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 to 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, Colorado. We conducted a total of 899 min 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 work 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.

RESUMEN.—*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, Colorado. 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* 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.

The persistence of many rare and endemic plant species relies on sexual reproduction within local populations (Bailey and Kevan 2017). Although many rare plants have developed selfcompatibility 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). Climateinduced 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% to 55% of alpine species and 31% to 51% of subalpine species will lose 80% of their habitat in European mountains by 2070–2100 (Engler et al.

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Fig. 1. *Telesonix jamesii* growing from a crevice in the alpine of Pikes Peak, Colorado. Photo: K. Barthell.

2011). This loss not only constricts habitat for high-elevation rare plants but is also likely to 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. Because *T. jamesii* has been reported at only 19 sites in Colorado, 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 4184 m (Beatty et al. 2004). *Telesonix jamesii* flowers from late June through July at lower elevations and from July through August at

higher elevations (Ackerfield 2015). It is an obligate chasmophyte, growing out of rock crevices and talus substrates to avoid interspecific competition and disturbances such as fire (Beatty et al. 2004, Antonsson 2012). This life history strategy facilitates persistence of stress-tolerant species with poor competitive abilities 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 as growing on granite tors in dry, nutrient-poor soils in areas with high exposure to wind and ultraviolet (UV) radiation (Beatty et al. 2004). These conditions offer unique habitats that are distinct 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), who noted that species of *Telesonix* are self-compatible to varying degrees. Despite *T. jamesii* being a species of conservation concern, there have been no studies focused on mechanisms of pollination and 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*? And (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



Fig. 2. Map of the Pikes Peak Region, Colorado, with points projected where each pollination survey was conducted.

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 easternfacing slopes. At lower elevations below tree line, *T. jamesii* was uncommon, predominantly growing only in isolated forest clearings with rocky substrate.

Floral community composition and abundance varied across locations. Scattered plants of *Heuchera hallii* (Saxifragaceae), *Ciliaria austromontana* (Saxifragaceae), *Jamesia americana* (Hydrangeaceae), 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 min. 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 (humming-

birds) 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 Messinger Carril 2015), as well as 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 were identified by sight using The Sibley Field Guide to Birds of Western North America (Sibley 2016). For insects, a clean aspirator was used to ensure that 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 a total of 837 min 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 min of observations was obtained from a related ongoing study that is investigating plant–pollinator interactions in the Pikes Peak region. These observations took place across 3 summers from 2019 to 2021. Because pollinators from this latter study were not collected with a freshly cleaned aspirator, 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 (Boulder, CO). 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, Colorado. One species from each genus of Saxifragaceae was selected for comparison. Confamilial species were Heuchera hallii, Micranthes rhomboidea, Ciliaria austromontana, and Saxifraga rivularis. Pollen grains were deposited onto slides by plucking one anther from a plant, swirling it in a glycerine solution for 10 s, and mashing the anther to release as much pollen as possible. Length \times width ratios of 5 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 No. 1 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 and 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 whether the grain 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 the purposes of this study.

Statistical Analysis

Rarefaction can be used to estimate species richness from field sampling and to 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 all species visiting T. jamesii and for 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 Material 1). Twenty-one were observed in the concurrent study across the summers of 2019, 2020, and 2021 (Supplementary Material 2). On average, T. jamesii was visited once every 16.4 min across the 899-min 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 bumble bees (Bombus), which constituted over half (60%) of all observed visitors. We recorded 7 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 3 visitations below tree line in total (Supplementary Material 1).

			Number of times	
Order	Family	Species	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	Lasioglossum 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	

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* are reported. No individuals of *Selasphorus platycercus* were collected and examined for pollen; thus, effectiveness is recorded as NA.

TABLE 2. Mean length \times width ratio for each representative species across genera of Saxifragaceae colocated with *Telesonix jamesii* in the Pikes Peak region, Colorado. Sample size and standard error are indicated for each species.

Species	Mean	SE	п
Telesonix jamesii	1.229	0.0394	5
Heuchera hallii	1.914	0.0482	5
Micranthes rhomboidea	1.785	0.155	4
Ciliaria austromontana	1.813	0.0787	5
Saxifraga rivularis	1.053	0.0228	5

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 have 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 3 distinct open colpi joining at the pole.

Effective Pollen Carriers

Of the 19 species observed visiting T. jamesii, only 3 bore pollen grains on their bodies that matched T. jamesii (Table 1). All of these species were bumble bees (Bombus bifarius, B. sylvicola, and B. huntii). Although only 3 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 Material 3), which was estimated at 35 species. Rarefaction analysis showed that our observed richness of 3 effective pollinator species represented approximately 60% of estimated effective pollinator species richness, which was 5 species (Supplementary Material 3). However, these 2 estimated unsampled species are not abundant visitors, so their importance to T. jamesii as pollinators is likely low.

DISCUSSION

Telesonix jamesii is visited by a wide variety of pollinators. This is consistent with other arctic and alpine members of Saxifragaceae, which are thought to attract a variety of dipteran



Fig. 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 rhomboidea* (Photo: D. Martin, 2021), *Ciliaria austromontana* (Photo: A. Gaier, 2022), *Saxifraga rivularis* (Photo: J. Toews, 2020).

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 9 saxifrage species in North America characterized by their small flowers. At least 2 members of Colletidae, Colletes aestivalis and Colletes andrewsi, are 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 determined that pollination from bees resulted in overall greater seed set (Ornduff et al. 1975). Bees made up the majority of visitors in our study. Bumble bees were both the most common visitors and the most effective at carrying conspecific pollen. Pollen grains may have more success attaching to the numerous setae covering bumble bee bodies. Even disregarding corbicular loads, bumble bees 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 species are the only effective pollinators. Bumble bees 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 bumble bees 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, Mola et al. (2020) found no evidence that changes in habitat structure or elevation restricted bumble bee movement. This suggests that while B. bifarius may be geographically limited in its role as a pollen disperser for T. jamesii, it is unlikely that the species is 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 of seed dispersal for *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 animalmediated 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 plant that is unknown. Gornall and Bohm (1985) concluded that T. jamesii is self-compatible, but they did not investigate the fitness cost of asexual versus sexual reproduction (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 description fits the life history strategy of T. jamesii, which has to colonize and establish roots in rock crevices with harsh ultraviolet light 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 characteristic is absent from other closely related species in the genera Saxifraga and Boykinia (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 the 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 defense against herbivores. 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 the range of T. jamesii. Further genetic studies could clarify metapopulation dynamics, indicate the extent of phenotypic plasticity, and improve our understanding of the relationship between this species and its only congener, T. heucheriformis (Beatty et al. 2004). Telesonix heucheriformis 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 2 species could provide insights into the causes 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, 2019). Another caveat is having only 55 observed pollination events, which is a limited sample size. With nearly 900 min of field surveys in our study, it is likely that T. jamesii is simply not visited by pollinators very often. Rarefaction can help us account for incomplete sampling efforts, but it 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 into this system by comparing pollination at other populations besides Pikes Peak to see whether the patterns we observed generalize beyond a local scale.

Our study provides a greater understanding of the breeding system of T. jamesii on Pikes Peak. To our knowledge, we provide the first ecological field data on the pollination of this species, specifically the importance of bumble bees 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 T. jamesii and its conservation status.

SUPPLEMENTARY MATERIAL

Three online-only supplementary files accompany this article (https://scholarsarchive.byu.edu/ wnan/vol83/iss1/7).

SUPPLEMENTARY MATERIAL 1. Details of all 36 surveys conducted in the summer of 2020.

SUPPLEMENTARY MATERIAL 2. Additional floral observations of *Telesonix jamesii* in the Pikes Peak region, Colorado. Surveys were conducted for an ongoing study by Resasco et al.

SUPPLEMENTARY MATERIAL 3. Species accumulation curves for all recorded floral visitors of *Telesonix jamesii* and the pollinators found carrying conspecific pollen.

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