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BIOGEOGRAPHY OF *AMMOPHILA* (HYMENOPTERA: SPHECIDAE) IN THE GRAND CANYON ECOREGION, SOUTHWESTERN USA

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ABSTRACT.—We compiled distribution data on *Ammophila* collected in the Grand Canyon ecoregion (GCE) in northern Arizona and southern Utah. We report 35 species occurring from 350 to 2865 m elevation. Three new state records are reported for Arizona and one for Utah. A total of 73.8%–80.5% of the 41 Arizona *Ammophila* species occur in the GCE, and 16 species were detected in Grand Canyon National Park. Four species in Utah's portion of the GCE are not known to occur in Arizona. Five *Ammophila* species were frequently captured (*A. azteca, A. pruinosa* complex, *A. breviceps, A. acuta,* and *A. strenua*), whereas most species were relatively infrequently encountered. Four species were detected only at single localities, but no evidence of localized endemism was found. Flight periods generally extended across the growing season, but 4 species appeared to fly in springtime and before the onset of the summer rainy season. Raw species richness was unimodally distributed across elevation, with a peak at 1750 m; however, adjustment of species richness by land area within 100-m elevation belts produced a linear decrease of species density across elevation (R^2 = 0.733). This pattern indicates conformance to the temperate-to-tropical negative relationship between species richness and latitude. Four species were found only below 1500 m elevation, whereas 5 species were detected at upper elevations, indicating that only 25.7% of the fauna appear to be constrained by elevation. Thus, we report relatively high GCE *Ammophila* species richness, relatively weak ecotonal impacts on the assemblage along the southern Colorado Plateau geologic province boundary, and modest corridor and barrier/filter landform impacts of Grand Canyon on this genus.

RESUMEN.—Reunimos información de la distribución de *Ammophila* en la ecoregión del Gran Cañón (GCE), en el norte de Arizona y el sudeste de Utah. Reportamos 35 especies que se encuentran entre los 350 y los 2865 metros de elevación. Se reportaron tres nuevos registros estatales en Arizona y uno en Utah. El 73.8% y 80.5% de las 41 especies de *Ammophila* de Arizona se encontraron en la GCE, y se detectaron 16 especies en el Parque Nacional del Gran Cañón. Cuatro especies de la parte de la GCE de Utah no se conocen en Arizona. Se detectaron con frecuencia cinco especies de *Ammophila* (*A. azteca, A. pruinosa, A. breviceps, A. acuta* y *A. strenua*), la mayor parte de las especies se registraron con una frecuencia relativamente moderadamente baja. Se detectaron cuatro especies sólo en una localidad, sin embargo no se encontró ningún indicio de endemismo localizado. Por lo general, los períodos de vuelo se extendían a lo largo de la temporada de crecimiento; sin embargo, se registró que cuatro especies volaron en primavera y antes del comienzo de la época lluviosa en verano. La riqueza de especies naturales se distribuía de manera unimodal en relación con la elevación, y el punto máximo se registró en los 1750 m; sin embargo, el ajuste de la riqueza de especies por área dentro de los cinturones de elevación de 100 m produjo una disminución lineal de la densidad de las especies en relación con la elevación (R^2 = 0.733). Este patrón indica una conformidad a la relación negativa templada-tropical entre riqueza de especies y la latitud. Se encontraron cuatro especies por debajo de los 1500 m de elevación, y se detectaron cinco especies en elevaciones superiores, lo cual indica que solo el 25.7% de la fauna está restringida por la elevación. Así, reportamos una riqueza relativamente elevada de especies de *Ammophila* en la GCE, impactos relativamente débiles en los ecotonos en el grupo que se extiende a lo largo del límite de la provincia geológica de la Meseta del Colorado en la zona sur y leves impactos de accidentes geográficos en forma de barreras/filtros y corredores del Gran Cañón en este género.

Ammophila (Sphecidae: Ammophilinae, Ammophilini) is a large, cosmopolitan genus of medium to large, slender, solitary, often red and black thread-waisted wasps. Contemporary taxonomy of the genus is based on Fernald (1934), Bohart and Menke (1976), Menke (1964, 1966a, 1966b, 1967, 1986, 1994, 2007), Krombein et al. (1979), and Pulawski (2009). *Ammophila* species are well known for their complex nesting and foraging behaviors (e.g., Peckham and Peckham 1898, Evans 1959, Ponder 1976, Brockman 1985, Hager and Kurcewski 1986, Field 1989). However, the regional distribution of *Ammophila* has not been examined in the Grand Canyon ecoregion (GCE) on the southern Colorado Plateau and at the ecotonal boundary of the Colorado Plateau and the Basin and Range geologic provinces (Fig. 1). The GCE

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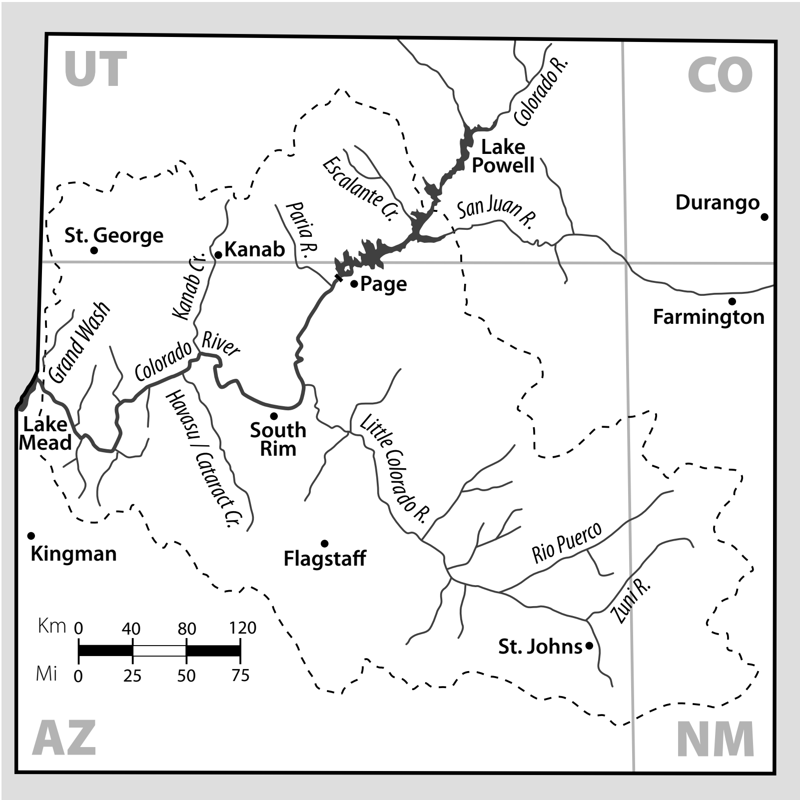

Fig. 1. The Grand Canyon ecoregion, southwestern USA.

contains numerous national parks, of which Grand Canyon is a UNESCO World Heritage Site and one of the world's largest, deepest canyons. Large, deep canyons juxtapose complex arrays of steep ecological gradients, including elevation, aspect, soils, and microclimate. They also affect assemblage composition and regional biogeography by functioning as barrier/filters, corridors, and refugia or in a null fashion (Stevens 2012). As part of a GCE invertebrate inventory, we present the first list of *Ammophila* species in the GCE, along with data on the species' elevation ranges, flight timing (i.e., seasonal activity periods), and relative collection frequency. We use these data to discuss the extent of landform impacts on *Ammophila* distribution in this large, complex landscape.

METHODS

Study Area

The GCE includes 145,000 km^2 of the southern Colorado Plateau in northern Arizona, southern Utah, and western New Mexico (Stevens 2012; Fig. 1). This landscape is topographically diverse, with elevations ranging from 350 m AMSL on Lake Mead to 3850 m at the top of the San Francisco Mountains near Flagstaff, Arizona. The highest point on the North Rim of Grand Canyon lies at approximately 2830 m. The climate of the GCE is continental and arid, with hot low-elevation desert summertime temperatures and cold high-elevation winter temperatures (Sellers et al. 1985). Precipitation is bimodal, with wintertime snowfall and rain and mid- to late-summer monsoonal rains. Most of the GCE is federally managed by the U.S. National Park Service, the Bureau of Land Management, the USDA Forest Service, and several Native American tribes, with little state or private land. Embedded wholly within the southwestern Colorado Plateau, Grand Canyon is a 445 km long, 2450 m deep canyon. Approximately two-thirds of Grand Canyon is managed by the National Park Service (Stevens 2012).

The Mogollon Rim forms the southern boundary of the Colorado Plateau and the GCE along the margin of the Basin and Range geologic province, and is a steep escarpment running diagonally southeast to northwest across central Arizona. The Mogollon Rim forms a biogeographic macro-ecotonal boundary known as the Lowe–Davis line between the Mexican-neotropical Madrean floristic region and the boreal Rocky Mountain floristic region (Lomolino et al. 2010, Stevens 2012). The GCE includes elements of 4 biomes, including the Madrean, Mohavean/Sonoran, Intermountain, and Cordilleran. The GCE is dominated by upland grassland, shrubland, woodland, ponderosa pine forest, and barren rock, which collectively cover 95% of the land area. Deserts below 1000 m and montane to alpine habitats above 2800 m each occupy only about 2.5% of the land area. The low desert habitats of the GCE are occupied by Madrean, Sonoran, and Mohavean Desert shrub vegetation, whereas middle elevations are 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. Elevations above 3600 m support <10 km^2 of Rocky Mountain alpine tundra habitat. *Ammophila* habitats in the GCE include sandy desert, riparian terraces, sand dunes, meadows, and exposed volcanic ash and gravel soils, which are widely distributed across elevation.

Data Sources and Analyses

Ammophila collection data were assembled from the literature, from inspection of museum specimens, and from field collections. We compiled a list of southwestern species from Krombein et al. (1979), Menke (1964, 1966a, 1966b, 1967, 1986, 1994, 2007), and Pulawski (2009). We examined >2500 specimens from the large regional collections of several institutions: the Ammophila Research Institute (ARI) in Bisbee, Arizona; the Monte L. Bean Life Science Museum at Brigham Young University (BYU); the Museum of Northern Arizona (MNA); and the University of Arizona Entomology Museum (UA). *Ammophila pruinosa* was distinguished from the *A. pruinosa* complex, which may include one or more undescribed species. The senior author collected *Ammophila* and other Hymenoptera during entomological field work in the GCE from 1974 to 2013 on more than 200 river trips through Grand Canyon and more than 5000 km of hiking through the region, including hiking trips to more than 400 springs in the region. Those trips often involved Malaise trapping and sampling of a wide array of habitats at and adjacent to the springs. More than 17,500 Hymenoptera specimens were collected during those expeditions at a total of 1390 localities. In all, 673 *Ammophila* specimens were examined from a total of 278 localities in the GCE. BYU *Ammophila* specimens were identified by H.E. Evans, and specimens collected during this study are databased and housed at MNA and ARI.

We sought to determine whether collection timing or elevation biased our results. Collect on was conducted during all months of the April–October growing season, with 9%–20% of all specimens collected each month. Elevation range was not related to the number of specimens among all species for which data were available (R^2 = 0.157), nor for those species for which >10 specimens were available (R^2 = 0.005). Therefore, although the sampling design of field collections was not systematic, it was not obviously biased by month or elevation, and it was conducted purposefully to determine aculeate wasp distribution across elevation throughout the GCE.

We used specimen-based locality data from field collections and museum specimens to determine flight dates and elevation ranges within the GCE. To investigate species-area relationships across elevation, we used a geographic information systems analysis to calculate the land area of each 100-m belt across the GCE. We calculated the ratio of $\log_{10}$ (*Ammophila* species richness + 1) to the $\log_{10}$ area (km^2) of each 100-m elevation belt and plotted that value against elevation.

We calculated the relative distributional frequency (RDF) of each GCE *Ammophila* species. RDF was calculated as the proportion of localities at which a species was detected in the GCE (Stevens and Polhemus 2008). RDF is an observational index and ranges in value from 0 (not present) to 1.0 (occurring at all localities sampled). For example, *Ammophila strenua* was collected at 37 of the 278 localities sampled at which *Ammophila* were found, resulting in an RDF of 0.133 (Table 1). RDF is a conservative estimate of capture frequency because it is based on the number of sites from which *Ammophila* species were detected, not the many sites sampled at which none were found. Also, RDF is suggestive of relative rarity, information that is otherwise unavailable. Based on inspection of histogram data, RDF values were grouped into categories of rarely captured (RDF < 0.01, 3 or fewer localities, 9 species), infrequently captured (0.01 < RDF < 0.05, 3–13 localities, 15 species), moderately regularly captured (0.05 < RDF < 0.1, 13–27 localities, 6 species), and frequently captured (RDF > 0.1, >27 localities, 5 species).

RDF may be biased by inadvertent focus on specific microhabitats, as well as by variation in a species' detectability and ease of capture. We examined the array of specimen-based elevation data by inspecting the histogram of sites sampled and found an approximately even distribution of specimens across elevation, but with slight undersampling between elevations of 1000–1600 m. However, those elevations in the GCE are largely dominated by vertical, barren cliff faces, habitats not occupied by *Ammophila.* Detection frequency and ease of capture does not appear to us to vary greatly among *Ammophila* species. Therefore, while mindful of these sampling design limitations, we conclude that RDF analyses provide a general indication of collection frequency.

RESULTS AND DISCUSSION

We detected 35 *Ammophila* species in the GCE distributed across elevations from 350 to 3048 m (Table 1). Two additional species may occur in the GCE on the basis of reported occurrence on 2 or more sides of the region: *A. nearctica* and *A. nefertiti.* We detected 4 species in Utah's portion of the GCE that are not known to occur in Arizona: *A. californica, A. dysmica, A. mediata,* and *A. polita.* Among the species reported here are apparently the first Arizona records for *A. mcclayi, A. parkeri,* and *A. varipes,* and the first Utah record for *A. extremitata.* These records add to the compendia of Krombein et al. (1979) and Pulawski (2009). A total of 41 *Ammophila* species have been reported in Arizona, and *A. nearctica* may occur there as well, but it has not been documented (Krombein et al. 1979, Menke 1964, 1966a, 1966b, 1967, 1986, 1994, 2007, Pulawski 2009; Table 1). Thus, 73.8%–80.5% of the *Ammophila* species known from Arizona also occur in the GCE. A total of 16 *Ammophila* species were detected within Grand Canyon National Park (Table 1).

Five *Ammophila* species were frequently captured: *A. azteca* (RDF = 0.21), *A. pruinosa* complex (total RDF = 0.16), *A. breviceps* (RDF = 0.14), *A. acuta* (RDF = 0.13), and *A. strenua* (RDF = 0.13). Most species were moderately infrequently encountered, with RDF values of 0.01–0.1 (Table 1). Nine species were rarely captured, having RDF values <0.01, among which 4 species were detected only at a single locality (RDF = 0.004): *A. hurdi, A. kennedyi, A. mediata,* and *A. mimica.* Additional collecting is needed, particularly in the northeastern GCE, to clarify these species' ranges.

Flight date ranges for more frequently captured species show that flight periods extended across the growing season, with no apparent restriction to the early summer dry period or the mid- to late-summer monsoon period (Table 1). Species such as *A. ferruginosa, A. fernaldi, A. parkeri,* and *A. wrightii* were captured only during the April to early July premonsoon period, but the flight dates of most species were broadly distributed across the growing season. For example, *A. strenua* was collected from 24 April to 4 October. The duration of the flight period was strongly negatively related to elevation due to the early onset of freezing conditions at upper elevations. These data suggest that most GCE *Ammophila* species are broad generalists in terms of flight timing.

Biological diversity is often strongly negatively related to elevation because elevation exerts impacts that are analogous to those of latitude. Raw *Ammophila* species richness in the GCE was more or less unimodally distributed across elevation, with a peak at 1750 m (Table 1, Fig. 2). Unimodal species richness maxima at middle elevations are often reported in elevation gradient analyses (reviewed by Lomolino et al. 2010); however, in complex landscapes such as the GCE, adjustment of species richness by land area across elevation often results in a linear decrease of species richness across elevation (e.g., Stevens and Polhemus 2008, Stevens and Bailowitz 2009). We found that the ratio of $\log_{10}$ (*Ammophila* species richness + 1) to $\log_{10}$ area (km^2) was strongly negatively linearly related to elevation ($R^2 = 0.733$; Fig 2). This pattern indicates that area-adjusted species density decreased in a manner consistent with the global temperate–tropic latitudinal gradient.

TABLE 1. *Ammophila* species, distribution, elevation range, flight dates, and relative distribution frequency (RDF). Distribution abbreviations: AZ = Arizona, GC = Grand Canyon, GCE = Grand Canyon ecoregion. RDF is the proportion of sites at which an *Ammophila* species was detected in relation to the total 273 sites at which any *Ammophila* were collected. Elevation and flight dates in parentheses are from specimens collected from the Southwest outside of the GCE. Species without elevation range and flight dates occur in Arizona but not in the GCE.

Species	Distribution	Elevation range (m)	Flight dates	RDF
Ammophila aberti Haldeman	AZ & GCE, GC	365–1902	6 May–21 Sep	0.076
Ammophila acuta (Fernald)	AZ & GCE	ca. 1150–2165	15 Jun–14 Sep	0.133
Ammophila aphrodite Menke	AZ	—	—	0.000
Ammophila azteca Cameron	AZ & GCE, GC	1648–3048	4 May–5 Oct	0.209
Ammophila bella Menke	AZ	—	—	0.000
Ammophila bellula Menke	AZ	—	—	0.000
Ammophila breviceps Smith	AZ & GCE, GC	375–1994	26 Apr–27 Oct	0.144
Ammophila californica Menke	UT – GCE	1470–1795	16 May–19 Sep	0.022
Ammophila cleopatra Menke	AZ & GCE, GC	454–2005	1 Jun–27 Oct	0.090
Ammophila dejecta Cameron	AZ	—	—	0.000
Ammophila dysmica Menke	UT – GCE	1774–2154	17 May–17 Jul	0.018
Ammophila extremitata Cresson	AZ & GCE, GC	2230–2700	20 Jun–29 Jun	0.011
Ammophila femurrubra Fox	AZ & GCE, GC	370–1872	4 May–28 Sep	0.036
Ammophila fernaldi (Murray)	AZ & GCE	1499–2130	4 Apr–24 Jul	0.018
Ammophila ferruginosa Cresson	AZ & GCE	(1310) 1678–1841	28 May–30 Jul	0.040
Ammophila formicoides Menke	AZ	—	—	0.000
Ammophila harti (Fernald)	AZ & GCE	1786–1916	5 May–29 Aug	0.040
Ammophila hermosa Menke	AZ	—	—	0.000
Ammophila hurdi Menke	AZ & GCE	1000	—	0.004
Ammophila imitator Menke	AZ	—	—	0.000
Ammophila juncea Cresson	AZ & GCE	1541–1997	8 Jun–15 Aug	0.025
Ammophila karenae Menke	AZ & GCE	(224)–2107	25 Jun	0.007
Ammophila kennedyi (Murray)	AZ & GCE	2133	25 Jun	0.004
Ammophila macra Cresson	AZ & GCE	1265–2133	5 May–17 Sep	0.079
Ammophila mcclayi Menke	AZ & GCE, GC	1370	5 May	0.007
Ammophila mediata Cresson	UT – GCE	2591	26 Jul	0.004
Ammophila mescalero Menke	AZ & GCE	1829	10 Aug	0.007
Ammophila mimica Menke	AZ & GCE	(159)–945	4 Jun–(1 Jul)	0.004
Ammophila moenkopi Menke	AZ & GCE	1456–2133	26 Jun	0.014
Ammophila nancy Menke	AZ & GCE, GC	(30) 355–1280	25 May–23 Oct	0.054
Ammophila nearctica Kohl	AZ?, GCE?	—	—	0.000
Ammophila nefertiti Menke	AZ, GCE?	—	—	0.000
Ammophila novita (Fernald)	AZ	—	—	0.000
Ammophila parkeri Menke	AZ & GCE, GC	465–1010	6 May–9 May	0.011
Ammophila peckhami (Fernald)	AZ & GCE	1644–2750	3 Jun–15 Sep	0.040
Ammophila picipes Cameron	AZ	—	—	0.000
Ammophila placida Smith	AZ & GCE, GC	385–630	28 Sep–8 Oct	0.007
Ammophila polita Cresson	UT – GCE	1829	29 May–27 Sep	0.007
Ammophila procera Dahlbom	AZ & GCE, GC	375–2250	7 Jun–27 Sep	0.058
Ammophila pruinosa Cresson	AZ & GCE, GC	(10) 940–1901	26 Apr–11 Sep	0.032
Ammophila pruinosa complex	AZ & GCE, GC	385–2012	23 Apr–27 Oct	0.158
Ammophila strenua Cresson	AZ & GCE, GC	(1599) 1615–2700	24 Apr–4 Oct	0.133
Ammophila unita Menke	AZ & GCE	930–1988	24 May–21 Sep	0.050
Ammophila varipes Cresson	AZ & GCE	1499–2133	4 May–29 Aug	0.036
Ammophila wrightii (Cresson)	AZ & GCE, GC	940–1608	26 Apr–5 Jul	0.018
Ammophila zanthoptera Cameron	AZ & GCE, GC	2100–2700	17 Jun–22 Aug	0.022

The slight flexure in the area-adjusted species density ratio at ~1750 m (Fig. 2) prompted us to examine assemblage composition below 1500 m and above 2000 m in the GCE. Species found only below 1500 m elevation included *A. mcclayi, A. nancy, A. parkeri,* and *A. placida.* Species primarily occurring above 2000 m elevation included *A. azteca, A. extremitata, A. kennedyi, A. mediata,* and *A. zanthoptera.* The remaining GCE species occurred relatively broadly across middle elevations (1000–2000 m). *Ammophila* species richness within Grand Canyon was equivalent across elevation, with 9 species collected at low-middle elevations and 5 species taken at middle-upper elevations ($P > 0.48$; Table 1). Overall, these data again demonstrate that most GCE *Ammophila* species are widespread across

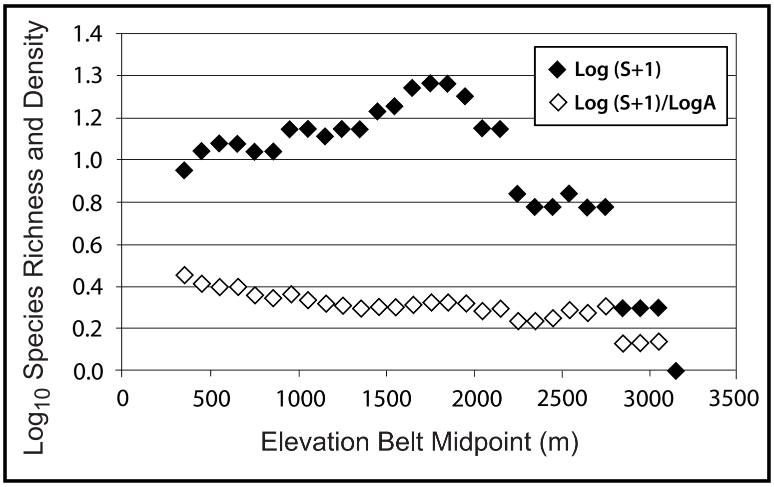

Fig. 2. *Ammophila* raw species richness (S) and $\log_{10}$ area (A)-adjusted species density in relation to 100 m elevation belt midpoints in the Grand Canyon ecoregion.

elevation; however, 9 of 35 species (25.7%) appear constrained by elevation to portions of the landscape with relatively little land area.

Previous studies of GCE invertebrate groups for which species' overall range data were known include work on Odonata, aquatic Hemiptera, tiger beetles (Cicindelinae), and mosquitoes (Culicidae; Stevens and Huber 2004, Stevens and Polhemus 2008, Stevens et al. 2008, Stevens and Bailowitz 2009). Those studies generally demonstrate that (1) low-elevation taxa tend to be neotropical in biogeographic affinity, (2) high-elevation species tend to be nearctic in affinity, and (3) GCE assemblages are more or less even mixtures of neotropical, range-centered, and nearctic species. However, some GCE assemblages are more strongly characterized by boreal and range-centered species (e.g., Gerridae water striders—Stevens and Polhemus 2008; Cicindelinae—Stevens and Huber 2004), rather than by neotropical or range-centered taxa. In the case of *Ammophila,* only a few low-elevation Mexican/neotropical species and a few high-elevation boreal/nearctic *Ammophila* species occur in the GCE, with most species in the assemblage appearing to be widespread and broadly range-centered. Thus, the extent of ecotonal and biogeographic influences appears to be weaker among *Ammophila* than in other GCE insect taxa studied, and the biogeographic influence of Grand Canyon as a large, deep canyon landscape is restricted to modest corridor and barrier/filter functions (e.g. for *A. cleopatra* and *A. mediata,* respectively).

More vagile (mobile, dispersive) groups of insects tend to be more species-rich in the GCE and have lower levels of endemism (Garth 1950, Polhemus and Polhemus 1976, Stevens 2012). As an at least moderately vagile genus, the large number of co-occurring, widespread *Ammophila* species in the GCE generally conforms to this pattern. Also, we found no clear evidence of local endemism among the 35 *Ammophila* species detected in our study. *Ammophila* species richness in the GCE thus appears to be related to the broad distributions and wide elevation ranges of most species in the genus.

Additional collecting will refine range and elevation patterns for GCE *Ammophila* species, as will more regional collecting, particularly in Mexico. Such efforts are needed to clarify biogeographic affinities among *Ammophila* species. Monitoring of upper-elevation species also may be relevant in light of projected climate change impacts on alpine habitats. Although the results and conclusions presented here may be refined with additional collecting, our data provide a contemporary biogeographic baseline of *Ammophila* composition and distribution in relation to future climate and habitat changes in the GCE.

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