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Floral Visitors of a Colorado Endemic Chasmophyte, Telesonix jamesii (Saxifragaceae)

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Floral Visitors of a Colorado Endemic Chasmophyte, *Telesonix jamesii* (Saxifragaceae)

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Abstract

Telesonix jamesii, a rare and imperiled species of perennial saxifrage, is restricted rocky habitats at high elevations across 21 isolated known populations in the southern Rocky Mountains of Colorado and New Mexico. Despite its imperiled conservation status, very little is known about the natural history of *T. jamesii*. We studied pollination of this species during the summers of 2019–2021 at multiple locations on Pikes Peak, CO. We conducted a total of 899 minutes of pollinator surveys, identifying all floral visitors during this time period. We then examined floral visitors for the presence of *T. jamesii* pollen to determine which species might be effective pollinators. We found that flowers of *T. jamesii* are visited by a diverse assemblage of insects and one species of hummingbird. Bumble bees (*Bombus*) were the most commonly observed species visiting flowers, as well as the only group found carrying *T. jamesii* pollen on their bodies. Our findings suggest that *T. jamesii* is infrequently pollinated and we speculate that gene flow for this species may be low. This constitutes the first investigation into the field pollination ecology of *T. jamesii.* Our study warrants future investigation into the population genetics of this species as well as surveys of historical occurrences and high suitability habitat for populations.

Telesonix jamesii, una especie perenne de saxífraga rara y en peligro, esta restringida a hábitats rocosos en altas elevaciones entre 21 populaciones aisladas conocidas en las sureñas Rocky Mountains de Colorado y New Mexico. A pesar de su estado de conservación arriesgado, se sabe muy poco sobre la historia natural de *T. jamesii*. Estudiamos la polinización de esta especie durante los veranos de 2019-2021 en múltiples sitios en Pikes Peak, CO. Realizamos un total de 899 minutos de muestreos de polinización, identificando a todos los visitantes florales durante este período de tiempo. Luego examinamos a los visitantes florales para detectar la presencia de

polen de *T. jamesii* para determinar cuales especies podrían ser polinizadores efectivos. Aquí, encontramos que las flores de *T. jamesii* son visitadas por un conjunto diverso de insectos y una especie de colibrí. Los abejorros (*Bombus*) fueron las especies más frecuentemente observadas visitando flores, así como el único grupo encontrado portando polen de *T. jamesii*. Nuestros descubrimientos sugieren que *T. jamesii* se poliniza con poca frecuencia y especulamos que el flujo de genes para esta especie puede ser bajo. Esto constituye la primera investigación de campo sobre la ecología de polinización de *T. jamesii*. Nuestro estudio justifica una investigación futura sobre la genética de poblaciones de esta especie, así como el estudio de ocurrencias históricas y de hábitats de alta idoneidad para poblaciones.

Introduction

The persistence of many rare and endemic plant species relies on sexual reproduction within local populations (Bailey and Kevon 2017). Although many rare plants have developed self-compatibility for reproductive assurance (Karron et al. 2012), effective pollinators are essential for maintaining gene flow and allowing populations to adapt to changing environments (Holsinger and Gottlieb 1991). Understanding plant-pollinator interactions has conservation implications, particularly for plant species found at high elevations (Kearns et al. 1998). Climate induced phenological mismatches between plants and pollinators can arise more rapidly at high elevations due to accelerated flowering times and short growing seasons (Gezon et al. 2016). Additionally, alpine and subalpine habitats are at greater risk of climate-driven habitat loss than those at lower altitudes (Inouye 2020). Warming of alpine areas may significantly reduce the diversity of microhabitats and suitable thermal refugia for high elevation species (Graae et al. 2018). One estimate predicted that 36-55% of alpine species and 31-51% of subalpine species will lose 80% of their habitat by 2070-2100 in European mountains (Engler et al. 2011). This not only constricts habitat for high elevation rare plants but is likely to also affect their interactions with pollinators (Burkle et al. 2013). These factors, coupled with worldwide declines of insect pollinators (Potts et al. 2010, Bartomeus et al. 2011, Breed et al. 2013), make identifying mechanisms that promote genetic diversity in high elevation endemics crucial for conserving global biodiversity (Jabis et al. 2011).

Telesonix jamesii (Saxifragaceae; Fig. 1) is a rare vascular plant species regionally endemic to the southern Rocky Mountains of Colorado and New Mexico. With only 19 sites in Colorado where this species has been reported, the Colorado Natural Heritage Program ranks this species as S2 (imperiled in state because of rarity; Beatty et al. 2004, Rondeau et al. 2011). *Telesonix jamesii* grows from montane to alpine life zones (see Ackerfield 2015 for description of life zones), with an elevational maximum of 4,184 m (Beatty et al. 2004). *Telesonix jamesii* flowers from late June through July at lower elevations and flowers from July through August at higher elevations (Ackerfield 2015). It is an obligatory chasmophyte, growing out of rock crevices and talus substrates to avoid interspecific competition and disturbances such as fire (Antonsson 2012, Beatty et al. 2004). This life history strategy facilitates stress-tolerant species with poor competitive abilities to persist in more extreme habitats (Sexton et al. 2009). However, the selective pressure from these extreme conditions narrows the distribution and adaptive potential of endemic chasmophytes such as *T. jamesii* (Hum 2017). The species has been described growing on granite tors in dry, poor nutrient soils in areas with high exposure to wind and UV radiation (Beatty et al. 2004). These conditions offer distinctly unique habitats from the surrounding forest matrix of the montane and subalpine life zones (Ackerfield 2015), often leaving patches of suitable habitat isolated from one another. At a larger scale, some mountain peaks occur as geographically isolated "sky islands" surrounded by a sea of unsuitable habitat at lower elevations (Wershow and DeChaine 2018). This lack of connectivity could potentially inhibit gene flow between populations (Jabis et al. 2011), making this rare and endemic species a strong candidate for a pollination biology investigation.

The reproductive biology of *T. jamesii* has been described briefly through horticultural work by Gornall and Bohm (1985), noting that species of *Telesonix* are self-compatible to varying degrees. Despite being a species of conservation concern, there have been no studies focused on mechanisms of pollination as well as identification of pollinators (Beatty et al. 2004). Here, we expand on what is known about the pollination system of this species by asking the following questions: (1) What animals visit flowers of *T. jamesii*? (2) Do these species collect pollen from *T. jamesii* in a manner that would likely make them effective pollinators?

Methods

Study site

Our study was conducted on Pikes Peak, located at the eastern edge of the southern Rocky Mountains in Colorado during the summers of 2019–2021. We sampled plants at 36 locations (Fig. 2) on the mountain that ranged in elevation from 2527.75 m (38.848521°N, -104.94812 °W) to 4129.18 m (38.840252°N, 105.03964°W). Locations occurred both above and below tree line. On Pikes Peak, *T. jamesii* is common above the tree line but does not extend to the summit (4302 m). All locations were on eastern facing slopes. At lower elevations below tree line, *T. jamesii* was uncommon, predominantly only growing in isolated forest clearings with rocky substrate.

Floral community composition and abundance varied across locations. Scattered plants of *Heuchera hallii* (Saxifragaceae), *Ciliara austromontana* (Saxifragaceae), *Jamesia americana* (Hydrangeacae), and *Draba streptocarpa* (Brassicaceae) were common community associates at locations below tree line. Common plant associates above tree line included *Geum rossii* (Rosaceae), *Bistorta bistortoides* (Polygonaceae), *Potentilla fruticosa* (Rosaceae), and *D. streptocarpa* (Brassicaceae).

Floral visitation

In 2020, we observed flowers of *T. jamesii* for periods of at least 15 minutes. Thirty-six observations were carried out by a single observer (AGG) from July through August. Individual plants were chosen haphazardly along trails where *T. jamesii* has been historically known to occur (GBIF 2020). During observations, we recorded avian visitors (hummingbirds) and collected all foraging insects observed contacting the reproductive parts of the flower. We identified insects in the lab using *Flies: The Natural History and Diversity of Diptera* (Marshall 2012), *The Bumble Bees of Colorado: A Pictorial Identification Guide* (Wright et al. 2017), *The Bees in Your Backyard* (Wilson and Carril 2015), as well and a reference collection from the Colorado Front Range (Resasco et al. 2021). Following analysis, we curated insects and submitted voucher specimens to the entomology collections at the University of Colorado Natural History Museum. Hummingbirds identified by sight using *Sibley Field Guide to Birds of Western North America* (Sibley 2016). For insects, a clean aspirator was used to ensure no residual pollen came into contact with insects. Aspirators were washed with water and dried with a cotton swab in between collections.

Observations for this study took place over 837 minutes between 08:15 and 16:46 Mountain Daylight Time. Observations were made during fair weather conditions, with air temperatures ranging from 6°C to 22°C. There was no precipitation during any of the observations. An additional 62 minutes of observation were made from a related ongoing study that is investigating plant-pollinator interactions in the Pikes Peak region. These observations took place across three summers from 2019 to 2021. Because pollinators from this latter study were not collected with a freshly cleaned aspirators, we omitted them from the pollen identification process.

Pollen identification

We collected pollen of *T. jamesii* from museum specimens at the University of Colorado Herbarium. To confidently distinguish pollen of *T. jamesii* from similar species found in the region, we mounted and examined pollen grains of confamilial species that occur in El Paso County, CO. One species from each genus of Saxifragaceae was selected for comparison. Confamilial species were *Heuchera hallii, Micranthes rhoda, Ciliara austromontana,* and *Saxifraga rivulus.* Pollen grains were deposited onto slides by plucking one anther from a plant, swirling it in a glycerine solution for 10 sec, and mashing the anther to release as much pollen as possible. Length x width ratios of five pollen grains were measured and averaged for each species and compared to *T. jamesii*. All length and width measurements were taken along the equatorial axis.

Once pollen of *T. jamesii* was differentiated from related species, we mounted body pollen from insects onto glycerine slides. A Safranin-O stain was added to the glycerine solution. We removed body pollen from insects using a number one artist's brush (Kearns and Inouye 1993). For all species of *Bombus*, we only considered pollen that could later be potentially deposited on another flower. This meant disregarding pollen carried in corbicula loads because that pollen would be brought back to the nests rather than being deposited on flowers (Macior 1967). After brushing pollen grains onto slides, we dipped forelimb appendages of each insect into the glycerine solution, as most pollinators were observed making contact with flowering parts with both their bodies and limbs. Slides were then systematically examined under the microscope for pollen grains by starting at one corner of the slide, scanning all the way from left to right one field of view at a time. On each occasion that a pollen grain was found, we took measurements and photographs to determine if it represented pollen of *T. jamesii*. If a pollen grain found on an individual insect specimen was determined to be *T. jamesii*, that insect species was considered an effective pollinator for purposes of this study.

Statistical analysis

Rarefaction can be used to estimate species richness from field sampling and assess thoroughness of sampling, especially given that raw species richness counts from surveys will almost always fail to account for the total number of species in a community (Gotelli and Colwell 2001). By resampling the pool of species from field surveys and plotting species richness as a function of individuals collected, species richness can be estimated as the accumulation curve reaches an asymptote (Gotelli and Colwell 2011). To assess the thoroughness of our sampling effort, we divided the observed species richness by the second-order jackknife estimator for both all species visiting *T. jamesii* and species found carrying conspecific pollen. The second-order jackknife estimator method has been demonstrated to work well for incidence data with a limited number of samples (Gotelli and Colwell 2001).

Results

Pollinator visitation

Fifty-five floral visitors spanning 18 different insect species or morphospeices were observed visiting flowers of *T. jamesii* (Table 1). During the summer of 2020, we observed 34 individual floral visitors (Supplementary Materials 1). Twenty-one were observed in the concurrent study across the summers of 2019, 2020, and 2021. On average, *T. jamesii* was visited once every 16.4 minutes across the 899-minute observation period (total minutes/total visits). Only one avian species was observed visiting *T. jamesii*, which was *Selasphorus platycercus,* the Broad-Tailed Hummingbird. Most of the insects observed were bees in the family *Apidae*, especially bumblebees (*Bombus*), which comprised over half (60%) of all observed visitors. We recorded seven different species of *Bombus*. Non-*Bombus* bees included *Lasioglossum, Anthophora,* and *Agapostemon*. Flies belonging to Muscidae*,* Syrphidae*,* Empididae*,* and Platypezidae were observed visiting flowers as well. Flies, ants, and halictid bees were identified to family or genus (Table 1). No pollinators were observed visiting flowers at our lowest elevation surveys in early July, and we only recorded three visitations below tree line in total (Supplementary materials 1).

Pollen characterization

We found clear morphological differences in pollen between species in closely related genera of Saxifragaceae in the Pikes Peak region, with each species bearing a distinct morphology (length, width, circularity, and shape factor or length/width ratio). These features facilitated accurate identification of pollen to species (Table 2; Kearns and Inouye 1993, Pospiech et al. 2021). While species from each genus all had spheroidal tricolpate pollen grains, the length to width ratios differ between species (Table 2). *Telesonix jamesii* is characterized as having oblate spheroidal tricolpate pollen grains with an average length to width ratio of 1.229 (Table 2; Fig. 3). Colpi of this species extend across the equatorial axis toward the poles. In the polar view, grains have three distinct open colpi joining at the pole.

Effective pollen carriers

Of the 19 species observed visiting *T. jamesii*, only three bore pollen grains on their bodies matching *T. jamesii* (Table 1). All of these species were bumblebees (*Bombus bifarius*, *B.*

sylvicola, and *B. huntii*). Although only three species were recorded carrying conspecific pollen, these species accounted for 29.1% of observed visitations (n = 16). For estimating total species richness of floral visitors, we included all 19 species observed on flowers. Rarefaction analysis showed that observed species richness represented approximately 53% of estimated total species richness (Supplementary Materials 3), which was estimated at 35 species. Rarefaction analysis showed that our observed richness of three effective pollinator species represented approximately 60% of estimated effective pollinator species richness, which was five species (Supplementary Materials 3). However, these two estimated unsampled species are not abundant visitors, so their importance to *T. jamesii* as pollinators is likely low.

Discussion

Telesonix jamesii is visited by wide variety of pollinators. This is consistent with other arctic and alpine members of Saxifragaceae, which are thought to attract a variety of dipteran and hymenopteran pollinators (Brochmann and Hapnes, 2001). While it has been suggested that an array of species pollinate members of Saxifragaceae, very few studies have investigated pollination ecology of this family in depth (Soltis, 2007). Okuyama et al. (2004) identified fungal gnats (Sciaridae) as an effective pollinator of *Mitella,* a genus of approximately nine saxifrage species in North America characterized by its small flowers. At least two members of Colletidae, *Colletes aestivalis* and *Colletes andrewsii*, have been shown to be oligolectic on *Heuchera* (Robertson 1925, Robson 2019), the latter of which is native to Colorado (Scott et al. 2011). Despite *Heuchera* being present in our study system and inhabiting similar chasmophytic microhabitats, we observed no members of Colletidae visiting *T. jamesii.* Ornduff et al. (1975) found that both halictid and syrphid pollinators carried pollen of *Jepsonia* in California. They also identified that pollination from bees resulted in overall greater seed set (Ornduff et al. 1975). Bees made up the majority of visitors in our study. Bumblebees were both the most common visitors and most effective at carrying conspecific pollen. Pollen grains may have more success attaching to the numerous setae covering bumblebee bodies. Even disregarding corbicular loads, bumblebees typically had more body pollen than the other species, so there may be a higher probability of finding conspecific pollen on those individuals.

Gene flow between populations of *T. jamesii* may be of concern if *Bombus* are the only effective pollinators. Bumblebees are central place foragers and seldom travel long distances while foraging (Wolf and Mortiz 2008, Hagen et al. 2011). Because *T. jamesii* often grows in isolated open patches of rock, there is low connectivity between areas of suitable habitat. In the montane and subalpine, subpopulations typically grow in exposed rocky outcrops that are surrounded by dense forest (Beatty et al. 2004). It is unlikely that many bumblebees move between these isolated patches. Mola et al. (2020) found that individuals of *B. bifarius* traveled a maximum of 362 m from their colony when foraging (Mola et al. 2020). Despite the limited foraging distance of this species, they found no evidence that changes in habitat structure or elevation restricted bumblebee movement (Mola et al. 2020). This suggests that while *B. bifarius* may be geographically limited in its role as pollen disperser for *T. jamesii*, it is unlikely that they are limited to the habitat patches where *T. jamesii* occurs. At a larger geographic scale, weak pollinator connectivity between populations could make dispersal a greater concern for the genetic diversity of this species (Levin 1981). Little is known about mechanisms for seed dispersal *T. jamesii* (Beatty et al. 2004). Unlike the seeds of closely related *Boykinia* species, which have tubercles that easily attach to fur or feathers, the seeds of *Telesonix* species are smooth and unfavorable for animal-mediated dispersal (Gornall and Bohm 1985). We speculate that *T. jamesii* is likely reliant on water and wind patterns for primary and/or secondary seed dispersal.

The extent to which *T. jamesii* relies on outcrossing is still unknown. While this study identified floral visitors of *T. jamesii* and those that are successful at carrying pollen, there is still much about the reproductive biology of this species that is unknown. Gornall and Bohm (1985) concluded that *T. jamesii* is self-compatible, but the fitness cost of asexual versus sexual reproduction was not investigated (Gornall and Bohm 1985). Moreover, promoting sexual reproduction via pollinators could be costly if a species has already depleted its store of genetic diversity to adapt to such narrow conditions (Kruckeberg and Rabinowitz 1985). Van Valen's niche-variation hypothesis, where precise adaptation to narrow ecological conditions favors reduced heterozygosity for a species (Van Valen 1965), is commonly cited as a cause of lower genetic diversity in endemic species (Kruckeberg and Rabinowitz 1985). Many stress-tolerant alpine perennials have the capacity to reproduce sexually yet continue to reproduce vegetatively to take advantage of resources and protection from the parent plant (Grime 1979). This fits the life history strategy of *T. jamesii*, having to colonize and establish roots in rock crevices with harsh UV and wind conditions. Sexual reproduction may nonetheless still play a role in this species survival. Plants of *T. jamesii* are covered in aromatic glandular trichomes that yield a spicy fragrance. This is absent from other closely related species in *Saxifraga* and *Boykinia* genera (Gornall and Bohm, 1985). Gornall and Bohm (1985) hypothesized that this trait may have evolved to attract pollinators. Nocturnal pollination systems can often be mediated by glandular floral scents (Cordeiro et al. 2017). While it is possible that nocturnal pollinators such as moths visit *T. jamesii*, the ruggedness of the terrain and the remoteness of study area made nighttime observations extremely difficult. Given that flowers are bright in color and visitations were observed during daytime hours, it is possible that the scent serves some other purpose – such as herbivory defense. A thorough investigation of the extent of sexual reproduction in this system would require an experimentally manipulated study using pollinator limitation to measure reproductive traits such as seed set.

A population genetics study may be warranted as well to assess gene flow and variability through their range. Further genetic studies could clarify metapopulation dynamics, indicate the extent of phenotypic plasticity, and help better understand the relationship between this species and its only congener, *T. heucheriformes* (Beatty et al. 2004). *Telesonix heucheriformes* occupies similar habitats as *T. jamesii* but is more widely distributed, ranging from western Nevada to Alberta (NatureServe 2022). Understanding the evolutionary relationship between these two species could provide insights for reasons of endemism in *T. jamesii*. Despite seemingly plentiful habitat, it remains unknown why populations of *T. jamesii* are so few and scattered. We recommend resurveying historical occurrences as well as surveying for new populations in high probability habitats. Niche modeling would be the next step for identifying potential new habitats and environmental factors affecting distribution.

Our study design bore a few limitations. Conspecific pollen found on an insect's body does not necessarily indicate that said species is an effective pollinator; rather, it only indicates that said species has the capacity to carry conspecific pollen. There may be certain animal behavioral traits prohibiting the successful deposition of pollen. However, this methodology remains a useful technique for analyzing pollinator efficiency from unmanipulated field surveys (Goldblatt et al. 1989, Kearns and Inouye 1993, Wiesenborn 2018, Wiesenborn 2019). Another caveat is having only 55 observed pollination events, which is a limited sample size. With nearly 900 minutes of field surveys, it is likely that *T. jamesii* is simply not visited by pollinators very often. Rarefaction can help us account for incomplete sampling efforts, but does not overcome these limitations. Another consideration is that surveys were conducted only during the daytime and the majority of our surveys were conducted during the summer of 2020. Due to interannual environmental variation, short-term studies may offer only a glimpse into the ecological processes occurring in a system, whereas long-term studies can provide stronger insights into these processes (Lindenmayer et al. 2012). We could gain stronger insights to this system by comparing pollination at other populations besides Pikes Peak to see if these patterns generalize beyond a local scale.

Our study provides a greater understanding of the breeding system of *T. jamesii* on Pikes Peak. We provide the first field ecological data on the pollination of this species to our knowledge, specifically the importance of bumblebees as effective pollinators. Populations of *T. jamesii* could suffer if suitable habitat for native bees (and plants) is not maintained, although a more in-depth study is required to investigate this further. Additionally, investigation into the extent of outcrossing as well as its effect on offspring fitness is also recommended to better understand the reproductive biology of this species. Further advancing this type of knowledge would require experimental manipulation of wild populations, which might present challenges due the rarity of this species and its conservation status.

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Figure Legends

Figure 1

Telesonix jamesii growing from a crevice in the alpine of Pikes Peak, CO. Photo: K. Barthell

Figure 2

Map of the Pikes Region with points projected where each pollination survey was conducted

Figure 3

Confamilial species to *Telesonix jamesii* (left) and their pollen (right). Species from top to bottom: *Telesonix jamesii* (Photo: A. Gaier, 2021), *Heuchera hallii* (Photo: K. Carragher, 2022), *Micranthes rhomboidei* (Photo: D. Martin, 2021), *Cilaria austromontana* (D. Hirt, 2022), *Saxifraga rivularis* (J. Toews, 2020).

Figure 3

Click here to access/download;

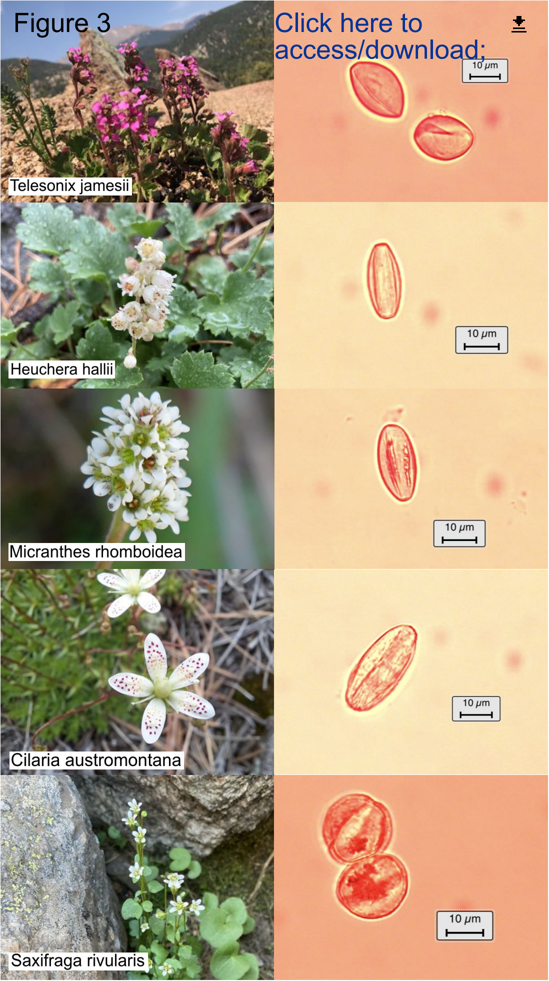

Figure 2

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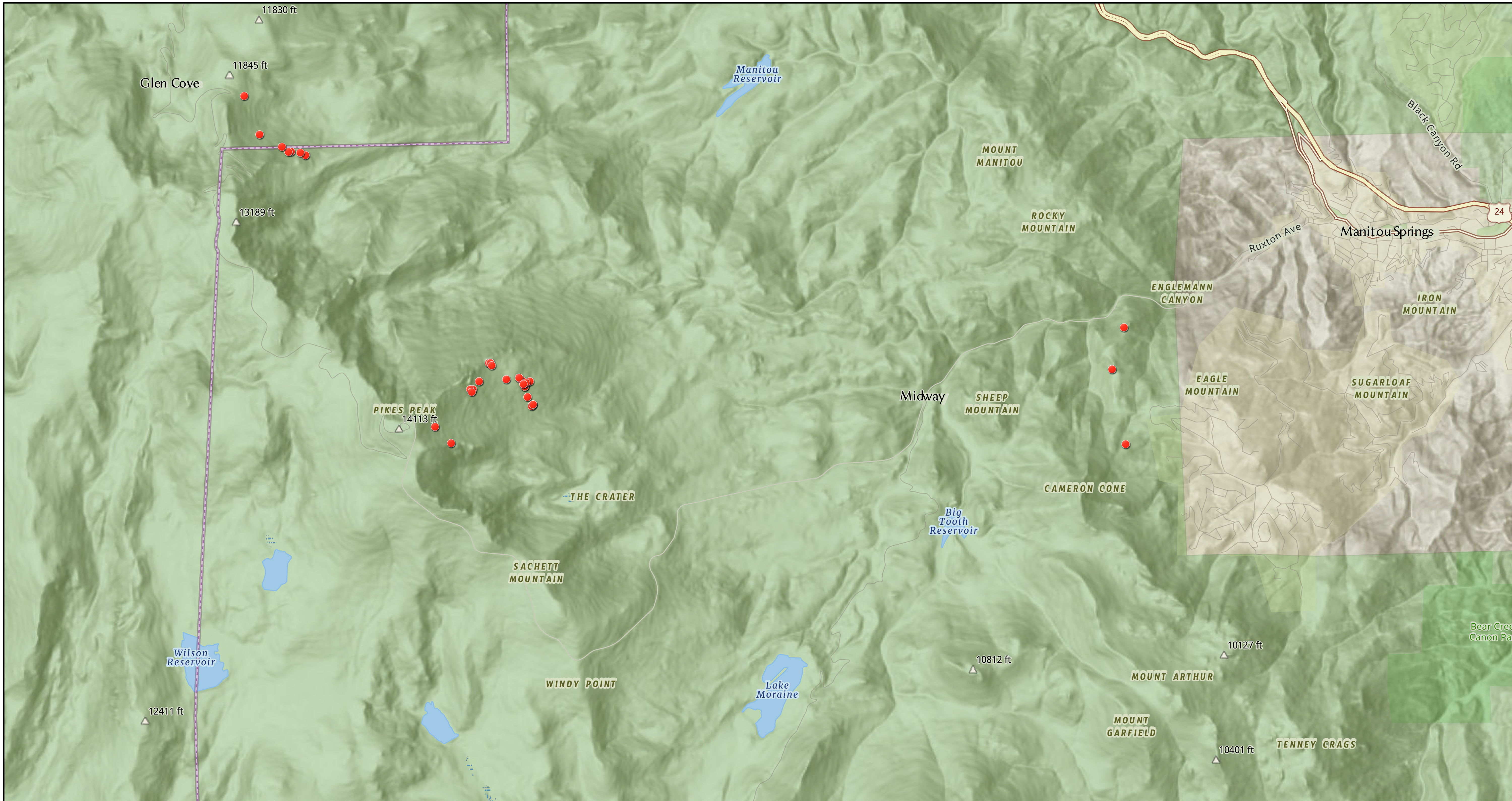
Survey Locations



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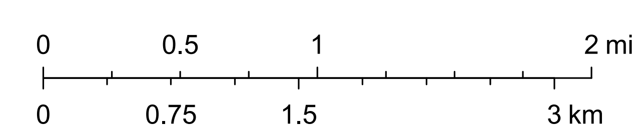

Table 1.

Species observed visiting flowers of *Telesonix jamesii*, and their relative number of occurrences, at Pikes Peak from 2019 to 2021. Thirty-eight of the interactions were from surveys conducted exclusively for this study. Seventeen were drawn from a concurrent study (see Methods). Species carrying pollen of *T. jamesii* is reported. No individuals of *Selasphorus platycercus* were collected and examined for pollen, thus effectiveness is recorded as NA.

Order	Family	Species	Number of times observed	Pollen Carrier
Hymenoptera	Halictidae	*Agapostemon sp.*	2	No
Hymenoptera	Apidae	*Anthophora montana*	4	No
Hymenoptera	Apidae	*Bombus balteatus*	4	No
Hymenoptera	Apidae	*Bombus bifarius*	10	Yes
Hymenoptera	Apidae	*Bombus centralis*	1	No
Hymenoptera	Apidae	*Bombus flavifrons*	7	No
Hymenoptera	Apidae	*Bombus huntii*	2	Yes
Hymenoptera	Apidae	*Bombus melanopygus*	5	No
Hymenoptera	Apidae	*Bombus sylvicola*	4	Yes
Diptera	Empididae	*Empididae sp.1*	1	No
Diptera	Empididae	*Empididae sp.2*	1	No
Hymenoptera	Formicidae	*Formica sp.*	1	No
Hymenoptera	Halictidae	*Lassioglossum sp.*	1	No
Diptera	Muscidae	*Muscidae sp.*	4	No
Diptera	Platypezidae	*Platypezidae sp.1*	4	No
Diptera	Platypezidae	*Platypezidae sp.2*	1	No
Apodiformes	Trochilidae	*Selasphorus platycercus*	1	NA
Diptera	Syrphidae	*Syrphidae sp.1*	1	No
Diptera	Syrphidae	*Syrphidae sp.2*	1	No
		Total:	55	

Figure 1

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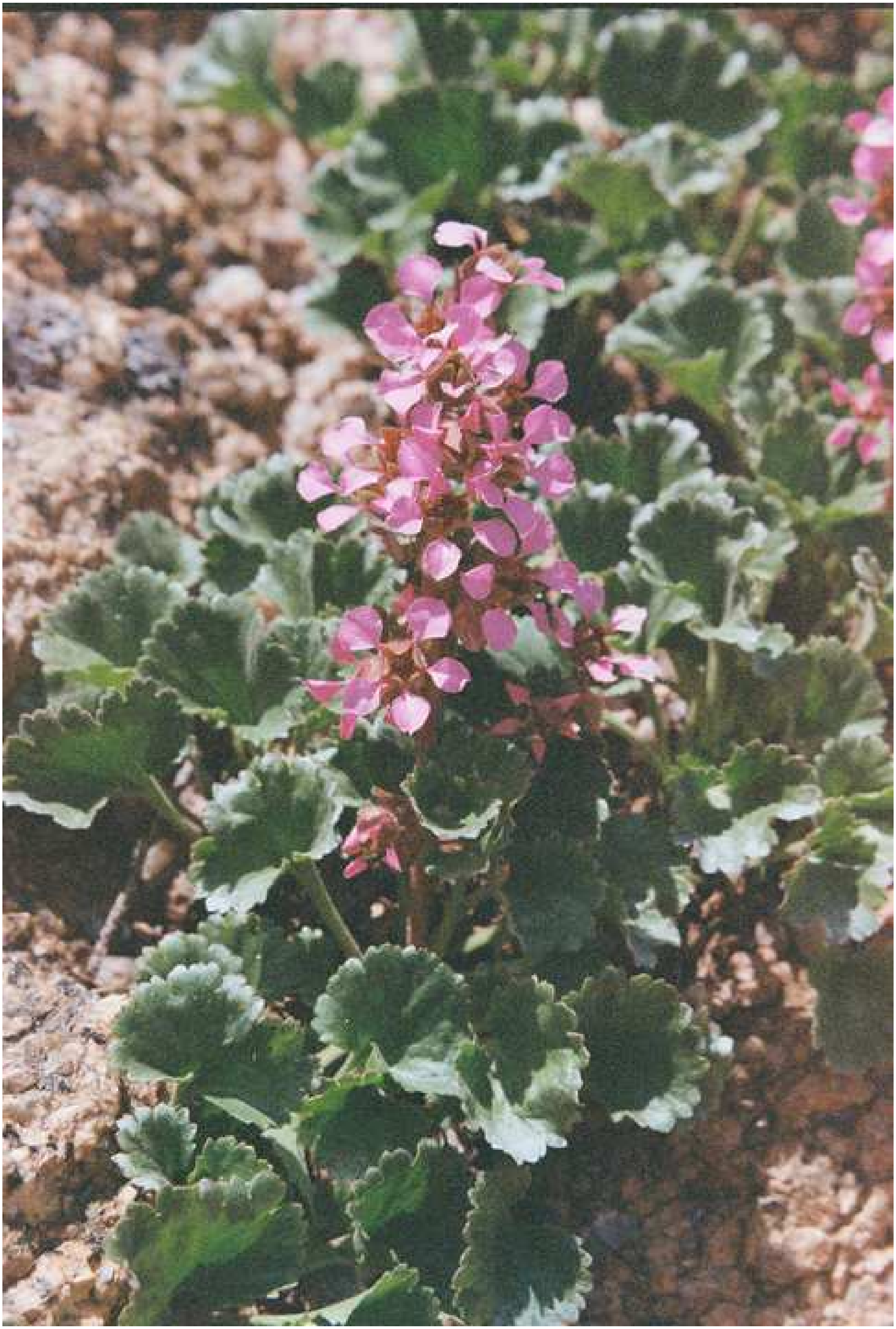

Table 2.

Mean length x width ratios for each representative species across genera of Saxifragaceae co-located with *Telesonix jamesii* in the Pikes Peak region. Sample size and standard error indicated for each species.

Species	Mean	SE	N
Telesonix jamesii	1.229	0.0394	5
Heuchera hallii	1.914	0.0482	5
Micranthes rhoda	1.785	0.155	4
Ciliara austromontana	1.813	0.0787	5
Saxifraga rivulus	1.053	0.0228	5