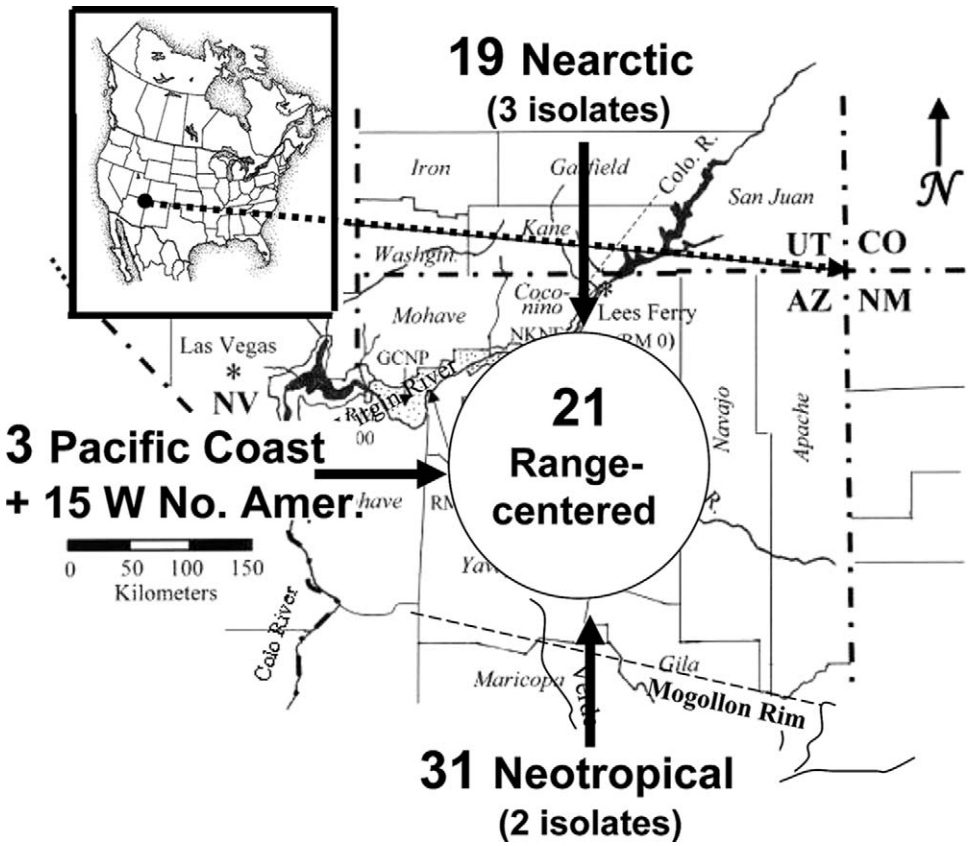


**Fig. 2.** Directional contribution of Anisoptera and Zygoptera species from surrounding biomes and from within the GCE. For example, 31 species including one isolated population are derived from the Mexico and Central America.

Selys in the Chuska Mountains of northeastern Arizona, and *C. dorsalis* in Arizona's White Mountains. However, genetic analyses of those isolated taxa remain outstanding. In total, this amounts to ≤5.6% potential Odonata endemism. Low levels of endemism are expected because vagility should ensure gene flow across the region. Other relatively vagile GCE taxa exhibit similar levels of at least subspecific endemism, including the butterflies and skippers (Lepidoptera; 3.8%; Garth 1950; L.E.S., unpublished data). Although many Lepidoptera are highly vagile, the endemic or rare taxa are closely associated with isolated host plant patches. The high levels of subspecific endemism and low species richness of GCE Cicindelidae (Coleoptera) may be related to their generally low vagility and confinement to

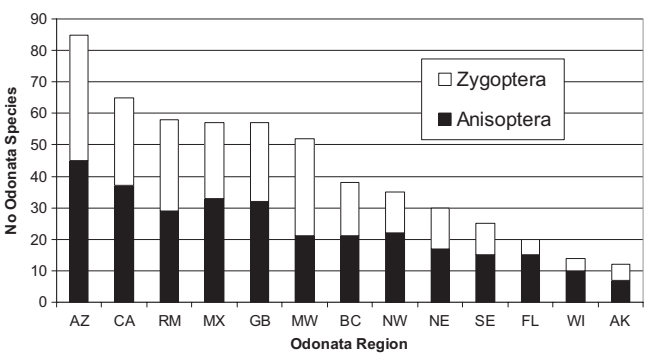


**Fig. 3.** Anisoptera and Zygoptera species richness in the GCE in relation to the Anisoptera bioregions of Needham et al. (2000). Most species are distributed in several to many biomes. Biome abbreviations follow state abbreviations, except BC, Baja California; GB, Great Basin; MW, Midwestern; MX, Mexican; NE, Northeast; NW, Pacific Northwest; and RM, Rocky Mountain.

desert riparian and some montane meadow habitats (Stevens and Huber 2004).

General support for the affinity hypothesis indicates that the relatively great species richness of the GCE Odonata assemblage is attributable to taxon mixing from adjacent biomes, with slightly more allochthonous (tropical and boreal) than autochthonous (range centered) taxa, and with a distinctive Pacific Coast influence among the endogenous taxa. With more Neotropical than Nearctic taxa, GCE Odonata affinity is similar to that of the region's vascular plants (Phillips et al. 1987), aquatic Heteroptera (Polhemus and Polhemus 1976, Stevens and Polhemus 2008), butterflies and skippers (Lepidoptera; Garth 1950; L.E.S., unpublished data), and mosquitoes (Diptera: Culicidae; Stevens et al. 2008). In contrast, Nearctic influences are stronger among the region's Salicaceae (Argus 1995), Chironomidae (Diptera; Sublette et al. 1998), Tenthrinidae (Hymenoptera; Lackner 1999), and Cicindelidae (Coleoptera; Stevens and Huber 2004). Differences in proportional affinity of allochthonous taxa may be attributable to differential responses to Quaternary climate changes (e.g., Stevens and Polhemus 2008). Overall, the GCE Odonata assemblage is the result of extraregional mixing and displays little apparent endemism, patterns that we attribute to the taxon's generally broad dispersal capability and its likely complex, but poorly understood, biogeographic history.

*Hypothesis 2—Elevation Effects: a) The GCE Odonata Assemblage Is Strongly Structured by Elevation.* As a primary landscape factor, elevation impacts on species richness are generally expected to be analogous to those of latitude, with more species found at lower elevations and latitudes. In support of this hypothesis, at least 21 (24.4%) of the 86 species for which elevation range data are available display discrete elevation ranges, whereas 50 (58.1%) of those species have moderately restricted elevation ranges (Table 1). Nonintuitively, the relationship between diversity and elevation range has been reported in many cases to be a unimodal curve, with the most species occurring at intermediate elevations (Lomolino et al. 2006). This unimodal pattern of maximum species richness at intermediate elevations is evident among the raw GCE Odonata data (Fig. 4a). This analysis reveals that approximately half of 86 GCE species occur between 750- and 2,250-m elevation (Table 1; Fig. 4a). Proportionally more Anisoptera than Zygoptera species are restricted to elevations <1,500 m. Anisoptera species richness is bimodally distributed, with a dip in richness at middle elevations (1,300–1,700 m), a zone dominated by desert cliff habitats that provide little Anisoptera habitat. In contrast, GCE Zygoptera species richness is unimodal across elevation, as the springs that emerge from desert cliffs often support damselfly species.

Land surface area varies across elevation, and therefore species–area relationships may affect the distribution of species richness across that gradient (Lomolino et al. 2006). Using GCE aquatic Heteroptera data, Stevens and Polhemus (2008) report that standardizing species richness against land area within elevation belts reveals the expected negative linear relationship. We report a similar effect for GCE Odonata: $\log_{10}$-transformed species richness divided by the $\log_{10}$ land surface area in each 100 m elevation belt from 350 to 3,850 m declines in a generally monotonic fashion when plotted against elevation for all Odonata together ($R^2 > 0.85$, $P < 0.0001$; Fig. 4b). The mid-elevation dip may be the result of cliff dominance that poorly supports Anisoptera. This analysis assumes that Odonata habitat area is related to overall land area within elevation belts; however, testing that assumption is beyond the scope of this study.

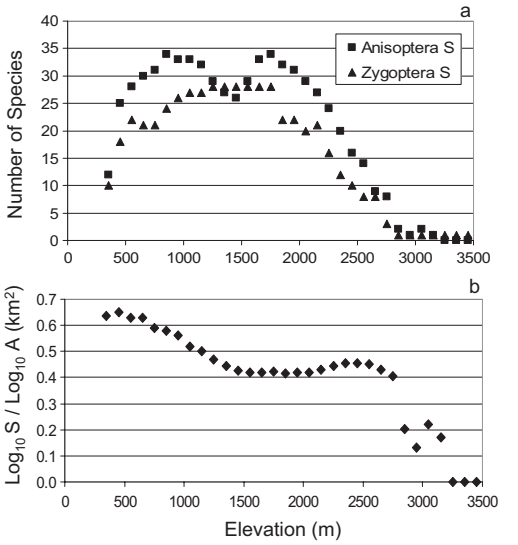


**Fig. 4.** (a) Raw area-unadjusted Anisoptera and Zygoptera species richness in 100-m elevation belts across the GCE. (b) $\text{Log}_{10}$-transformed species richness (S)/$\log_{10}$ belt area (A; square kilometers) in 100-m elevation belts across the GCE (linear regression line, $R^2 = 0.847$).

Elevation influences climate, which governs many aspects of invertebrate life history and phenology. Likely in relation to elevationally based climate differences, the first appearance of Odonata species in the GCE generally lags at least a month behind that in southern Arizona. Similarly, the duration of activity in southern Arizona usually extends at least a month later than that in the GCE. The exceptions to this pattern are Odonata (especially Zygoptera) associated with warm-stenothermal springs, which have more generations or other phonological traits that are at least partially decoupled from climate [e.g., *Telebasis salva* (Hagen) in Montezuma Well, Blinn 2008]. Although not specifically studied here, we observed that the first date of detection for widespread GCE species similarly was at least a month before that at upper elevations; however, aeshnids, larger libellulids, and other widespread taxa may begin moving upslope promptly after emergence, a behavior that obfuscates understanding of elevation-based life history phenology.

We also predict that Odonata assemblage similarity should vary across elevation, with tropical taxa at low

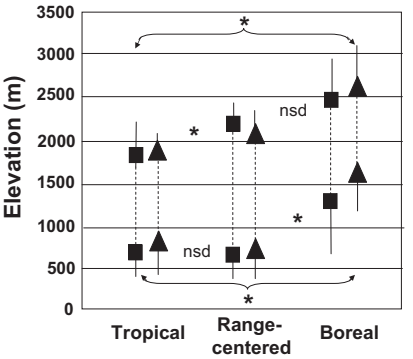


**Fig. 5.** Average minimum and maximum and 95% confidence intervals of elevation ranges of tropical and Mexican, range-centered, and boreal Anisoptera (filled squares) and Zygoptera (filled triangles) in the GCE. Asterisks indicate significant differences in elevation ranges of all Odonata species pooled within affinity groups after Bonferroni adjustment ($P$ values <0.05).

elevations and a rather different assemblage at boreal elevations. Analysis of Sørensen's coefficient of community ($CC_S$) similarity among low- (<1,200 m), medium- (1,200–2,100), and high (>2,100)-elevation assemblages reveals highest similarity between low and medium elevation assemblages ($CC_S$ = 78.3%), slightly lower similarity between medium and high elevations ($CC_S$ = 76.8%), and far lower similarity between low- and high-elevation assemblages ($CC_S$ = 56.2%). The pattern of decreasing similarity across elevation is consistent with the affinity and elevation range relationships reported above and supports the hypothesis that elevation exerts strong impacts on the GCE Odonata assemblage.

*Hypothesis 2b: Elevation Range Patterns Recapitulate Biogeographic Affinity.* The elevation ranges of GCE Odonata reflect their biogeographic affinity. A comparison of the elevation range limits of tropical, range-centered, and boreal taxa demonstrates that the average minimum and maximum elevation ranges of tropical species are both lower than those of boreal species, but the average elevation ranges of range-centered and Pacific Coast species largely overlap those of the allochthonous taxa (Bonferroni-adjusted $P < 0.05$; Table 1; Fig. 5). Thus, Odonata species elevation ranges generally reflect biogeographic affinity and latitudinal distribution, findings that are consistent with hypotheses 1 and 2.

From our data, at least 56.1% of the fauna is allochthonous to the GCE, nearly equal to the 56.8% of the fauna that have restricted elevation ranges (Table 1; Figs. 2 and 4). Not only is biogeographic affinity as important as elevation in structuring the GCE Odonata assemblage but also the two factors are intimately related, as demonstrated by elevational zonation of boreal and tropical taxa.

*Hypothesis 3: Landforms Should Exert Little Influence across Spatial Scale on GCE Odonata Ranges.* To what extent do landform and vicariance influence Odonata assemblage composition? Given their generally great vagility, we predict that null and corridor landform effects on Odonata should strongly dominate over barrier refuge effects across spatial scale from that of the Southwest to the GCE to the GC. In total, 39 (30.5%) of the 128 Arizona Odonata taxa have not been detected in the GCE, suggesting a stronger than expected barrier effect at the spatial scale of geologic provinces in the Southwest. For example, the ranges of the macromiinine libellulid *Macromia magnifica* McLachlan in Selys, and the libellulinine *Pseudoleon superbus* (Hagen) reach northern range boundaries on the southern and southwestern edges of the Colorado Plateau. Analogously, the corduliinine *Somatochlora semicircularis* (Selys) and the coenagrionid *Argia emma* Kennedy enter the extreme northern portion of the GCE (the latter species range wraps around the northern and western boundaries of the GCE), and the GCE exerts a barrier effect on these boreal western North American taxa. We exclude from the GCE species list some otherwise widespread western North American taxa, such as the libellulids *Leucorrhinia intacta* (Hagen) and *Erythemis vesiculosa* (F.), and conenagrionids *Enallagma anna* Williamson and *Ishnura ramburii* (Selys) because they have yet to be reported from the GCE. *L. intacta* occurs immediately SE of the GCE; *E. vesiculosa* and *I. ramburii* occur immediately south of the GCE (Abbott 2007); and the range of *E. anna* wraps around the northern boundary of the GCE. These species ranges likely represent additional cases of GCE barrier effects. Overall, hypothesis 3 is falsified at a subcontinental scale, but other factors likely affect barrier-related exclusions, including the poorly known phenomenon of Odonata migratory behavior.

At the spatial scale of the GCE, the following order of biogeographic landform effects on the fauna is observed (Table 3): null > barrier/filter ≫ refuge. This pattern supports the predictions of hypothesis 3. However, under the prediction that approximately two thirds of GCE species should reveal null range effects, and the remaining third may equally demonstrate barrier and refuge effects, the hypothesis is falsified ($\chi^2_{df = 2} = 37.02$, $P < 0.0001$), with lower than expected null impacts (<49.4% of species), lower than expected refuge effects (9.0% of species), and far higher than expected barrier effects (41.8% of species). Even if model assumptions are relaxed to expected percentages of 50% null:25% barrier:25% refuge impacts, barrier effects remain considerably higher than expected (overall $\chi^2_{df = 2} = 16.48$, $P = 0.0001$). Ranges demonstrating clear evidence of barrier/filter constraints particularly involved species reaching either the northern or southern extent of their continental ranges in the GCE (Table 3). Despite failed statistical support for this hypothesis, slightly more than half of the GCE Odonata species meet the general expectations of the hypothesis. Therefore, we consider overall support for hypothesis 3 to be equivocal at the spatial scale of the GCE, with more robust landform-related barrier/filter effects than expected.

At the spatial scale of GC, support for hypothesis 3 also is falsified, although the findings vary in relation

**Table 3. GC and GCE biogeographic landform effects on richness of Anisopera, Zygoptera, and all Odonata species**

| | GC Anisoptera | GC Zygoptera | All GC spp. | GCE Anisoptera | GCE Zygoptera | All GCE spp. |
|---|---|---|---|---|---|---|
| Biogeographic effect | | | | | | |
| GC—full corridor through Colorado R. in GC | 7 (21.2) | 8 (32.0) | 15 (25.9) | | | |
| GC—partial corridor up Colorado R. in GC | 11 (33.3) | 7 (28.0) | 18 (31.0) | | | |
| GC—partial corridor down Colorado R. in GC | 4 (12.1) | 0 (0.0) | 4 (6.9) | | | |
| *Pooled full and partial corridor effects* | *22 (66.7)* | *15 (60.0)* | *37 (63.8)* | | | |
| GC—barrier: GC desert divides range N-S | 4 (12.1) | 1 (4.0) | 5 (8.6) | | | |
| GCE—barrier: northern range limit | | | | 8 (16.3) | 3 (7.5) | 11 (12.4) |
| GCE—barrier: southern range limit | | | | 7 (14.3) | 10 (25.0) | 17 (19.1) |
| *GCE or GC—all barrier and filter effects* | *19 (57.6)* | *8 (32.0)* | *27 (46.6)* | *19 (38.8)* | *16 (40.0)* | *35 (39.3)* |
| GCE or GC—null effect (no landform effect) | 6 (18.2) | 0 (0.0) | 6 (10.3) | 26 (53.1) | 20 (50.0) | 46 (51.7) |
| GCE or GC—refuge effect | 1 (3.0) | 9 (36.0) | 10 (17.2) | 4 (8.2) | 4 (10.0) | 8 (9.0) |
| Total no. of species | 33 | 25 | 58 | 49 | 40 | 89 |

Numbers in parentheses are column percentages, except the pooled full and partial corridor effects and the GCE and GC—all barrier effects rows (in italics), which present the sum (and percentage) of species demonstrating some form of corridor or barrier impact, respectively. Missing values represent biogeographic effects that do not exist in that regional scale.

to alternative interpretations of range patterns. In total, 31 (34.8%) species detected in the GCE have not been detected in or around the immediate rims of GC (Tables 1 and 3). Therefore, even with relatively open access to the Mojave Desert to the west, GC is a relatively isolated landform. If partial corridor effects (ranges extending either part way up or down the Colorado River) are regarded as evidence of corridor effects through the landscape, the following ordering of GC landform effects is obtained: partial or full corridor (63.8% of species) $\gg$ refuge (17.2%) $>$ null (10.3%) $>$ barrier/filter (8.6%). Assuming that null and corridor effects should equally prevail (expected values of 33.3% each) and that barrier and refuge effects should be half as important (expected values of 16.7% each), the hypothesis is falsified ($\chi^2_{df = 3} = 32.31$, $P < 0.0001$). Although corridor effects dominate, in accord with our predictions, there are far fewer than expected cases of null effects. Cases of barrier effects include upland species whose ranges are divided by the strip of desert habitat on the canyon floor that separates the two GC rims. Thus, under the assumption that partial corridors are evidence of corridor effects, the hypothesis is falsified at the spatial scale of GC.

An alternative interpretation of our data are that partial corridor effects in GC are evidence of barrier/filter effects. Under this interpretation, the ordering of landform impacts shifts to: barrier/filter (46.6% of species affected) $>$ full corridor (25.9%) $>$ refuge (17.28%) $>$ null (10.3%; $\chi^2_{df = 3} = 41.57$, $P < 0.0001$; Table 3). Thus, the dominant impact of GC shifts from a corridor to a barrier/filter effect, an even stronger falsification of Hypothesis 3. Therefore, both interpretations falsify the hypothesis at the scale of GC, and indicate robust landform impacts of GC on its Odonata, with relatively minor null range effects. For example, all Aeshnidae in the region are widespread at the GCE spatial scale, but primarily exist in GC as corridor species (Table 1). Also, although only 3.3% of GCE Zygoptera are restricted to refugia, nearly one third of those have restricted ranges within GC.

GC exerts discrete range constraints on two pairs of congeneric Odonata species, both of which demonstrate adjacent but nonoverlapping range boundaries in Grand Canyon. *Hetaerina americana* (F.; Calopteryidae) is generally regarded as a common, low-moderate elevation stream-dwelling species throughout the Southwest. It is fully replaced by *H. vulnerata* upstream from Colorado River Mile 204 in GC, and *H. vulnerata* is the only calopterygid detected in central and eastern GC. Elsewhere in the GCE and Arizona, *H. vulnerata* seems to prefer smaller, more shaded streams than does its congener. Although *H. americana* has not been detected in GC upstream from Mile 204, it is common in the middle elevation reaches of the Little Colorado River near St. Johns, AZ, and in southern Nevada (Stevens and Bailowitz 2008). The exclusion of *H. americana* from the eastern basin of GC may be attributable to: failed dispersal by *H. americana* through the steep and narrow Muav Gorge that separates the two GC basins; drought (Johnson 1973); or unrecognized biotic interactions between these species.

In another case, *Brechmorhoga mendax* (Hagen) is widely distributed at low-middle elevations south of the Colorado Plateau, ascending the Colorado River up to Colorado River Mile 132. Upstream from that point to Nankoweap Creek (CR Mi. 52R) it is replaced by isolated populations of *B. pertinax* (Stevens and Bailowitz 2005). As with *Hetaerina*, the two *Brechmorhoga* species have regionally similar overall elevation ranges and flight times (Table 1), the congener excluded from eastern GC is generally more widespread and common to the south, and the excluded congener is associated with larger, more open streams. The eastern basin of Grand Canyon supports several endemic species, including *Euphorbia aaron-rossii* (A. & N. Holmgren; Euphorbiaceae; Phillips et al. 1987) and *Crotalus oregonus abyssus* Klauber (Crotalidae; Miller et al. 1982). Restricted to the eastern GC basin, the range of *B. pertinax* rather precisely overlaps that of GC's population of regionally endemic *Cicindela hemorrhagica arizonae* Wickham (Cicindelidae; Stevens and Huber 2004). At least one endemic GC plant

species, *Flaveria mcdougallii* Theroux, Pinkava & D. J. Keil (Asteraceae; Phillips et al. 1987), bridges the eastern and western GC basin boundary. Similarly, *B. mendax* breaches the Muav Gorge boundary between the two GC basins, and its range ends abruptly near the west side of the eastern GC basin. However, the causes for the displacement of *B. mendax* by *B. pertinax* between Deer Creek and Stone Creek (Colorado River miles 136–132) remains enigmatic, perhaps representing an ongoing northward and upstream expansion of *B. mendax* into the congener's refugial range, or a case of competitive exclusion. Additional morphological, genetic similarity, and biotic interaction analyses of GC *B. pertinax* are needed to understand its isolation and this range anomaly.

If hypothesis 3 obtains and Odonata are generally unaffected by landform, we predict little difference in the extent of range restriction among species across the spatial scale from the GCE to GC. We test this by scoring whether constraints on each species ranges became more or less severe as spatial scale fines. In total, 54 (60.7%) species showed evidence of additional range restriction in GC compared with the GCE ($X^2_{df = 3} = 50.5$, $P < 0.0001$; Table 1). This finding agrees with our previous conclusion that GC exerts strong landform impacts on the Odonata fauna.

The extent and form of biogeograhic landform impacts on Odonata are related to spatial scale, in a manner consistent with other invertebrate biogeography studies in the GCE (Stevens and Polhemus 2008). Hypothesis 3 is partially supported at a moderately coarse, intermediate spatial scale, but not at the subcontinental (Arizona) scale or the subregional spatial scale of GC. The proportion of species showing null biogeographic effects decreases as spatial scale fines, and the proportion of barrier/filter and refuge effects increases as well. This is primarily attributable to increasing resolution of environmental grain at finer scales: actual habitat area is reduced and barriers become more obvious at finer spatial scales than at coarser scales, even for highly vagile species.

Although contrary to the assumptions of hypothesis 3, the increase in the proportion of Odonata species demonstrating barrier effects in GC is not surprising. As a desert landform, GC is generally inhospitable to aquatic taxa, and although it has many small, highly isolated springs, stock tanks, and natural ponds, <2% of the overall land area consists of wetland or open water habitat. For example, *C. resolutum* is restricted in Arizona to several perennial North Rim ponds. Also, much of the existing aquatic habitat in the region has been anthropogenically altered or is artificial (e.g., the large reservoirs of the Colorado River; Stevens et al. 1997, Grand Canyon Wildlands Council 2002). Therefore, actual Odonata habitat in the GC and GCE is naturally and anthropogenically isolated and fragmented, and is much smaller in area than is suggested by regional or subcontinental scale Odonata range maps.

**Conservation.** None of the species detected in this study previously has been regarded as obviously rare or at risk at the subcontinental scale, with the possible exceptions of: *B. pertinax* and *C. resolutum* in GC; *C. dorsalis* and *O. s. montanus* in eastern and northeastern Arizona, respectively; and *A. hinei* around the southern margins of the Colorado Plateau. However, our regional range analyses reveal a very different portrait of Odonata population status in the GCE. RDF rarity values varied greatly among GCE Odonata: many Odonata species are widely scattered in distribution or are somewhat rare, with a median and mean RDF = 0.03 and 0.043, respectively (found at fewer than 15 and 22.3 of 505 localities, respectively) and with a 95% confidence limit = 0.01 (five or fewer localities; Table 1). *A. vivida* (RDF = 0.307), *Sympetrum corruptum* (Rambur) (0.248), and *Libellula saturata* Uhler (0.202) are widespread and common in appropriate GCE habitats. However, 15 (16.9%) species are restricted to three or fewer localities, and four (4.5%) of GCE species have been detected only at a single locality.

In all, we consider 15 Odonata species to be rare in GCE, with several species highly restricted in Arizona: *Ishnura cervula* Selys (Coenagrionidae) in central northern Arizona, *O. s. montanus* in the Chuska Mountains, *C. dorsalis* in the White Mountains, *C. resolutum* in perennial North Rim ponds, and the subregionally rare or possibly crytically endemic *B. pertinax* in six small, springfed GC tributary streams in central GC. *B. pertinax* and *C. resolutum* are the only two rare species in, or on the rims immediately around GC. Although most of the 15 species we consider to be rare in the GCE are regarded as widespread and not rare in their overall ranges, few monitoring data are available to verify their status.

As everywhere in the West, most natural GCE water bodies are at risk of degradation or outright elimination (Kreamer and Springer 2008). The spring-fed streams in central GC that support *B. pertinax* may be at risk of dewatering due to groundwater pumping or pollution through mining on the Coconino Plateau south of GC (Grand Canyon Wildlands Council 2002, Stevens and Bailowitz 2005). In addition to that species, 9 GC Zygoptera appear restricted to refugia: these generally less vagile taxa may be at higher risk than Anisoptera in GC. In most cases, habitat preservation and restoration are of paramount importance for the conservation of such rare or at-risk populations. Many, but not all, Anisoptera are habitat generalists, dispersing so widely that they may seem to be relatively resilient to environmental change. Although the region's Odonata assemblage may seem to be relatively secure, habitat degradation, intensifying surface water development, regional groundwater pumping and pollution, and global climate change may quickly change the conservation status of even relatively common, widespread species.

Although more easily observed than most insect taxa, some Odonata species have considerable dispersal ability, a factor that may limit their usefulness as indicators of environmental change. By the time population declines in wide-ranging species can be confirmed, it is often too late to recover them. Odonata monitoring efforts may be usefully and efficiently

focused on less wide-ranging taxa (e.g., endemic and range-restricted taxa); however, such monitoring may not detect declines among wide-ranging taxa. Many uncertainties in population dynamics are associated with global climate change: refugial populations are likely to disappear, elevation ranges may rise, the timing of first or last appearance may change, and Nearctic species richness may decrease in the face of increasing advance of Neotropical taxa (e.g., Colwell et al. 2008). The four high- elevation Nearctic Odonata species that have been detected at single localities in the GCE may be at risk due to climate change impacts on their habitats (Table 1). Baseline data, such as those presented in this study, are essential to detect population declines or range shifts, and to improve land and water resource stewardship.

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