

RIBES (GROSSULARIACEAE) POLLINATION IN NORTHERN CALIFORNIA:
STRONG OVERLAP IN VISITOR ASSEMBLAGES DESPITE FLORAL DIVERSITY

By

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ABSTRACT

RIBES (GROSSULARIACEAE) POLLINATION IN NORTHERN CALIFORNIA: STRONG OVERLAP IN VISITOR ASSEMBLAGES DESPITE FLORAL DIVERSITY

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The genus *Ribes* displays extensive floral diversity. The pollinator shift model suggests that such diversity is an outcome of species shifting to specialize on new pollinators. To test this model, I surveyed the flower visitors of 14 *Ribes* species at 44 sites in northern California and southern Oregon. Visits to sympatric species in other genera were also counted at each site. For purposes of analysis, visitors were placed into one of ten functionally equivalent groups. *Ribes* species were chosen to maximize differences in flower size and form; ten floral traits were measured for each species to characterize these differences. Ordination and correlation approaches were used to compare visitor assemblages, both within and between species, as well as to examine the match between differences in flower morphology and visitor assemblages. I found only weak support for the pollinator shift model. Despite the marked differences between *Ribes* flowers, most of the 14 species were visited primarily by bees. In general, differences in floral morphology were poor predictors of differences in visitor assemblage, but flower depth and width were both correlated with the ordination of species in visitor space. Most *Ribes* species are not strong pollination specialists. Visitor assemblages varied as much

between sites for individual species as they did between different species. Although shifts between pollinators may account for some of the differences between *Ribes* flowers, it appears that other factors play a greater role in floral diversification.

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INTRODUCTION

The idea that pollinators play a role in the evolution and diversification of flowers is almost as old as the idea of natural selection (Darwin, 1862). This evolutionary linkage between pollinators and flowers provides an explanation for why some groups of closely related plants have flowers that differ in morphology, scent, visitor reward, bloom time, and other attributes that affect interactions with pollinators. The pollinator shift model is one of the leading hypotheses used to explain floral diversity. This model postulates that flowers diverge as they respond to selective pressures exerted by novel pollinators. Specialization on different pollinator species, or different groups of functionally similar pollinator species, has been invoked to explain floral diversity in many genera and families of angiosperms (Pijl, 1960; Grant & Grant, 1965; Stebbins, 1970; Faegri & Pijl, 1979; Kiestler, 1984; Sakai et al., 1999; Bradshaw & Schemske, 2003; Fenster et al., 2004; Wilson et al., 2004; Thomson & Wilson, 2008; Schlüter et al., 2009; Wester and Classen-Bockhoff, 2011). For example, different species of *Aquilegia* have adapted to different sets of pollinators (bees, hummingbirds and hawk moths) via changes in color and nectar spur length (Whittall & Hodges, 2007).

The genus *Ribes* L. (currents and gooseberries, Grossulariaceae) has one of the broadest ranges of floral morphology of any temperate zone woody genus (M. Mesler, personal communication). Flowers differ strongly in color, shape, size, angle of presentation, nectar accessibility, and degree of anther and stigma exertion (Figure 1). Such diversity provides an excellent opportunity to test the pollinator shift model, which

predicts that differences in floral traits across species will be matched by corresponding differences in pollinator assemblages. In fact, some *Ribes* species have sets of floral features suggestive of classical fly, moth, bee, or hummingbird floral syndromes, but very little work has been conducted on the pollination of *Ribes* in the wild. Known pollinators include bumblebees (*Bombus*: Thorp, 1983; Thorp et al., 2002), *Osmia* bees (Torchio, 1976), anthophorid bees (Cole, 1978), hummingbirds (Grant & Grant, 1968; Pojar, 1975), butterflies (Davidson, 1898), fungus gnats (Mycetophilidae: Okuyama et al., 2008), small and large syrphid flies, bombyliids, and day-flying hawkmoths (M. Mesler, personal observation). To date, no study has documented the visitor assemblages of multiple species of *Ribes* with divergent flowers across several sites.

I compared the flowers and visitor assemblages of 14 species of *Ribes* at several sites in northern California and southern Oregon (Table 1, Figure 2). My specific objectives were to determine: (a) which insects and birds, organized by functional group, visit each species; (b) the degree to which differences in floral morphology predict differences in pollinators; and (c) for each species, the degree of consistency in pollinator assemblages across several sites. Unfortunately, a well-resolved phylogeny is not yet available for *Ribes* (Messinger, 1999; Senter & Soltis, 2003; Schultheis & Donoghue, 2004), precluding certain kinds of tests of the pollinator shift model for the genus. Nevertheless, my findings address fundamental predictions of the pollinator shift model – that pollinator assemblages vary with flower morphology and pollinators are consistent across multiple sites.



Figure 1. *Ribes* flowers (clockwise from the top left): *R. roezlii*, *R. cereum* (with leaf), *R. sanguineum* var. *sanguineum*, *R. lasianthum*, *R. bracteosum*, and *R. montigenum*. Illustration by Jade Paget-Seekins

METHODS:

Study Species

Pollinator visits to 14 *Ribes* taxa (hereafter referred to as species; Table 1) were surveyed at three to eight sites each, depending on the taxon. Two of those species received too few visits (< 25 at most sites) to be used in the data analysis (Table 1). Species were chosen to include as much diversity in flower form and color as possible within the geographic constraints of northern California and adjacent southern Oregon (Figure 2). Species that tended to grow sympatrically and bloom concurrently were favored. Comparisons of the visitor assemblages of sympatric species should be especially informative because these species share a common visitor pool.

Study Sites

This study was conducted at 44 sites, nine of which had two to five sympatric *Ribes* species blooming during field observations. The sites extended from southwestern Oregon near Cave Junction to south of Lake Tahoe in California (Figure 2) at elevations ranging from 6m to 2,662m. I visited each site once between 28 February and 23 July 2010, and collected data on flower visitation and flower morphology at each site (see Flower Morphology and Visitor Surveys for details).

Table 1. *Ribes* species included in the study, subgenera follow Berger (1924). Sepal colors are listed; petals are more-or-less white unless otherwise noted.

Species	Sepal Color
Subgenus <i>Calobotrya</i>	
<i>Ribes cereum</i> Douglas	White to pale pink
<i>Ribes sanguineum</i> var. <i>glutinosum</i> (Benth.) Loudon	Pink
<i>Ribes sanguineum</i> var. <i>sanguineum</i> Pursh	Dark pink
<i>Ribes viscosissimum</i> Pursh	Off-white
Subgenus <i>Coreosma</i>	
<i>Ribes bracteosum</i> Douglas*	Greenish-brown
Subgenus <i>Grossularia</i>	
<i>Ribes divaricatum</i> Douglas	Deep red to green
<i>Ribes inerme</i> Rydb.	Deep red to green
Subgenus <i>Grossularioides</i>	
<i>Ribes lacustre</i> (Pers.) Poir.*	Dull yellow (reddish petals)
<i>Ribes montigenum</i> McClatchie	Dull yellow (dull red petals)
Subgenus <i>Hesperia</i>	
<i>Ribes roezlii</i> Regel	Deep red
Subgenus <i>Lobbia</i>	
<i>Ribes binominatum</i> A. Heller	Green
<i>Ribes lasianthum</i> Greene	Bright yellow (yellow petals)
<i>Ribes lobbii</i> A. Gray	Deep red
<i>Ribes marshallii</i> Greene	Deep red (bright yellow petals)

* received too few visits to analyze

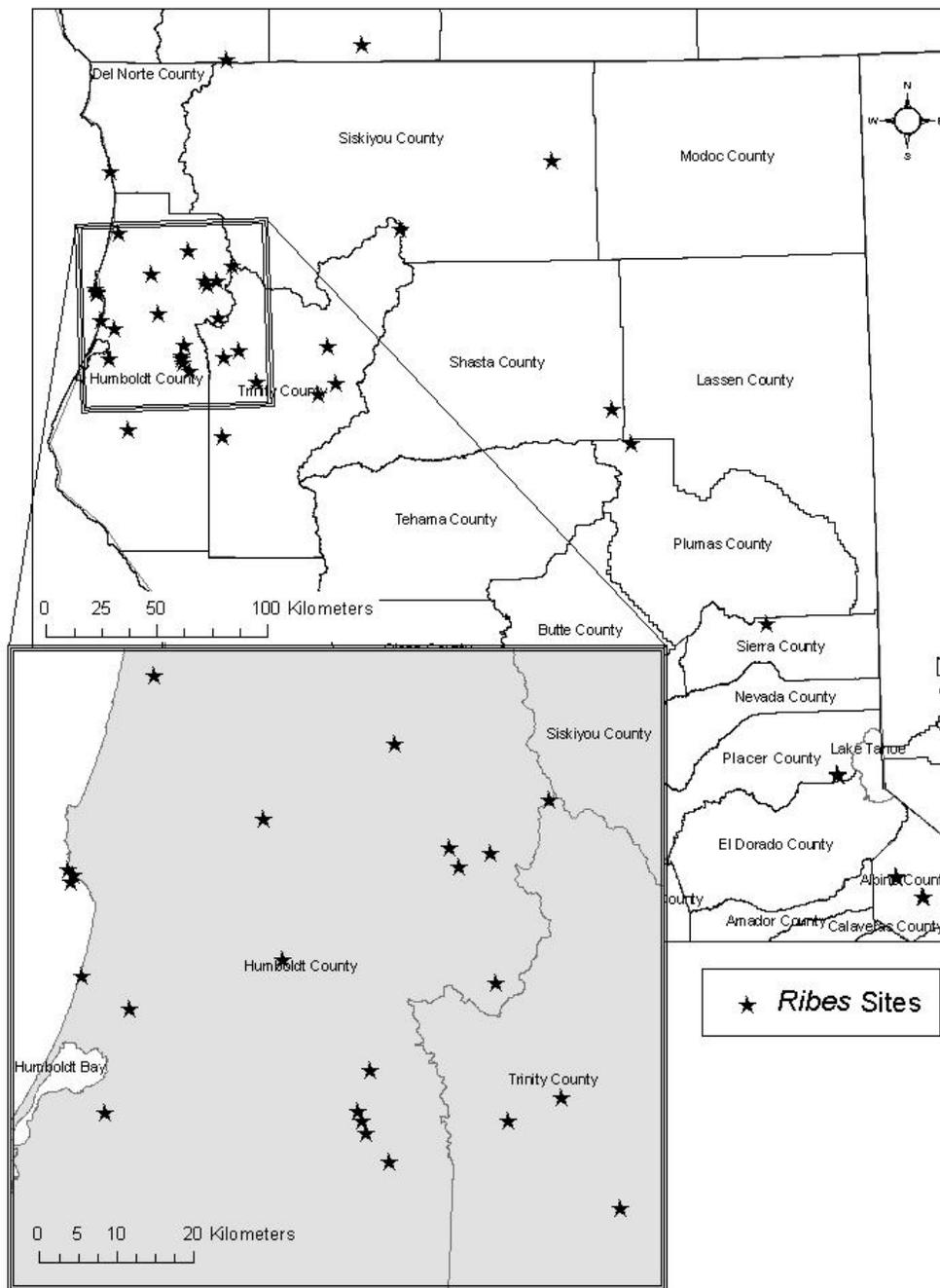


Figure 2. Map of northern California and southern Oregon. Black stars represent study sites.

Flower Morphology

Five representative flowers (usually from different shrubs) were measured from each *Ribes* species at each site. Floral features relating to three aspects of pollination were deemed important – attractiveness to visitors, visitor access to nectar rewards, and placement of pollen on visitor bodies. I chose to measure SEPAL LENGTH, since sepals are the showiest part of *Ribes* flowers and thus an important attribute in attracting visitors. SEPAL and PETAL COLORS were recorded, using a Munsell color chart. Color is an important visual attractor with different pollinator classes generally being attracted to different colors (Faegri and Pijl, 1979). I took five measurements relating to nectar accessibility. PETAL LENGTH, measured from the rim of the hypanthium, was included because petals often point forward and constrict access to nectar in this genus. HYPANTHIUM LENGTH was measured from the point where the sepals and petals separate to the top of the inferior ovary. This important feature is related to access to nectar. Unless flower tissue is torn, consumption of nectar from the base of a deep hypanthium is limited to visitors with long mouth-parts or ones small enough to crawl to the base of the flower. HYPANTHIUM WIDTH was measured at the mid-point of the hypanthium tube, or just above the ovary for the flat-faced flowers. Because petals and/or sepals extend forward beyond the hypanthium in most taxa and thus more-or-less block the opening of the flower, effective FLOWER DEPTH was measured from the distal edge of the perianth parts to the top of the inferior ovary. Effective FLOWER WIDTH was measured at the narrowest point of access to the flower. This position generally corresponded to gaps

between closely apposed petals and/or the width of narrow tube-shaped petals, although larger visitors could readily push petals apart to gain access to nectar. Except for the three flat-faced flowers, flower width was less than hypanthium width. STIGMA and ANTHHER EXSSERTION were both measured from the distal edge of the petals (or the sepals if they were farther forward) to the tip of the stigma or anther. Placement of the stigma and anthers in relation to the rest of the flower is important for pollen deposition on and retrieval from visitor's bodies. The above measurements, except color, were all taken using digital calipers precise to a tenth of a millimeter.

I calculated Euclidean distances based on seven of the above traits to express degree of morphological difference between pairs of species (PC-ORD, McCune and Mefford 2006). Color was not included in the analysis because it was not scored numerically. Anther exsertion was also omitted, because it was strongly correlated with stigma exsertion. The calculations used trait averages standardized by subtracting the lowest value for that trait then dividing by the highest value (the range). I also compared floral morphology visually using a graph incorporating FLOWER DEPTH, STIGMA EXSSERTION, SEPAL LENGTH, and SEPAL COLOR.

Visitor Surveys

At every site, I counted the number of visits to flowers of each *Ribes* species during three 1/2-hour long census periods, generally all in the same day. In some cases, student volunteers helped with the censuses. Sites were only surveyed if at least 100

Ribes flowers were in bloom and if weather conditions were favorable to pollinator visits. At the start of each census, I measured wind speed, temperature and approximate cloud cover. Census periods were spaced throughout the day and were generally divided into six 5-minute blocks or occasionally three 10-minute blocks, to allow observation of different shrubs or groups of shrubs. At sites with only a few exceptionally flower-rich shrubs, or with closely spaced groups of shrubs, the same three to six observation points were used for each of the census periods. At other sites, each survey used a different location. When possible, shrubs with dozens to hundreds of open flowers were chosen, but the number of flowers observed varied based on species and site. Only potential pollinators were included in the counts; obvious nectar thieves and other visitors that did not look likely to contact anthers or stigmas were not recorded as visitors. Brief descriptions of each visitor were made. Sites with fewer than 25 visits were not used in subsequent analyses due to insufficient data.

When two or more *Ribes* species were present at a site, each was still observed for 1.5 hours, but in 5- or 10-minute censuses. These censuses were interspersed, so that the time of day each species was observed would be approximately the same. At three sites with more than two *Ribes* species in bloom, observations were made over consecutive days, with each species observed each day.

After each *Ribes* census I surveyed visitors to non-*Ribes* flowers for half-an-hour, to judge the degree to which *Ribes* species specialized on a subset of the available

pollinators at that site. When possible I counted visits to the three non-*Ribes* species with the greatest number of open flowers for one 10-minute census period each, but at some sites only one or two species were available. A total of 1.5 hours of observations were made at co-flowering plants at all sites. When three or more *Ribes* species were surveyed at a site, the co-flowering censuses were broken up into smaller blocks of time (5- or 10-minutes long) and interspersed with the *Ribes* censuses.

Floral Visitors

After each census, I collected at least one voucher specimen for most of the insect flower visitors for identification and documentation. Bird visitors were not collected, and several species identifiable in the field were not collected at every site. Vouchers have been deposited at Humboldt State University.

Visitors were identified to family and genus when possible, but for purposes of analysis they were grouped according to size and other features that influence access to floral rewards, pollen movement, and flower handling. Such a functional-group approach has the merits of grouping species that likely exert the same or similar selective pressures on flower traits (in spite of taxonomic differences) and of providing a more meaningful measure of degree of specialization (Fenster et al., 2004). Visitors to flowers of *Ribes* and co-flowering species were placed into ten functional groups (Table 2). Most of the groups are very different from each other; however, SMALL BEES gradates into MEDIUM BEES, which in turn gradates into LARGE INSECTS. Honeybees, which would be in

MEDIUM BEES, were treated as a separate functional group distinct from the others since *Ribes* in California have only interacted with them for a few hundred years. If these two groups of bees were lumped together into one group the significance of the analyses would not change.

Insects not collected or identified were put into functional groups based on descriptions made at the sites. One percent of the total visits (175/16317) did not have enough information about visitors recorded to group them without specimens; these visits were excluded from analysis.

Analysis of Floral Visitors

I performed a 10×12 contingency table analysis to test for differences in the composition of pollinator assemblages among the 12 *Ribes* species, using the function `chisq.test (simulate.p.value=T)` (R Development Core Team, 2009). Since many observed values were < 5 , it was necessary to calculate p values using a randomization approach; I used 99,999 replicate runs. The randomization approach works by populating each cell randomly while keeping row and column totals constant. The p value was obtained by comparing the χ^2 value for the original table against the distribution of χ^2 values generated by the randomization. Similar contingency table analyses compared the visitor assemblages for each *Ribes* species across sites.

Table 2. Families/genera/orders included in the 10 functional groups.

large insects: *Bombus*, *Criorhina*, Vespinae (including *Vespula acadica*, *Dolichovespula arenaria*), *Xylocopa*, large *Anthophora*, *Habropoda miserabilis*, other *Habropoda*

medium bees: larger *Osmia*, most *Andrena*, *Eucera* (long horn bees), *Halictus*, smaller *Anthophora*, *Anthophora urbana*, smaller *Habropoda* (male)

honey bee: *Apis mellifera*

small bees: most male and some smaller female *Osmia*, *Lasioglossum* (*Dialictus*, *Evyllaesus*, and *Lasioglossum*), *Nomada*, small *Andrena*, small Halictid, *Ceratina*, *Hoplitis*, small Megachilidae, *Stelis*, *Megachile*, small wasps

tiny bees: tiny *Lasioglossum* (*Evyllaesus* and *Dialictus*), tiny *Nomada*, tiny Megachilidae, *Hyllaeus*, tiny wasps

medium/small flies: most Diptera unless listed elsewhere, including many Syrphidae

tiny fly: nematoceros or lower flies (the former suborder Nematocera), Empididae

beetle: (visited co-flowering plants) Coleoptera, including Cleridae, Buprestidae, Cantharidae, Cerambycidae, Melyridae

long proboscis: *Bombylius*, Lepidoptera (butterflies and moths including day flying hawkmoths), Geometridae, *Proserpaus clarkiae* (when it was not a nectar thief)

hummingbird: Anna's Hummingbird (*Calypte anna*), Rufous Hummingbird (*Selasphorus rufus*), another bird (possibly American Goldfinch)

Equation 1. Proportional Similarity (PS) = $1 - 1/2 \sum |P_{ai} - P_{bi}|$

i = a functional group, a and b = *Ribes* species (or sites), P = proportion of visits

I calculated proportional similarity (PS) values (Equation 1; Smith et al., 2008) to quantify degree of overlap in visitor assemblages for pairs of *Ribes* species or for pairs of populations of the same species. These similarity values were used to examine the correlation between degree of floral and visitor similarity for pairs of *Ribes* species, as well as to further quantify the consistency of visitor assemblages across sites for a given species, and to compare the visitor assemblages of sympatric species. Proportional similarities were converted to differences by subtracting each value from 1, and used in a Non-metric Multidimensional Scaling (NMS) ordination (in R with the packages MASS {Ripley et al., 2012} and vegan {Oksanen, et al. 2012}). A secondary matrix of seven floral traits was then correlated to the NMS plot (9,999 permutations were used to obtain p -values for these correlations). A table of the proportion of visits from each functional group was also correlated with the NMS plot.

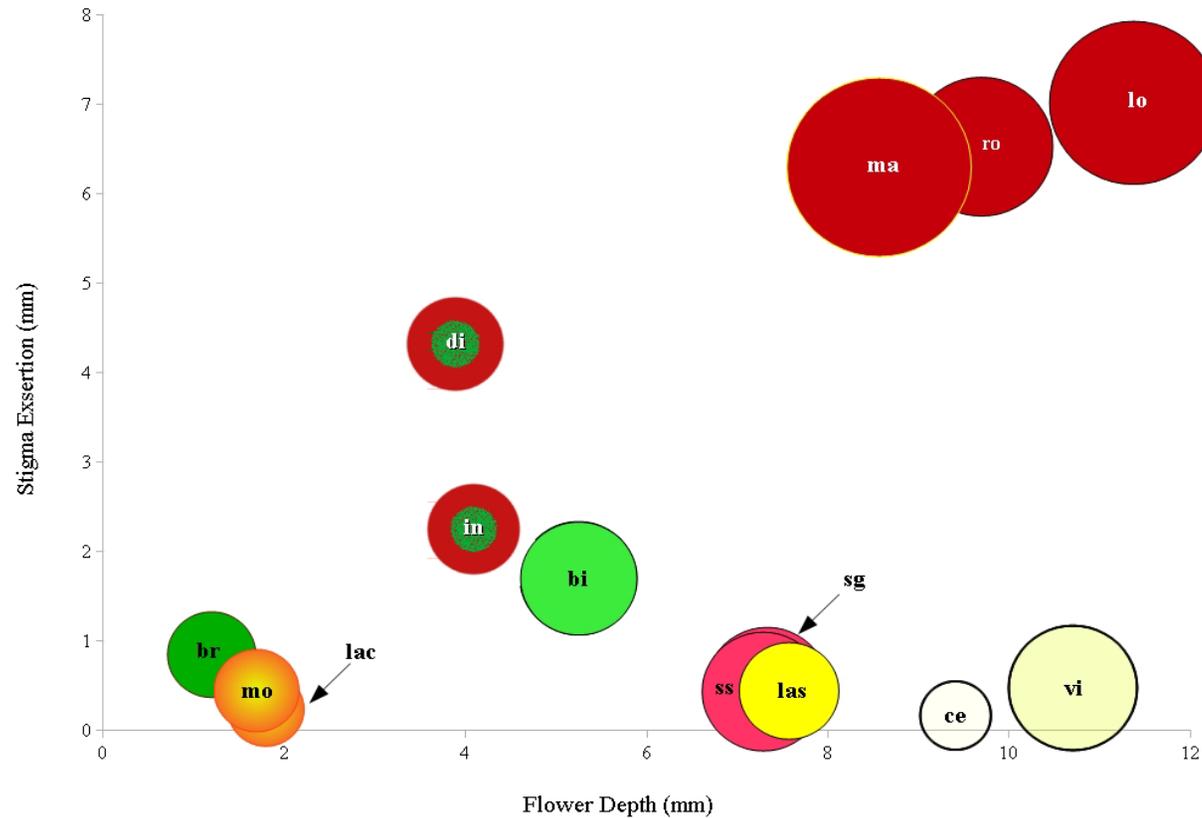


Figure 3. A graph representing four *Ribes* flower traits. Color roughly corresponds to sepal color, and size corresponds to sepal length.

bi = *R. binominatum*, br = *R. bracteosum*, ce = *R. cereum*, di = *R. divaricatum*, in = *R. inerme*, lac = *R. lacustre*, las = *R. lasianthum*, lo = *R. lobbii*, ma = *R. marshallii*, mo = *R. montigenum*, ro = *R. roezlii*, sg = *R. sanguineum* var. *glutinosum*, ss = *R. s. sanguineum*, vi = *R. viscosissimum*

Table 3. Mean morphological measurements of *Ribes* flowers, all numbers are millimeters. Species ordered by flower depth.

<i>Ribes</i> species	Sepal	Petal	H length	H width	F depth	Stigma	Anther	F width
<i>R. lobbii</i>	11.51	6.13	5.28	3.97	11.37	7.02	5.59	1.65
<i>R. viscosissimum</i>	6.72	3.45	7.52	5.33	10.7	0.48	0.03	2.18
<i>R. roezlii</i>	8.34	4.14	5.66	3.56	9.69	6.53	3.52	1.53
<i>R. cereum</i>	2.04	0.96	9.41	2.27	9.41	0.17	0	1.60
<i>R. marshallii</i>	13.83	4.97	3.70	3.98	8.56	6.30	6.16	0.06
<i>R. lasianthum</i>	4.04	2.78	5.11	2.69	7.57	0.44	0	0.79
<i>R. s. var. glutinosum</i>	6.01	3.21	4.29	3.34	7.33	0.49	0.12	2.71
<i>R. sanguineum var. s.</i>	6.11	3.88	3.71	2.85	7.29	0.43	0	1.72
<i>R. binominatum</i>	5.58	2.57	3.04	3.70	5.24	1.70	1.40	2.09
<i>R. inerme</i>	3.51	1.59	2.56	2.93	4.13	2.27	2.05	2.54
<i>R. divaricatum</i>	3.89	1.71	2.45	2.95	3.91	4.32	3.86	2.50
<i>R. lacustre</i>	2.38	1.38	1.01	2.77	1.80	0.24	0.39	2.89
<i>R. montigenum</i>	2.94	1.21	0.52	3.12	1.69	0.45	0.50	4.95
<i>R. bracteosum</i>	3.18	1.14	0.97	2.13	1.20	0.85	0.83	2.33

Sepal = sepal length, Petal = petal length, H length = hypanthium length, H width = hypanthium width, F depth = flower depth, Stigma = stigma exsertion, Anther = anther exsertion, F width = effective flower width

RESULTS

Characterization of Flower Morphology

Using four morphological traits the *Ribes* flowers fall into three tight groups, with five ungrouped species (Figure 3, see Table 3 for all the trait measurements). *Ribes marshallii*, *R. roezlii* and *R. lobbii* are similar; the shape and length of their petals restricts access to nectar, they have crimson sepals, and exerted stigmas and anthers. The two *R. sanguineum* varieties and *R. lasianthum* have flowers with slightly exerted stigmas, and petals that extend beyond the hypanthium, lengthening the flower depth. *Ribes bracteosum*, *R. montigenum* and *R. lacustre* all have open flowers with very short hypanthia, tiny petals, and almost no nectar. The distance between *R. inerme* and *R. divaricatum* on the figure is the one detail that is misleading; they are actually very similar to each other, except for stigma and anther exertion.

Floral Visitors

We observed more than 16,000 visits to *Ribes* flowers by potential pollinators across the 44 study sites. The number of visits per site varied between species (Table 4). Two species, *R. bracteosum* and *R. lacustre*, received very few visits. With the exception of one individual syrphid fly that visited 67 flowers in succession, we recorded only 29 visits to flowers of *R. lacustre* in 4.5 hours of observation (three sites). At one site we saw only two visits, despite many open flowers and fair weather. *Ribes bracteosum*, also observed in full bloom, received only 18.5 visits per site. Both species were observed additionally at dawn and dusk, as well as mid-day. Since so few visits were observed,

these two species are not included in data analysis. Of the remaining species, *R. viscosissimum*, *R. inerme* and *R. montigenum* had the fewest visits, with an average of only about 68 per site. At the other extreme, *R. cereum* had the most visits per site, with a mean 658 visits (in 1.5 hours). The other eight species were between these two extremes, with on average 273 visits per site (Table 4).

The visitor assemblages of the 12 analyzed *Ribes* species differed significantly ($\chi^2=15740$, $p<0.0001$), but there was considerable overlap in the visitors to different species (mean pairwise proportional similarity=0.497, SD=0.203, n=66 pairs, Table 5). *Ribes lasianthum* and *R. viscosissimum* had the most similar sets of visitors (PS=0.870). In contrast, *R. montigenum* had the most distinct visitor assemblage. Its visitors were most similar to *R. binominatum* (0.360) and least similar to *R. marshallii* (0.062). Interestingly, *R. sanguineum* var. *sanguineum* shared as many visitors with *R. roezlii* (0.768) as with *R. s. var. glutinosum* (0.757). The former two taxa occurred sympatrically at three sites. Results of the ordination analysis also suggest strong overlap in visitor assemblages (Figure 4), with the exception of *R. montigenum*, *R. inerme* and to a lesser extent *R. divaricatum*, and *R. binominatum*.

Table 4. The mean proportion of visits to *Ribes* flowers by functional group, and the mean number of visits per site. Species ordered by flower depth, deepest flowers on top.

	large	LP	medB	HB	smB	tinyB	mFly	tinyF	hum	btl	visits per site
<i>R. lobbii</i>	0.52	0.02	0.03	0.36	0.06	0.00	0.01	0.00	0	0.00	563.0
<i>R. viscosissimum</i>	0.56	0.01	0.31	0.01	0.06	0.01	0.04	0	0	0	67.2
<i>R. roezlii</i>	0.47	0.09	0.24	0.08	0.05	0	0.07	0	0	0	206.2
<i>R. cereum</i>	0.62	0.06	0.21	0.00	0.09	0	0.00	0	0.01	0	649.3
<i>R. marshallii</i>	0.90	0	0.05	0	0.03	0.01	0.00	0	0	0	148.3
<i>R. lasianthum</i>	0.46	0	0.32	0	0.15	0	0.08	0	0	0	348.7
<i>R. s. var. glutinosum</i>	0.46	0.13	0.01	0.10	0.01	0	0.06	0.01	0.22	0	201.4
<i>R. sanguineum</i> var. <i>s.</i>	0.39	0.10	0.11	0.13	0.13	0.00	0.06	0	0.09	0	475.1
<i>R. binominatum</i>	0.40	0	0.03	0.16	0.22	0.19	0.00	0	0	0	143.8
<i>R. inerme</i>	0.11	0	0.13	0.45	0.02	0	0.29	0.00	0	0	67.7
<i>R. divaricatum</i>	0.48	0	0	0.00	0	0	0.42	0.10	0	0	98.0
<i>R. montigenum</i>	0.01	0	0	0	0.16	0.19	0.20	0.42	0.02	0	69.4

large = large insects, LP = long proboscis, medB = medium bees, HB = honeybees, smB = small bees, tinyB = tiny bees, mFly = small-medium flies, tinyF = tiny flies, hum = hummingbirds and other birds, btl = beetles

Table 5. Similarity matrix -- pairwise similarities of the mean proportion of visits by the 10 functional groups to *Ribes* species, calculated using Equation 1. For each site the proportion of visits by each functional group was found, these were used to calculate mean proportions, giving sites equal weight despite receiving different numbers of visits. Numbers in bold are more similar pairs, with similarity values greater than 0.6. Underlined numbers are for pairs with visitor similarities less than 0.3.

	<i>s. glut</i>	<i>mars</i>	<i>cere</i>	<i>visc</i>	<i>lobb</i>	<i>lasi</i>	<i>roez</i>	<i>s. sang</i>	<i>bino</i>	<i>iner</i>	<i>diva</i>
<i>R. marshallii</i>	0.480										
<i>R. cereum</i>	0.559	0.698									
<i>R. viscosissimum</i>	0.539	0.649	0.850								
<i>R. lobbii</i>	0.607	0.587	0.629	0.635							
<i>R. lasianthum</i>	0.536	0.538	0.760	0.870	0.548						
<i>R. roezlii</i>	0.706	0.550	0.793	0.821	0.650	0.821					
<i>R. sanguineum</i> var. <i>s.</i>	0.757	0.475	0.670	0.622	0.633	0.680	0.768				
<i>R. binominatum</i>	0.522	0.481	0.530	0.513	0.645	0.581	0.564	0.686			
<i>R. inerme</i>	<u>0.290</u>	<u>0.171</u>	<u>0.258</u>	0.302	0.522	0.330	0.405	0.412	0.315		
<i>R. divaricatum</i>	0.529	0.481	0.483	0.524	0.491	0.534	0.544	0.450	0.405	0.405	
<i>R. montigenum</i>	<u>0.115</u>	<u>0.062</u>	<u>0.121</u>	<u>0.126</u>	<u>0.083</u>	<u>0.238</u>	<u>0.134</u>	<u>0.221</u>	0.360	<u>0.232</u>	0.307

s. glut = *R. sanguineum* var. *glutinosum*, *roez* = *R. roezlii*, *diva* = *R. divaricatum*, *iner* = *R. inerme*, *bino* = *R. binominatum*, *lobb* = *R. lobbii*, *s. sang* = *R. sanguineum* var. *sanguineum*, *visc* = *R. viscosissimum*, *cere* = *R. cereum*, *mars* = *R. marshallii*, *mont* = *R. montigenum*, *lasi* = *R. lasianthum*

The visitor assemblages of most of the species were dominated by bees. With the exception of *R. montigenum* and *R. inerme*, each species received at least 39% of its visits from members of the LARGE INSECTS functional group (Table 4), which consisted mainly of *Bombus* and other large bees, but occasionally included large wasps or flies. When the LARGE INSECTS group is combined with the other bee groups, it accounts for greater than 70% of the visits to nine of the *Ribes* species. The remaining species received a relatively greater proportion of their visits from flies or hummingbirds. More than 60% of visits to *Ribes montigenum* were made by flies (TINY FLIES, and MEDIUM/SMALL FLIES). *Ribes inerme* and *R. divaricatum* received the greatest percent of visits from small-to-medium-sized flies, 29% and 42%, respectively. Both varieties of *R. sanguineum* were visited by hummingbirds at almost all sites. Hummingbirds made up 21% of total visits to *R. s. var glutinosum*, and 8.4% to *R. s. var sanguineum*. The ordination analysis provides additional support for a separation of large and small visitors with the LARGE INSECTS vector and TINY FLIES vector pointing in roughly opposite directions (Figure 4).

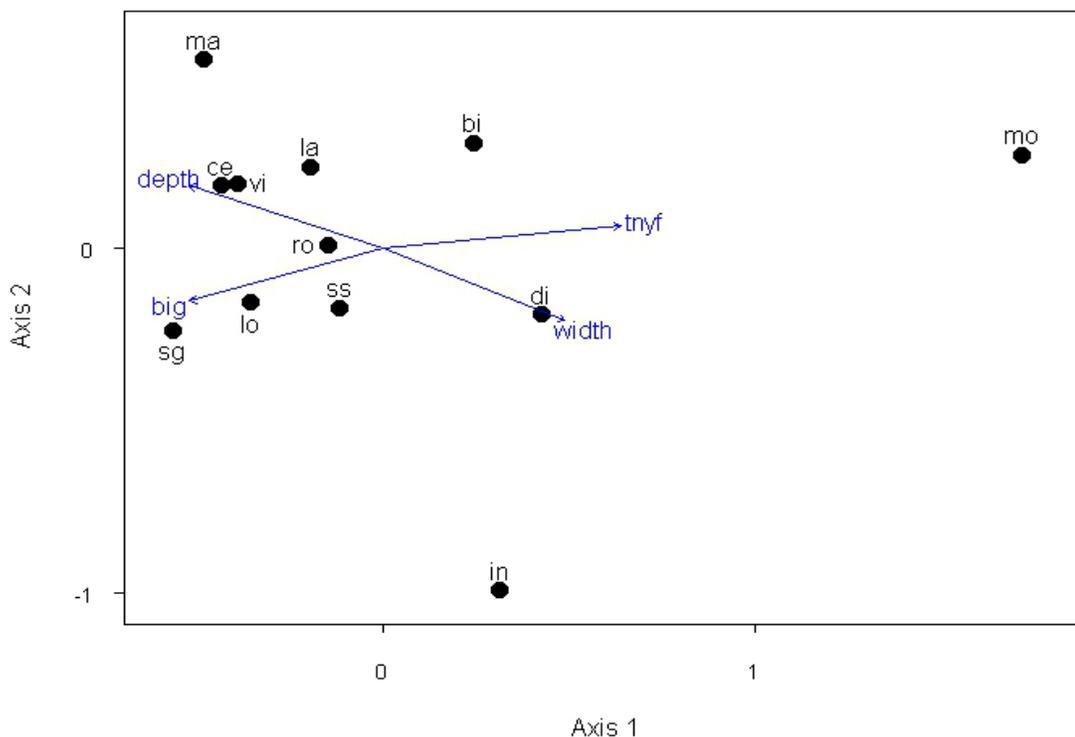


Figure 4. Non-metric Multidimensional Scaling (NMS) ordination of *Ribes* based on the composition of their visitor assemblages. Stress = 11.7. The two floral traits correlated with the ordination scores are overlaid as vectors {FLOWER DEPTH ($r=0.86$, $p=0.003$); FLOWER WIDTH ($r=0.82$, $p=0.020$)}. Moving from the upper left to lower right, flowers get wider and shorter. Two visitor functional groups are also significantly correlated to the ordination scores, LARGE INSECTS (big; $r=0.75$, $p=0.034$) and TINY FLIES (tnyf; $r=0.88$, $p=0.023$), with more visits from large insects on the left and tiny flies on the right.

bi = *R. binominatum*, ce = *R. cereum*, di = *R. divaricatum*, in = *R. inerme*, la = *R. lasianthum*, lo = *R. lobbii*, ma = *R. marshallii*, mo = *R. montigenum*, ro = *R. roezlii*, sg = *R. sanguineum* var. *glutinosum*, ss = *R. s.* var. *sanguineum*, vi = *R. viscosissimum*

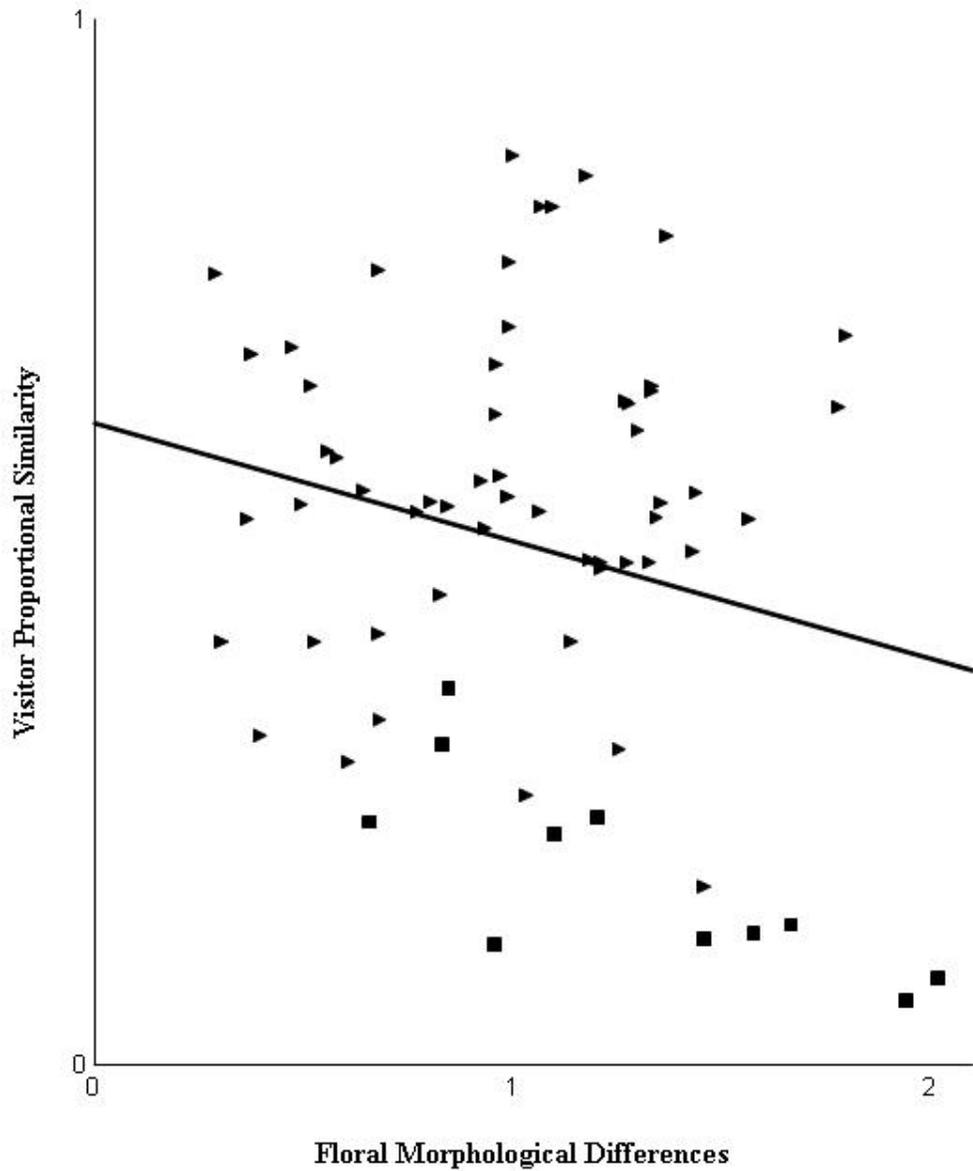


Figure 5. Correlation of pairwise morphological differences (Euclidean distances), and similarities in the proportion of floral visitors (visitor similarity matrix) is weakly significant ($r=0.23$, $p=0.069$). Squares represent comparisons of *R. montigenum* with one of the other *Ribes* species.

Correlation Between Floral Traits and Visitor Assemblages

Pairs of *Ribes* species with similar flowers were not necessarily visited by the same kinds of pollinators. The correlation between degree of morphological difference (Euclidean distances, Table 6) and degree of visitor similarity was weak and only marginally significant (Figure 5, $r=0.25$ $p=0.069$). If *R. montigenum*, which has the most distinctive flowers and the most distinctive visitor assemblages, is removed from the analysis, the suggestion of a relationship is completely eliminated ($r=0.07$, $p=0.612$). While the analysis using the distance matrix, which combined all floral traits, was only weakly significant, results of the ordination analysis (Figure 4) suggest some floral traits individually are correlated with visitor assemblages. The vectors for FLOWER WIDTH and FLOWER DEPTH are both significantly correlated to the visitor ordination scores; larger insects are more likely to visit narrower, deeper flowers and tiny insects to visit wider, shallower flowers.

Similarity of Visitors to the Same *Ribes* Species at Different Sites

The visitor assemblages of individual *Ribes* species differed significantly across sites (χ^2 values ranged from 23 to 3642, all $p \leq 0.0015$). The mean proportional similarity value for all pairs of sites within a species portrays degree of spatial consistency in pollinator assemblages. This value ranged from 0.26 for *R. montigenum* to 0.90 for *R. marshallii* (Table 7), with an overall grand mean of species' means of 0.453 (SD=0.173, $n=12$, 122 total pairs of sites). By comparison, the mean similarity between all pairs of species (when site variation is eliminated by averaging) is 0.497.

Table 6. A Euclidean distance matrix of 14 *Ribes* species using seven measured morphological traits. Numbers in bold are smaller (<0.5), representing pairs with similar flowers, underlined numbers are larger (≥ 1.5), representing especially different pairs of species.

	<i>lobb</i>	<i>mars</i>	<i>visc</i>	<i>roez</i>	<i>s. sang</i>	<i>s. glut</i>	<i>lasi</i>	<i>cere</i>	<i>bino</i>	<i>diva</i>	<i>iner</i>	<i>brac</i>	<i>lacu</i>
<i>mars</i>	0.56												
<i>visc</i>	1.27	1.33											
<i>roez</i>	0.52	0.64	1.10										
<i>s. sang</i>	1.28	1.21	0.96	0.99									
<i>s. glut</i>	1.30	1.27	0.80	0.99	0.29								
<i>lasi</i>	1.44	1.36	1.00	1.07	0.38	0.49							
<i>cere</i>	<u>1.78</u>	<u>1.80</u>	1.18	1.37	0.96	0.93	0.68						
<i>bino</i>	1.33	1.21	0.93	0.97	0.47	0.37	0.58	1.06					
<i>diva</i>	1.43	1.33	1.34	0.99	0.83	0.77	0.85	1.18	0.53				
<i>iner</i>	1.57	1.46	1.25	1.14	0.68	0.61	0.68	1.03	0.40	0.31			
<i>brac</i>	<u>1.95</u>	<u>1.78</u>	<u>1.64</u>	<u>1.55</u>	0.92	0.93	0.92	1.27	0.76	0.67	0.48		
<i>lacu</i>	<u>1.94</u>	<u>1.80</u>	<u>1.50</u>	<u>1.55</u>	0.88	0.83	0.91	1.25	0.67	0.68	0.44	0.27	
<i>mont</i>	<u>2.02</u>	<u>1.94</u>	<u>1.58</u>	<u>1.67</u>	1.10	0.96	1.20	1.46	0.85	0.83	0.66	0.63	0.44

s. glut = *R. sanguineum* var. *glutinatum*, *roez* = *R. roezlii*, *diva* = *R. divaricatum*, *iner* = *R. inerme*, *bino* = *R. binominatum*, *lobb* = *R. lobbii*, *s. sang* = *R. sanguineum* var. *sanguineum*, *visc* = *R. viscosissimum*, *cere* = *R. cereum*, *mars* = *R. marshallii*, *mont* = *R. montigenum*, *lasi* = *R. lasianthum*

Table 7. Proportional similarities in visits, between sites for each *Ribes* species. The mean similarity for all species is 0.453 (SD=0.173). n = number of pairwise similarities. CV = coefficient of variation (mean/standard deviation).

species	mean	CV	n	No. of sites
<i>mars</i>	0.897	0.047	3	3
<i>lobb</i>	0.637	0.267	21	7
<i>cere</i>	0.561	0.444	6	4
<i>roez</i>	0.452	0.343	15	6
<i>diva</i>	0.443	0.691	3	3
<i>s. sang</i>	0.400	0.520	28	8
<i>visc</i>	0.390	0.905	10	5
<i>iner</i>	0.373	0.673	3	3
<i>lasi</i>	0.370	0.841	3	3
<i>bino</i>	0.330	0.836	10	5
<i>s. glut</i>	0.322	0.922	10	5
<i>mont</i>	0.264	0.962	10	5

s. glut = *R. sanguineum* var. *glutinosum*, *roez* = *R. roezlii*,
diva = *R. divaricatum*, *iner* = *R. inerme*, *bino* = *R. binominatum*,
lobb = *R. lobbii*, *s. sang* = *R. sanguineum* var. *sanguineum*,
visc = *R. viscosissimum*, *cere* = *R. cereum*, *mars* = *R. marshallii*,
mont = *R. montigenum*, *lasi* = *R. lasianthum*

Table 8. The number of sites with pairs of species blooming sympatrically. Species not listed were never observed at the same site.

	<i>roez</i>	<i>iner</i>	<i>bino</i>	<i>lobb</i>	<i>s. sang</i>	<i>visco</i>
<i>lobb</i>	1	1	3			
<i>s. sang</i>	3	1	3	4		
<i>visco</i>	0	0	3	2	1	
<i>mars</i>	0	0	1	1	0	1
<i>mont</i>	0	0	0	0	0	1

roez = *R. roezlii*, *iner* = *R. inerme*, *bino* = *R. binominatum*,
lobb = *R. lobbii*, *s. sang* = *R. sanguineum* var. *sanguineum*,
visc = *R. viscosissimum*, *mars* = *R. marshallii*, *mont* = *R. montigenum*

Similarities of Visitors to Flowers at the Same Site

Sympatric *Ribes* species tended to attract the same kinds of visitors even though their flowers were usually quite different. The mean similarity for pairs of sympatric species (0.56, SD=0.249, n=26) was not significantly higher than the mean similarity of the same *Ribes* species at different sites (0.45; $t=1.50$, $df=29.93$, $p=0.144$). Since some species pairs were never observed sympatrically (Table 8), the mean of 0.56 is not representative of all possible species pairs, and pairs which were observed more often had a greater influence on the mean. This and subsequent significance tests are problematic because some of the same data goes into both means, nevertheless I feel they are useful.

Visitors to *Ribes* flowers tended to be different from visitors to sympatric co-flowering plants in other genera. These non-*Ribes* flowers were often morphologically very different from *Ribes*, and generally had more accessible nectar. The mean pairwise proportional similarity between visitors to *Ribes* flowers and sympatric non-*Ribes* flowers (mean=0.337, SD=0.229, n=56 sites) was lower than the between-*Ribes*-species similarities ($t=4.04$, $df=111.05$, $p<0.0001$). Even the mean between-site similarity for all *Ribes* species was marginally significantly higher ($t=1.97$, $df=20.17$, $p=0.062$). In other words, on average *Ribes* species shared fewer members of their visitor assemblages with sympatric non-*Ribes* species than with themselves (between-site) and than with each other (between-species).

DISCUSSION

My study provides only weak support for the hypothesis that shifting between pollinators played a major role in the diversification of *Ribes* flowers. Despite the marked interspecific diversity in the shape, size, and color of flowers, most *Ribes* species studied were mainly visited by bees. If pollinators have been the main drivers of morphological change, flowers with different shapes would be expected to have different sets of pollinators. For the most part, *Ribes* flowers with a higher degree of morphological difference did not have a higher degree of difference in visitor assemblages. Additionally, visitors to a given *Ribes* species varied from site to site about as much as visitors to different species of *Ribes* or to sympatric *Ribes*. However, *Ribes* species did generally share more visitors with one another than with co-flowering non-*Ribes*.

Although flower morphology is only weakly correlated with floral visitors when comparing species pairs (Figure 5), some floral traits are correlated to visitor assemblages. The visitor ordination analysis (Figure 4) showed that deeper narrower flowers are more likely to be visited by bigger insects, mainly bees, whereas wider flatter flowers received more visits from smaller insects, especially flies.

There is some support for an association between tiny fly pollinators and flat-faced flowers. Forty-two percent of visits to the flat-faced *R. montigenum* were by tiny flies. Another 20% of visits were by small-to-medium-sized flies, and 19% by tiny bees.

Of the 12 analyzed *Ribes* species, *R. montigenum* is the most morphologically distinct. Two species with similar flowers, *R. bracteosum* and *R. lacustre*, received too few visits to be included in the data analysis, despite extra care taken to find their pollinators. Since fungus gnats could be attracted to the flat-faced low-nectar-producing flowers, and are often active early and late in the day (Okuyama et al., 2008), censuses for these flowers were done near dawn and dusk as well as during the middle of the day. These extra censuses did not reveal additional visits. Of the few visits to *R. bracteosum* and *R. lacustre*, almost all were from small-to-medium- or tiny-flies. Flowers from all three of these flat-faced species have characteristics consistent with the fly pollination syndrome. This syndrome is characterized by small relatively pale and dull colored, flat-faced flowers, with short styles and filaments, and little nectar (Danieli-Silva et al., 2011; Faegri and Pijl, 1979).

Hummingbirds were consistent visitors to both varieties of *R. sanguineum*, visiting them at almost every site (and they supplied a mean of 21% of the visits to *R. s. var. glutinosum* and 8.4% of visits to *R. s. var. sanguineum*). Hummingbirds were, with two exceptions, never observed visiting any other *Ribes* species during this study (Table 4). Nevertheless, aside from their pink to dark pink color, the flowers of *R. sanguineum* are not highly distinct morphologically. These two varieties are especially similar in shape to *R. lasianthum* and *R. binominatum* (Table 6, Figure 3). Red has been shown to be an important indicator of hummingbird visitation (Grant & Grant, 1968; Faegri & Pijl, 1979; Wilson et al., 2004). Flower color may influence hummingbirds to visit *R.*

sanguineum, yet it is not the only *Ribes* species I studied with reddish flowers. *Ribes marshallii*, *R. lobbii* and *R. roezlii* all have deep red sepals, although a darker shade of red than the *R. sanguineum* sepals. No hummingbird visits to any of the dark red flowers were observed, even at sites where I observed hummingbird visits to *R. sanguineum*. *Ribes speciosum*, not included in this study, has been shown by others (Stiles, 1976; Grant & Grant, 1968) to be visited by hummingbirds and does look like a traditional hummingbird flower, being bright red with strongly exerted anthers and stigmas and a relatively long floral tube made of the hypanthium and extended (not reflexed) sepals.

Degree of Pollinator Specialization Varied Between *Ribes* Species

Shifting pollinators implies specializing on the new pollinator group. While *Ribes* species are not complete generalists, using all pollinators at a site, most are not strict specialists, with one type of pollinator predominately and consistently visiting different populations. The flowers of most *Ribes* species had a substantial proportion of visits by more than one type of pollinator. Additionally, for most species there was little consistency in visitor type between sites (Table 7).

Species with less accessible nectar appear to have more spatially consistent visitor assemblages than other species (Table 7). Bumblebees and large bumblebee-mimicking flies (*Criorhina*) made up 90% of visits to *R. marshallii*. Accessing nectar of *R. marshallii* requires a visitor to push open tightly appressed petals and have long enough mouth parts to reach the end of the hypanthium tube. Unlike nectar, pollen is freely available to visitors on the exerted anthers, and smaller bees were occasionally observed

collecting it. The three other species with the most consistent visitor assemblages, *R. lobbii*, *R. cereum*, and *R. roezlii*, also all have less accessible nectar than most *Ribes* species. These four species also all had more than 24% of visits by LARGE INSECTS at every site (except one *R. roezlii* site with 11%); this was not true for any of the other species, many of which had no visits by large insects at some sites. These deeper flowers additionally had no or very few visits by tiny insects at any site. These deeper flowers consistently exclude tiny insects from accessing nectar and pollinating, and attract large visitors leading to more overall visitor consistency.

Other Reasons Flowers May Diverge

Since it appears pollinator shift was not the main driver of floral divergence in *Ribes*, other models must be examined to explain the floral diversity. Some studies have shown divergence in floral form without changing pollinators. For example, selection against pollen loss to heterospecific stigmas can drive divergence in the relative position of anthers and stigmas in species that share the same pollinators (Muchhala and Potts, 2007). North American *Pedicularis* species are primarily pollinated by *Bombus* species despite much diversity and complexity in floral form (Macior, 1982). Yet these species appear to have diverged due to pressure from pollinators. Where pollen is placed, anatomically, on visitors varies, as does floral depth and bloom time (Macior, 1982).

Another mechanism that might account for floral diversification without pollinator shifts is selection on correlated traits (Strass & Whittall, 2007). For example, two recent studies suggest flower color polymorphism is maintained by a combination of

pollinator and herbivore preference; the same chemical compounds affect flower hue and foliage defense, thus linking herbivory and flower color (Irwin et al. 2003; Frey 2004). This could lead to divergence if herbivory defense mechanisms vary between species, and some are not correlated with floral traits, such as leaves with highly scented glands.

Only a limited number of the diverse traits seen in *Ribes* flowers can easily be accounted for by these other models of divergence. In the genus *Ribes* the degree of anther and stigma exertion varies, so where pollen contacts a visitor's body can also vary. However, since the styles and filaments do not arch over the flower opening, pollen is normally only placed on the head or underside of insects. I happened to notice pollen was placed on different parts of bees visiting *R. sanguineum* and *R. roezlii* (or *R. lobbii*) at sites they shared, mostly around the head versus on the underside of the thorax. I did not notice differences in pollen placement in other species pairs. For many pairs it would be difficult for pollen to be consistently placed on different regions of a pollinator's body, since for most *Ribes* species insects stick their head into the flowers, contacting anthers with only their head. Selection on correlated traits could explain the diversity of flower colors in *Ribes*, but it is harder to see what non-floral traits the other diverse floral characteristics (such as hypanthium length or petal shape) would be correlated with. I have seen the same shade of deep red that colors the sepals of some *Ribes* species on foliage in both *Ribes* and other plants, and speculate there might have been selection for presence of the compound in leaves. On the other hand, perhaps *Ribes* flowers simply have a high degree of evolvability due to a lack of genetic or developmental constraints

(such as minimal pleiotropy in the genes dictating floral morphology) allowing genetic drift and other non-selective explanations to account for more of the diversity. Since I did not study any other reasons for floral divergence, further research would be needed to support their potential role in *Ribes* flower diversification.

Potential Limitations of this Study

My study evaluated current visitors to *Ribes* flowers to ascertain whether past visitors influenced the evolution of floral morphology. While current visitors are not necessarily representative of past visitors, they are the best proxy available and may be a very good one. However, after *Ribes* flowers diverged, much could have changed both in available pollinators and in the flowers themselves. Perhaps the flowers diverged by changing pollinators, then became generalists, adapting to additional pollinators without affecting interactions with their primary pollinator (Aigner, 2001; Aigner, 2004). For example, *R. sanguineum* could have added hummingbirds to its pollinator suite without losing bees as a major source of pollination, possibly by changing color. This model could lead to divergent floral forms that all attract similar visitor assemblages, possibly with the efficiency of a given pollinator varying between species.

I tried to exclude visits by non-pollinators from the analysis. However, I could not measure how effective visitors were at pollinating *Ribes* flowers. Without these data all visits from potential pollinators had to be weighted equally, despite the fact that more effective pollinators likely apply more selective pressure on plants.

The small flat-faced flowers of *R. bracteosum* and *R. lacustre* had fewer and significantly different pollinators. This needs further study. Arasu (1970) and Offord (1944) studied a total of 11 uncultivated *Ribes* species (including *R. viscosissimum*, *R. roezlii* and both varieties of *R. sanguineum*) and found them to be self-incompatible with the exception of *R. bracteosum*. Only some *R. bracteosum* plants were found to be self-compatible and the selfed flowers had a lower fruit and seed set, averaging fewer than 4 seeds per fruit, instead of roughly 30 for outcrossed flowers (Arasu 1970). *Ribes bracteosum* does have extensive fruit set in Humboldt County, California (M. Mesler, personal observation). Those compatibility studies did not include *R. montigenum* or *R. lacustre*, so it is unknown if they are self-compatible. While I did see some visits to *R. montigenum*, many of the visitors had limited contact with anthers and stigmas, and most visitors did not travel often between flowers, leaving questions about sufficient pollen movement for outcrossing to take place often.

In conclusion, limited evidence exists to support the pollinator shift model as an explanation of diversification in *Ribes* flowers. Visitor assemblages vary widely between populations of a single species, although less widely for species with less accessible nectar. The most similar flowers are not visited by the most similar suites of animals. However, some floral features are correlated with the likelihood of a flower being visited by a particular type of animal. Small, flat-faced flowers do appear to have a distinct visitor assemblage compared to *Ribes* species with larger, more complex flowers. The hunt is still on to find reasons for all the beautiful diversity of *Ribes* flowers.

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