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### Authors

Chamberlain, Scott A  
Cartar, Ralph V  
Worley, Anne C  
[et al.](#)

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## **Traits and phylogenetic history contribute to network structure across Canadian plant-pollinator communities**

Scott A. Chamberlain <sup>1</sup>

Ralph V. Cartar <sup>2</sup>

Anne C. Worley <sup>3</sup>

Sarah J. Semmler <sup>3</sup>

Grahame Gielens <sup>1</sup>

Sherri Elwell <sup>1</sup>

Megan E. Evans <sup>2</sup>

Jana C. Vamosi <sup>2</sup>

Elizabeth Elle <sup>1</sup>

<sup>1</sup> Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada, V5A 1S6

<sup>2</sup> Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada, T2N 1N4

<sup>3</sup> Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba, Canada, R3T 2N2

1 **Abstract**

2 Interaction webs, or networks, define how the members of two or more trophic levels interact.  
3 However, the traits that mediate network structure have not been widely investigated.  
4 Generally, the mechanism that determines plant-pollinator partnerships is thought to involve  
5 the matching of a suite of species traits (such as abundance, phenology, morphology) between  
6 trophic levels. These traits are often unknown or hard to measure, but may reflect phylogenetic  
7 history. We asked whether morphological traits or phylogenetic history were more important in  
8 mediating network structure in mutualistic plant-pollinator interaction networks from Western  
9 Canada. At the plant species level, sexual system, growth form, and flower symmetry were the  
10 most important traits. For example, species with radially symmetrical flowers had more  
11 connections within their modules (a subset of species that interact more among one another  
12 than outside of the module) than species with bilaterally symmetrical flowers. At the pollinator  
13 species level, social species had more connections within and among modules. In addition,  
14 larger pollinators tended to be more specialized. As traits mediate interactions and have a  
15 phylogenetic signal, we found that phylogenetically close species tend to interact with a similar  
16 set of species. At the network level, patterns were weak, but we found increasing functional  
17 trait and phylogenetic diversity of plants associated with increased weighted nestedness. These  
18 results provide evidence that both specific traits and phylogenetic history can contribute to the  
19 nature of mutualistic interactions within networks, but they explain less variation between  
20 networks.

21 **Keywords:** network, mutualism, plant-pollinator, trait, phylogeny

## 22 **Introduction**

23 Interaction webs define how the members of two or more trophic levels interact with one  
24 another. Comparisons of the structure of different mutualistic interaction webs reveal some  
25 consistent patterns, suggesting common mechanisms by which communities are assembled.  
26 For example, the degree distribution (distribution of number of interactions per species) of  
27 mutualistic networks has a consistent pattern, despite differences in species composition across  
28 networks (Bascompte and Jordano 2007). In addition, a pattern of many weak, and few strong  
29 species interactions is pervasive across not only mutualistic networks (Bascompte et al. 2006),  
30 but food webs as well (Paine 1980). However, despite consistent structural patterns, there is  
31 still no consensus on what mediates the production of these patterns. Generally, traits of the  
32 species within networks are thought to either encourage or prevent interactions (Santamaría  
33 and Rodríguez-Gironés 2007; Vázquez et al. 2009; Junker et al. 2010; Cagnolo et al. 2011;  
34 Donatti et al. 2011; Danieli-Silva et al. 2012), yet stochastic processes may also play a role.  
35 Because the traits themselves are evolving at varying rates, phylogenetic history of any given  
36 assemblage of species can therefore influence network structure.

37         There are two ways in which traits can mediate linkage rules in a plant-pollinator  
38 bipartite community: barrier (the difference between traits of plants and pollinators prevents  
39 interaction), and complementarity (the degree to which traits are similar allows interaction).  
40 Traits involved in mediating species interactions are likely to be specific; for example the  
41 maximum length a pollinator's tongue can extend will determine the nectar tube lengths and  
42 therefore plant species it can visit. Junker *et al.* (2013) showed that flower traits have a large  
43 impact on the pollinators that visit them, and the resulting network structure; however, they

44 didn't compare the ability of traits to explain structure compared to other factors (e.g.,  
45 abundance). Stang *et al.* (2006) showed that both abundance (plant and pollinator) and flower  
46 traits independently contributed to network structure, but the combination of the two better  
47 predicted network structure. There are few studies that have been able to use many traits of  
48 both sides of a network to ask how traits contribute to network structure. Furthermore, a  
49 limitation of most studies exploring how traits relate to network structure is small size of  
50 datasets: it is difficult to combine a large set of networks with trait data for the component  
51 species. Because of this difficulty, we explore the possibility of using phylogenetic information  
52 as a surrogate representing unmeasured differences among species.

53         Many species traits are phylogenetically conserved (Blomberg *et al.* 2003); in which case  
54 closely related species tend to have more similar traits than distantly related species. Thus, if  
55 species traits are the result, at least in part, of their phylogenetic history, traits and phylogeny  
56 should predict network structure to similar degrees. However, differences can arise because (1)  
57 some important traits are evolutionarily labile and show little phylogenetic signal and (2) some  
58 traits do show a phylogenetic signal, yet may not have been regularly measured, either due to  
59 perceptual differences (e.g., UV reflectance in flowers that insects can see but humans cannot)  
60 or because we simply did not appreciate their importance (e.g., electrical fields; Clarke *et al.*  
61 2013). Considering the possibility for the presence of "unknown" important traits, as well as the  
62 large amount of time it takes to collect data on a suite of potentially important traits, it would  
63 be useful if phylogenetic history can be a proxy for describing a list of traits that mediate  
64 species interactions. Thus far, several studies have shown that phylogenies do influence

65 network structure and specific species interactions, but the effect of phylogeny overall appears  
66 to be modest relative to traits (Rezende et al. 2007; Vázquez et al. 2009).

67         There is a temptation to reduce all of the interactions observed in a community into  
68 summary metrics, such as connectance, nestedness and interaction asymmetry and link these  
69 summary metrics to some value of vulnerability of the community to invasion or disturbance  
70 (Elle et al. 2012). While these observations are intriguing, the mechanisms that may cause these  
71 metrics to be associated with stability are often unclear and an investigation of traits can be a  
72 good place to begin to tease apart mechanistic influences. Here we use 47 mutualistic plant-  
73 pollinator interaction networks from Western Canada to ask what mediates their structure.  
74 Specifically, we ask: 1) How do phylogeny and traits affect individual species interaction  
75 patterns, as measured by several commonly used metrics?; and 2) How do phylogeny and traits  
76 affect structural properties of whole networks? We list empirically-based predictions, where  
77 possible, for question 1 in Table 1.

78

## 79 **Methods**

### 80 *Study sites*

81 A total of 47 mutualistic plant-pollinator networks were studied in four regions of western  
82 Canada, from west to east: oak savannah (British Columbia; 12 networks), shrub-steppe (British  
83 Columbia; eight networks), foothills rough fescue prairie (Alberta; 21 networks), and upland tall  
84 grass prairie and sedge meadow habitat (Manitoba; six networks) (see Table A1 for site  
85 information). Our original dataset included 52 networks, but five from very degraded rough

86 fescue prairie were excluded because they had less than 10 species in total (no. plant +  
87 pollinator species).

88

### 89 *Collection of mutualistic network data*

90 Two sampling methods were used in this study: transects and plots. Plots are generally more  
91 appropriate when the plant species in the community are very patchily distributed (Gibson et  
92 al. 2011). In the plot method, sampling focuses on individual plant species, with an attempt to  
93 observe each plant species for an equal amount of time. The transect method is more  
94 appropriate for communities in which plant species are relatively homogenously distributed so  
95 that a few transects can capture most of the plant species. An observer walks each transect for  
96 an equal amount of time. The tendency of the plot method is to pick up rare pollinators, while  
97 the transect method can be biased towards observing common pollinators. We attempt to  
98 correct for the different methods by including collection method as a categorical variable in  
99 analyses (see *Data analyses* below). The following are details of collection methods in each  
100 region (See Appendix Table A1 for details).

101       Oak savannah sites. We collected data on species interactions in 1-ha plots at each of six  
102 sites in both 2009 and 2010. Each plot was surveyed 10-12 times per season between late April  
103 and early July, the majority of the flowering period. Over the flowering period we attempted to  
104 visit sites morning, midday, and afternoon on different survey dates to reduce bias due to flight  
105 time differences among visiting insects. During each survey, each plant species in flower was  
106 observed for a 10 min period by each of two surveyors, on haphazard walks throughout the  
107 plot.

108 Shrub-steppe sites. Data were collected in 2010 for 8 sites using the same methodology  
109 as for oak-savannah sites, but surveys occurred from the beginning of April through the end of  
110 July for a total of 12 samples per site.

111 Foothills rough fescue prairie. We collected data on species interactions in six parallel  
112 100 m transects at each of 21 sites. Bees were sampled over a 2 m wide area centered on each  
113 transect. We visited sites twice per survey date (AM and PM), walking at a pace to cover 600 m  
114 in 30 minutes. Each site was sampled three to eight times (median = 5) during the flowering  
115 season, but different sites were sampled in each of 2009 and 2010.

116 Tall grass prairie. Sampling occurred in four upland tall grass prairie sites and two sites  
117 in sedge meadow. Insect observations took place within two 4 x 90 m parallel belt transects in  
118 each site. Transects were walked by two researchers for one hour between 09:00 and 15:00.  
119 Start times for observations in each site were rotated over survey dates. Each plot was  
120 sampled eight times between June and mid-September 2010.

121 With the exception of the tall grass prairie networks, all pollinators were collected for  
122 identification in the lab to the lowest taxonomic level possible (species or genus). For the tall  
123 grass prairie networks some pollinators could be identified to morphospecies on the wing; all  
124 other specimens were collected for identification in the lab.

125

#### 126 *Plant and pollinator traits*

127 Using information in published floras, we collected the following traits for plant species: flower  
128 symmetry (radial, bilateral), flower colour (blue, pink, white, yellow, green), sexual system  
129 (dioecious, gynodioecious, gynomonecious, perfect, and other, which includes monoecy,



130 andromonoecy, androdioecy, etc.), life-span (short-lived [annual,biennial] or long-lived  
131 [perennial]), growth form (herbaceous and other [including sub-shrubs, shrubs, trees, and  
132 woody vines]), and flower size. Flower size was determined by taking the midpoint of the  
133 minimum and maximum range of flower size given in each species' description in the flora (in  
134 mm). Flower colours available in floras do not include UV reflectance in flowers that insects can  
135 see but humans cannot. However, it is worth asking if flower colour classes do drive any  
136 variation in network structures because the spectrum humans see is at least part of the  
137 spectrum pollinators can see. Plant trait data were collected from various sources, including the  
138 Flora of North America (Flora of North America Editorial 2002) and the E-Flora of British  
139 Columbia (Klinkenberg 2012).

140         For pollinators, we collected the following life history traits, also from the literature:  
141 sociality (solitary; social; unknown), parasitism (not parasitic; social parasite; cleptoparasite),  
142 nest location (aboveground, belowground, above-/below-ground), and nest type (rent or  
143 excavate). Renters construct nests within existing tunnels or other cavities regardless of nest  
144 location, while excavators dig or bore the chamber/tunnel within existing substrate (Michener  
145 2007). Life history data were collected from Michener (2007). We also estimated body size for  
146 some of the bees and flies collected in this research. We measured intertegular distance  
147 (ITwidth) for bees, which correlates with body size (Cane 1987; Greenleaf et al. 2007), and with  
148 foraging distance (Greenleaf et al. 2007). We calculated bee mass (mg) using the equation:  
149  $mass = 0.77 \times ITwidth^{0.405}$  following Cane (1987). For flies, we measured body length (tip of the  
150 head to the end of the abdomen), and used the following equation to convert body length to

151 mass (mg):  $\text{mass} = 0.032 \times \text{length}^{2.63}$  following Sabo *et al.* (2002). Body size was not estimated  
152 for other taxa.

153

#### 154 *Plant and pollinator phylogenetic reconstruction*

155 Plant phylogenies were built using Phylomatic (<http://phylodiversity.net/phyloomatic/>; Webb  
156 and Donoghue 2004). Phylomatic is an online interface used to retrieve a phylogeny based on a  
157 user-defined set of plant species taxonomic names. Branch lengths were estimated for the  
158 master plant phylogeny using the algorithm for branch length adjustment (BLADJ) in the  
159 software Phylocom (Webb *et al.* 2008), which fixes a set of nodes in the tree to specified ages  
160 (Wikstrom *et al.* 2001) and evenly distributes the ages of the remaining nodes. The file (in  
161 multiple formats) we used to run the `bladj` command in Phylocom is provided in Appendix B.  
162 See the master plant phylogeny in Appendix B and on Figshare.org  
163 ([http://figshare.com/articles/Canadian\\_Networks/1014346](http://figshare.com/articles/Canadian_Networks/1014346)).

164 Animal phylogenies were built using a variety of tools, similar to that implemented in  
165 Phylomatic for plant phylogenies. First, we built a topology of all animal pollinators across all  
166 networks in the study in Mesquite v.2.75 (Maddison and Maddison 2011), based on a variety of  
167 published phylogenies (Appendix B). Second, we collected 33 node age estimates (in millions of  
168 years) from TimeTree.org (Hedges *et al.* 2006), which are provided in Appendix B. Last, we used  
169 the algorithm for branch length adjustment (BLADJ) as described above for plants, except that  
170 we used our node age estimates retrieved from TimeTree.org. See the master pollinator  
171 phylogeny in Appendix B and on Figshare.org  
172 ([http://figshare.com/articles/Canadian\\_Networks/1014346](http://figshare.com/articles/Canadian_Networks/1014346)).

173 We pruned the master phylogenies made above for both plants and pollinators for each  
174 network, to produce phylogenies for each site/year combination.

175

#### 176 *Species level network metrics*

177 For species level metrics of interaction, we calculated direction of interaction strength  
178 asymmetry (hereafter *IA*), a measure of specialization (Blüthgen's  $d'$ ; Blüthgen et al. 2006),  
179 degree (number of other species the focal species interacts with), within-module degree ( $z$ ),  
180 among-module connectivity ( $c$ ), and ecological similarity. We used the *specieslevel* function in  
181 the bipartite R package (Dormann 2011). Positive values of *IA* show that a focal species affects  
182 an interactor more than the interactor affects the focal species; negative values of *IA* indicate  
183 that a focal species is, on average, affected more by the interactor than the converse (Vázquez  
184 et al. 2007). The  $d'$  metric of specialization measures how specialized a species is with respect  
185 to available resources. Within-module degree ( $z$ ) is the standardized number of links to other  
186 species in the same module, and among-module connectivity ( $c$ ) is the extent of connections of  
187 the species to other modules (Olesen et al. 2007). Ecological similarity of any two species was  
188 calculated following Rezende *et al.* (2007) as the number of species with which both species  
189 interact divided by the total number of species with which they separately interact. A large  
190 value means the two species share interactions with the same species, while a small value  
191 indicates they share relatively few of the same species. This measure is necessarily one that  
192 depends on comparing two species – thus, this measure is only used when investigating how  
193 phylogenetic history relates to species traits (see below).

194

195 *Network structural properties and trait diversity*

196 For both plants and pollinators, we quantified trait diversity within each network using a  
197 measure of functional dispersion (Laliberté and Legendre 2010). FDis computes the mean  
198 distance of a species in ordination space from the mean for all species, where the ordination  
199 space is defined by a set of traits. This is in effect a multidimensional measure of functional  
200 diversity. FDis is highly correlated with Rao's quadratic entropy (Q; Botta-Dukát 2005), but FDis  
201 has better properties than Q (Laliberté and Legendre 2010). FDis can be weighted by the  
202 abundance of each species, but we did not do this because FDis is used in analyses in which the  
203 measures of abundance are the sums of cell values in the interaction matrices; this lack of  
204 independence would confound analyses. In these network level analyses, we did not include  
205 traits individually because many traits were categorical/nominal, which would leave few  
206 residual degrees of freedom and low statistical power.

207 For both plants and pollinators, we calculated one network level measure of  
208 phylogenetic diversity: mean pairwise distance (MPD) (Webb et al. 2008) between all taxa. We  
209 calculated four measures of network level structure: weighted nestedness, modularity,  
210 weighted connectance, and network level specialization ( $H_2'$ ). For nestedness, we used the  
211 weighted NODF measure, proposed by Almeida-Neto and Ulrich (2011). We used a modified  
212 version, NODF2, which sorts the matrix before calculating the measure, ideal for comparisons  
213 across different networks as it is independent of the initial matrix. Values of zero indicate non-  
214 nestedness, those of 100 are perfect nesting. Modularity ( $M$ ) measures the extent to which a  
215 network is organized into clearly delimited modules, where a module is a subset of species that  
216 interact more among one another than outside of the module (Bascompte and Jordano 2007).

217 We used the modularity-detecting algorithm, which maximized modularity using simulated  
218 annealing (SA) implemented in the command line function *netcarto\_cl* in the C library Rgraph  
219 (Guimera and Amaral 2005a; Guimera and Amaral 2005b). Weighted connectance is the  
220 quantitative version of linkage density divided by number of species in the network, following  
221 Tylianakis *et al.* (2007). Network level specialization (H2') was introduced by Blüthgen *et al.*  
222 (2006), and characterizes the degree of specialization in a network, while not being affected by  
223 network size or sampling intensity. A summary table of these network level metrics is presented  
224 in Appendix C.

225

226 *Data analyses*

### 227 **Phylogenetic signal**

228 We calculated phylogenetic signal for a subset of traits that were either binary (plants:  
229 life-span, growth form, and flower symmetry; pollinators: nest location, parasitic, and sociality)  
230 or continuous (plants: flower size; pollinators: body size). For binary traits we calculated the D  
231 statistic proposed by Fritz and Purvis (2010), while for continuous traits we calculated the K  
232 statistic proposed by Blomberg *et al.* (2003). For both methods we performed 1000 simulations  
233 to compare the observed statistic to a distribution of values from species randomized on the  
234 tips of each phylogeny. We calculated phylogenetic signal for each trait in each site, for both  
235 plants and pollinators. For D, we determined whether D was significantly greater than 0  
236 (indicating trait is more phylogenetically conserved than under a Brownian motion model), and  
237 whether it was significantly less than 1 (indicating trait is phylogenetically overdispersed). The K  
238 statistic tests whether K is significantly different from 1; less than 1 indicates trait is

239 phylogenetically overdispersed, while greater than 1 indicates trait is phylogenetically  
240 conserved. We could not calculate signal for some site/organism/trait combinations because  
241 trait values were the same for all species. Thus, sample sizes are less than 47 for some tests. We  
242 summarized these analyses by presenting proportion of networks that had D values significantly  
243 greater than 0 or less than 1, and K values significantly less than or greater than 1. A potential  
244 source of bias in detecting phylogenetic signal was that some networks had fewer than 20  
245 species, which Blomberg et al. (2003) showed have less than 0.8 statistical power.

246

#### 247 **How do phylogeny and traits affect species-level interaction metrics?**

248 For species-level analyses we tested for a relationship between species-level interaction metrics  
249 and phylogenetic history within individual networks, and separately tested for a relationship  
250 between species-level network metrics and traits across the entire dataset. For phylogenies, we  
251 calculated pairwise phylogenetic distance between each species pair in the phylogeny for each  
252 network using the *cophenetic.phylo* function in the ape R package (Paradis et al. 2004) and  
253 compared them to distance matrices based on interaction metrics using Mantel tests. Separate  
254 analyses were done for plants and pollinators. Although there are some drawbacks to Mantel  
255 tests (Harmon and Glor 2010), we use them with caution, recognizing that, relative to the  
256 alternative K statistic, Type I error is unaffected, but that Type II error is inflated. We used the  
257 function *mantel* in the vegan R package (Oksanen et al. 2013).

258         For our analysis of trait effects, we used mixed linear models for all variables, some with  
259 Gaussian error distributions (response variables: IA, and z) and others with binomial  
260 distributions ( $d'$  and c). Models were run separately for plant traits and pollinator traits. All

261 plant models were: *network metric* ~ *symmetry* + *colour category* + *flower size* + *sexual system*  
262 + *life-span* + *growth form* + *collection method*. All pollinator models were: *network metric* ~  
263 *sociality* + *parasitism* + *nest location* + *nest type* + *mass* + *collection method*. In both models,  
264 region (e.g. oak savannah, rough fescue) and network (i.e., site) were included as random  
265 effects. The explanatory variable mass was  $\log_{10}$  transformed to improve assumptions of  
266 normality and homoscedascity of residuals. In the case of significant effects of categorical  
267 variables, we performed post-hoc Tukey tests to determine what levels within a variable differ  
268 from one another. For the  $d'$  and  $c$  response variables, we used generalized linear mixed  
269 models with binomial error distribution with a logit link function, using the function *glmer* in the  
270 package *lme4* (Bates et al. 2012).

271

272 ***How do phylogeny and traits affect network structures?*** To address the extent to which  
273 phylogeny and traits influence community-level network structures, we modeled each of the  
274 five network structures with the model: *NetworkStructure* ~  $N_{TOT}$  +  $FDis_{PO}$  +  $FDis_{PL}$  +  $MPD_{PO}$  +  
275  $MPD_{PL}$ , where  $N_{TOT}$  is total network size (no. pollinator species + no. plant species);  $FDis_{PO}$  is  
276 pollinator functional trait dispersion;  $FDis_{PL}$  is plant functional trait dispersion;  $MPD_{PO}$  is mean  
277 phylogenetic diversity of pollinators, and  $MPD_{PL}$  is mean phylogenetic diversity of plants. As all  
278 response variables were continuous and bounded between 0 and 1, we used beta regression  
279 models for each network metric, using the *betareg* R package (Cribari-neto and Zeileis 2010),  
280 which are appropriate for this kind of data. Z-tests were used to perform significance tests of  
281 model coefficients. Nestedness was calculated as between 0 and 100, but is essentially a

282 proportion by dividing the nestedness value by 100. Network level data used in analyses are  
283 provided in Appendix C.

284

## 285 **Results**

### 286 *Phylogenetic signal*

287 Plants. Overall, the two traits that showed phylogenetic signal the most frequently were plant  
288 growth form (herb, woody) and flower symmetry (radial, bilateral). Life-span was  
289 phylogenetically conserved in 17% (six of 35) of trees, and overdispersed in 17% of trees (see  
290 Appendix E). Growth form was phylogenetically conserved in 6% (two of 34) of trees, and  
291 overdispersed in 12% of trees. Flower symmetry was phylogenetically conserved in 41% (19 of  
292 46) of trees, and overdispersed in 0 trees. Flower size had a significant phylogenetic signal in  
293 28% (13 of 47) of trees, with phylogenetic conservation in 7 trees, and overdispersion in 6.

294

295 Pollinators. Overall, the two traits that showed phylogenetic signal most frequently were  
296 sociality and nest location (above- vs. below-ground). For nest location, 73% (22 of 30) of trees  
297 were phylogenetically conserved, while no trees were overdispersed (see Appendix E). For  
298 parasitism, 38% (3 of 8) of trees were phylogenetically conserved, while 13% (1 of 8) of trees  
299 were overdispersed. For sociality, 93% (38 of 41) of trees were phylogenetically conserved,  
300 while no trees were overdispersed. Body size had a significant phylogenetic signal in 55% (25 of  
301 47) of trees, with two trees showing phylogenetic conservation, and 24 showing overdispersion.

302



303 *Phylogenetic history.* For plants, ecological similarity was most frequently related to plant  
304 phylogenetic distance, with significant relationships in 17% of networks. Specialization ( $d'$ ) was  
305 significantly related to pollinator phylogenetic distance in 10% of networks, while within-  
306 module degree ( $z$ ) was related to pollinator phylogenetic distance in 5% of networks. For  
307 pollinators, ecological similarity was most frequently related to pollinator phylogenetic  
308 distance, with significant relationships in 16% of networks (Table 2; Fig. 1).  $IA$  was related to  
309 pollinator phylogenetic distance in 14% of networks. Within-module degree ( $z$ ) was significantly  
310 related to pollinator phylogenetic distance in 5% of networks.

311

312 *How do phylogeny and traits affect species-level interaction metrics?*

313 *Plant traits.* Sexual systems, plant growth form, and flower symmetry were important traits for  
314 species-level network metrics (Appendix Table D1; Fig. 3). Species with a perfect sexual system  
315 (symbol “p”) had greater specialization ( $d'$ ) and interacted with fewer insect species (lower  
316 degree) than did gynomonecious species (symbol “gm”). Sexual system also significantly  
317 influenced within-module degree ( $z$ ), but post-hoc tests showed no differences among levels of  
318 either factor. For growth form, woody plant species had greater interaction asymmetry and  
319 higher within-module degree ( $z$ ) than species with an herbaceous growth form. Finally, species  
320 with radial flowers had greater within-module degree ( $z$ ) than those with bilaterally  
321 symmetrical flowers. Flower size was important in one network metric. There was a significant  
322 negative relationship between within-module degree ( $z$ ) and flower size, such that species with  
323 larger flowers had smaller values of  $z$ , or interacted less within their modules.

324

325 *Pollinator traits.* Sociality was by far the most important pollinator trait for species-level  
326 network metrics (Appendix Table D1; Fig. 2). Social species had higher values of within- module  
327 degree ( $z$ ) and among-module connectivity ( $c$ ) than solitary species, indicating that they interact  
328 with more plant species overall, and have more interactions both within- and among- modules  
329 than do solitary species. Solitary species also had significantly more negative values of  
330 interaction strength (IA) asymmetry than social species. That is, solitary species were affected  
331 more by their interactors on average than were social species. Body size also affected some  
332 network traits. Larger species had more positive values of interaction strength asymmetry,  
333 while smaller species tended to have more negative values. In addition, specialization ( $d'$ ) was  
334 higher in larger species.

335  
336 Surprisingly, we found no association between the networks where phylogeny significantly  
337 determined ecological similarity of interactions and the networks where there was a  
338 phylogenetic signal in important traits such as floral symmetry ( $P = 0.441$ ; Fisher's two-tailed  
339 exact test) or sociality ( $P = 0.323$ ; Fisher's two-tailed exact test) indicating that there are further  
340 unmeasured or unappreciated traits with a phylogenetic signal that determine network  
341 structure more than the traits included here.

342  
343 *How do phylogenetic and trait diversity affect whole-network structures?*  
344 Modularity, weighted network connectance, and network-level specialization ( $H2'$ ) were all  
345 significantly negatively related to network size (Table 3). There were no other significant main  
346 effects for  $H2'$ , but there was a significant interaction between pollinator functional trait

347 dispersion and pollinator phylogenetic diversity (Table 3), such that the effects of trait diversity  
348 and phylogenetic diversity interact to influence network structures. There was a significant and  
349 positive effect of plant functional diversity on weighted nestedness, such that more diverse  
350 communities with respect to plant traits, lead to more nested networks. In addition, there was  
351 a relatively weak, but significant effect of plant phylogenetic diversity on weighted nestedness,  
352 such that communities with a more phylogenetically diverse set of plant species are associated  
353 with more nested networks. Last, there was a significant negative interaction between plant  
354 functional trait diversity and phylogenetic diversity. Because we were concerned about the  
355 possible effect of differences in sampling and focus on certain functional groups on our results,  
356 we reran these analyses excluding networks where the sampling was restricted to the bee  
357 community. We obtained qualitatively similar results for most of the analyses, with the  
358 exception of a stronger effect of mean phylogenetic plant diversity ( $MPD_{PL}$ ) on  $H2'$ .

359

## 360 **Discussion**

361 We asked whether species traits or phylogenetic history were more important in mediating  
362 network structure in 47 mutualistic plant-pollinator networks. At the plant species level, sexual  
363 system, growth form, and flower symmetry were the most important traits. At the pollinator  
364 species level, social species had more connections within and among modules, and larger  
365 pollinators tended to be more specialized. Given some traits mediated species interactions and  
366 had a phylogenetic signal, we found that phylogenetically close species tend to interact with a  
367 similar set of species. At the network level, we found increasing functional trait and

368 phylogenetic diversity of plants associated with increased weighted nestedness. We explore our  
369 findings in further detail below.

370

### 371 *Species-level network metrics*

372 A minority of networks (17% or fewer) showed significant relationships between phylogeny and  
373 species-level metrics for either plants or pollinators. This was surprising given that the most  
374 important traits influencing these metrics were phylogenetically conserved in 41% (floral  
375 symmetry) and 93% (pollinator sociality) of networks examined. However, the finding that  
376 there was no association between the networks where important traits had a strong  
377 phylogenetic signal and the networks where phylogeny determined mutualistic partnerships  
378 indicates that phylogeny is accounting for the effects of unmeasured traits to some degree. The  
379 large amount of remaining unexplained variance, however, suggests that other unmeasured  
380 factors that are not correlated with phylogeny (e.g., abundance, phenology) are of even greater  
381 importance than phylogenetic effects on species-level interaction metrics. More detailed  
382 examination of individual networks where abundance is measured independently of interaction  
383 frequencies would be needed to distinguish among these explanations.

384         For pollinators, the only traits that were important for species-level network structures  
385 were sociality and body size. As expected (see Table 1), among-module connectivity was  
386 greater in social than in solitary species. This likely reflects the fact that social species are active  
387 longer in the season, thus interacting with more plant species, and individuals within a colony  
388 can specialize on different plant species (Fontaine et al. 2008), making the colony as a whole  
389 quite generalized (Cane and Sipes 2006). As expected (Table 1), we found that interaction

390 asymmetry was greater (more positive) in social species than solitary species. Thus, solitary  
391 species visit mostly a few generalists, while social species visit multiple plant species, many of  
392 which are generalists. This pattern contributes to the nested pattern found in many mutualistic  
393 networks (Bascompte et al. 2003).

394 Pollinator body size was important in specialization ( $d'$ ) and asymmetry, both of which  
395 were associated with an increase in body size (larger species are more specialized, and larger  
396 species have more positive asymmetry values meaning that other species depend on them  
397 more than they depend on others). These findings also fit our expectations (Table 1), and the  
398 results of other studies (Woodward et al. 2005; Chamberlain and Holland 2009).

399 For plants, three traits, sexual system, growth form, and flower symmetry, were often  
400 important in explaining species-level network structures. We lacked a clear expectation with  
401 respect to sexual system, yet found that gynomonecious plants (having both bisexual and  
402 female flowers on the same plant) had larger degree and were less specialized than plants with  
403 a perfect sexual system (each flower has both male and female structures). However, all  
404 gynomonecious plant species in our study were Asteraceae, raising the possibility that  
405 unmeasured trait(s) could be driving this difference between Asteraceae and plants from other  
406 families. Plant species that had an herbaceous growth form had lower within-module degree ( $z$ )  
407 than woody species, which fit our expectation (Table 1). In addition, although we had no  
408 expectation, woody plants had a more positive mean asymmetry value, suggesting that other  
409 species depend on them more than they depend on other species. The importance of woody  
410 species (mostly subshrubs and shrubs, in our dataset) may reflect larger plant size and  
411 therefore flower number, or a longer flowering period.

412

413 *Network-level properties*

414 Overall, plant traits and their phylogenetic history emerged as slightly more important to  
415 network-level structures than those of pollinators. This result is inconsistent with that of  
416 Rezende *et al.* (2007), who showed that phylogenetic history was more often significantly  
417 related to network structure in animals than in plants. Rezende *et al.* (2007) suggested that  
418 differences in mobility or “evolvability” could be involved in the difference between animals  
419 and plants (Bronstein *et al.* 2006), with the presence of certain pollinator clades in networks in  
420 accordance to their preferences for particular suites of floral traits.

421         In general, the overall effect of phylogeny on whole-network structures was generally  
422 weak compared to what was found in species-level metrics. This is not surprising because the  
423 species-level and network-level metrics examine different biological processes. The MPD  
424 parameter provides a metric of the overall amount of phylogenetic diversity in the community.  
425 The positive association of MPD of plants with nestedness could arise if some networks have a  
426 preponderance of certain clades where overlap in pollinators is especially low (e.g., monocots;  
427 Cortis *et al.* 2009).

428         A stronger pattern was observed with species-level metrics where phylogeny  
429 determines the number and identity of partnerships to some degree. We found little evidence  
430 that our included traits were driving this pattern because networks where phylogeny predicted  
431 interaction similarity were not the same networks where important traits had a strong  
432 phylogenetic signal, suggesting that other unmeasured traits that do have a phylogenetic signal  
433 are driving network structure.

434           We found that nestedness increased with increasing plant functional diversity but  
435 otherwise found little to suggest that increased trait diversity was associated with whole-  
436 network metrics. This is a surprising result given that trait diversity is often thought to enhance  
437 maintenance of biodiversity and ecosystem function (Cardinale et al. 2012). There is evidence  
438 that high nestedness, connectance, and modularity can contribute to robustness in mutualistic  
439 networks (Dunne et al. 2002; Thébault and Fontaine 2010; Donatti et al. 2011). Our results  
440 suggest that increased trait diversity is only weakly associated with networks that are  
441 potentially less robust to species loss.

442

#### 443 *Caveats*

444           When considering how traits influence ecological response variables, it is difficult to be  
445 sure that all possible important traits were measured. In this study, we included traits that were  
446 likely to be important variables in structuring communities. However, we were unable to  
447 include phenology or local abundance due to differences in the level of detail among data  
448 sets—basically sacrificing greater detail for the power that comes from including many different  
449 networks. Both phenology and local abundance have influenced visitation patterns in other  
450 pollination networks (Vázquez et al. 2007; Encinas-Viso et al. 2012). A more geographically-  
451 restricted focus would be needed to enable this kind of in-depth analysis. And, although we  
452 could have used the data we collected in each community to quantify network structure as a  
453 measure of abundance, this would mean that the same data would be used in the response and  
454 predictor variables in our models, violating a basic statistical assumption.

455           We combined networks described as part of different research projects, and with two  
456 different collection methods, which could bias results. However, we have accounted for these  
457 differences by including region (where each region comprised a single study) and collection  
458 method in our models.

459           Another potential source of error is variation in taxonomic sampling and level of  
460 identification – some taxonomic groups were sampled more thoroughly than others and some  
461 taxonomic groups were identified to species while others were identified to genus or higher.  
462 However, taxonomic identification was specific enough to unambiguously assign traits to taxa.

463

#### 464 *Conclusion*

465 We found that certain traits (namely, sociality and body size in pollinators, and flower  
466 symmetry and growth form in plants) were important in mediating network structure in  
467 mutualistic plant-pollinator interaction networks in Western Canada. Many networks showed  
468 no evidence that phylogeny was important in determining species-level interaction metrics. At  
469 the network level, both functional trait and phylogenetic diversity had only weak effects on  
470 overall network structure. In contrast to previous studies, pollinator traits and phylogenetic  
471 history appear to be less important than those of plants in determining community-level  
472 network structure.

473

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482

483

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602 Table 1. Description of traits included in this study, and expectations on how each trait should  
 603 relate to four pollinator or plant network structures: c: among-module connectivity; z: within-  
 604 module degree; ia: interaction asymmetry; d': specialization. Up arrows mean we expect the  
 605 value of the network metrics (e.g., c: among-module degree) to go up if the value of the trait is  
 606 that listed in the "Expectation at" column; we expect those with down arrows to go down in  
 607 value, and we do not have a prediction for those with an X.  
 608

<b>Trait</b>	<b>Description</b>	<b>Expectation at</b>	<b>c</b>	<b>z</b>	<b>ia</b>	<b>d'</b>
<b>Pollinators</b>						
Sociality	solitary, social	Social	↑	↑	↑	↓
Nest location	above- or belowground	Aboveground	X	X	X	X
Nest type	renters or excavators	Renters	X	X	X	X
Parasitism	parasitic, non-parasitic	Non-parasitic	X	X	X	↓
Body size	intertegular distance	Larger size	↑	↑	↑	↓
<b>Plants</b>						
Flower symmetry	zygomorphic, actinomorphic	Actinomorphic	↑	↑	↑	↓
Flower color	flower color	Yellow flowers	↑	↑	↑	↓
Sexual system	perfect, monoecious, dioecious	Perfect	X	X	X	X
Growth form	herbaceous, woody	Herbs	↓	↓	X	↑
Life-span	short-lived, long-lived	Annual	↓	↓	X	↑
Flower size	flower size	Larger size	↑	↑	X	↓

609  
610



611 Table 2. Summary of results of species level analyses of the relationship between species level  
 612 interaction metrics and phylogenetic distance. The numbers in each cell are the number of  
 613 networks with significant ( $P < 0.05$ ) relationships between species level interaction metrics (IA,  
 614 d, c, z, and ecosim) and phylogenetic distance; percents are percent of total networks with  
 615 significant relationships  
 616

Network Structure	Phylogenetic	
	Pollinators	Plants
<i>IA</i>	13 (14%)	2 (2%)
<i>d'</i>	2 (2%)	9 (10%)
<i>c</i>	3 (3%)	2 (2%)
<i>z</i>	5 (5%)	5 (5%)
Ecosim	15 (16%)	16 (17%)

617  
 618

619 Table 3. The joint effects of trait diversity and phylogenetic diversity on network level structures  
 620 (H2: network level specialization, weighted nestedness, modularity, weighted connectance).  
 621 See methods for more details. *P*-values < 0.05 are bolded  
 622  
 623

Term	H2'		W. Nestedness		Modularity		W. Connectance	
	Est	<i>P</i>	Est	<i>P</i>	Est	<i>P</i>	Est	<i>P</i>
N <sub>TOT</sub>	-1.11	<b>0.019</b>	0.77	0.133	-0.76	<b>0.006</b>	-1.09	<b>&lt;0.001</b>
FDis <sub>PO</sub>	-0.93	0.707	-1.38	0.603	1.77	0.236	-1.28	0.171
FDis <sub>PL</sub>	-5.50	0.342	14.92	<b>0.008</b>	-2.64	0.449	1.67	0.466
MPD <sub>PO</sub>	0.00	0.543	0.00	0.106	0.00	0.096	0.00	0.928
MPD <sub>PL</sub>	0.00	0.254	0.01	<b>0.036</b>	0.00	0.417	0.00	0.516
FDis <sub>PO</sub> ×MPD <sub>PO</sub>	0.01	<b>0.049</b>	-0.01	0.069	0.00	0.892	0.00	0.631
FDis <sub>PL</sub> ×MPD <sub>PL</sub>	0.01	0.527	-0.03	<b>0.048</b>	0.00	0.858	0.00	0.463

624

## Figure legends

Fig. 1 The relationship between phylogenetic distance and species level network metrics for plants and pollinators, in relationship to network size for five network metrics: a) ia – interaction asymmetry, b) d - specialization, c) c - among-module connectivity, d) z - within-module degree, and e) ecosim. Circle fill: empty circles are non-significant; filled circles were statistically significant (Pearson correlation coefficient;  $P < 0.05$ ). We used Mantel tests of distance matrices

Fig. 2 The relationship between species level network metrics (c, d', IA, and z) and pollinator sociality across all networks. Bars are least square means of the mean values for each network. Error bars are 1 SE. Asterisks show differences among levels within a variable (i.e., panel); letters are not shown where no differences occurred in post-hoc Tukey tests. We only show data for sociality here (other categorical variables were not significant – but see discussion of body size in *Results*). Abbreviations: S: solitary, SO: social. Network variables: c: among-module connectivity; z: within-module degree; ia: interaction asymmetry; d': specialization

Fig. 3 Relationship between species level interaction traits (c, d', IA, and z) and plant traits across all networks. See Fig. 2 for more information. Variables: sexual system (p: perfect; d: dioecious; gm: gynomonocious; gd: gynodioecious; o = other, including monoecy, andromonoecy, androdioecy, etc.); life-span (long: long-lived, short: short-lived); colour category (P: pink and red, W: white, Y: yellow-orange, B: purple-blue, G: greenish/brown/burgundy); growth form (h: herb, w: woody); symmetry (b: bilaterally symmetrical; r: radially symmetrical)

Fig. 1.

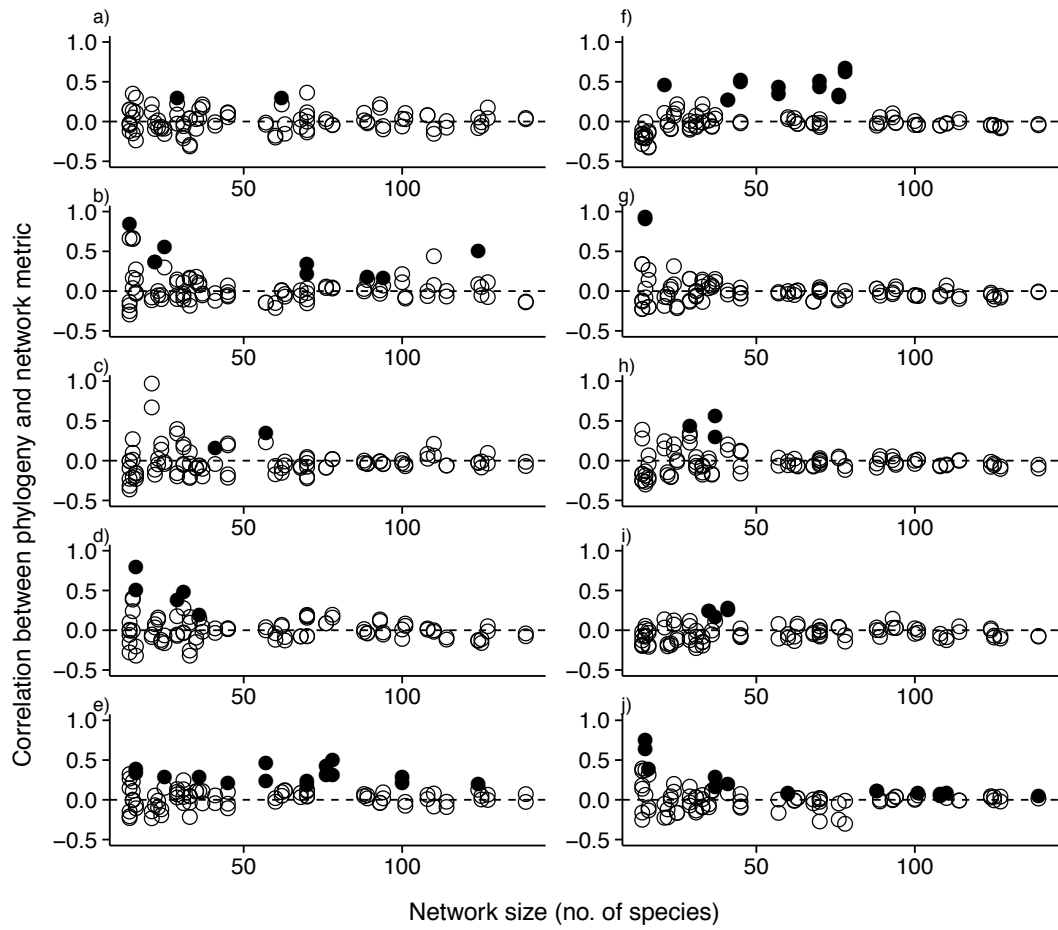


Fig. 2.

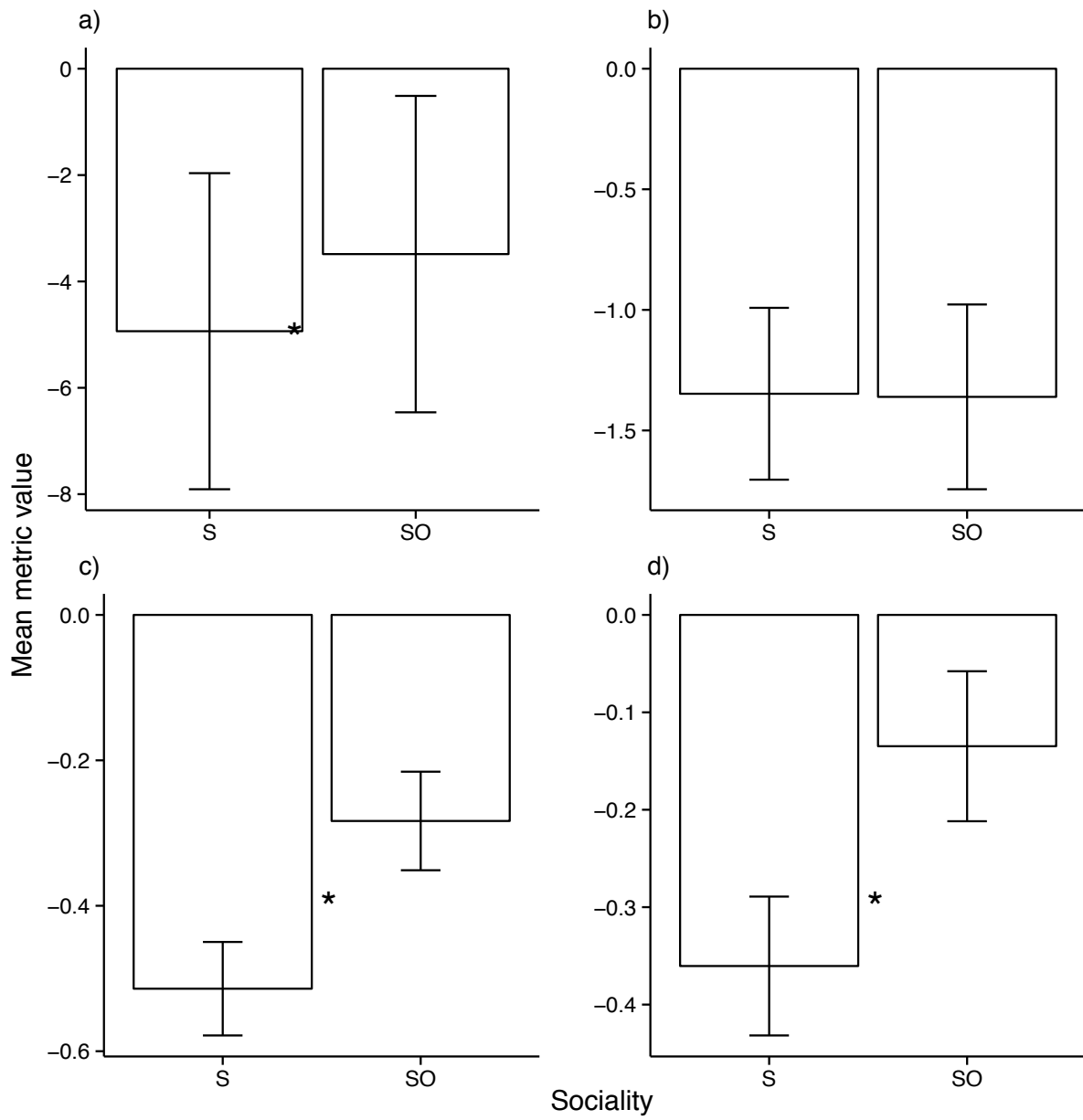


Fig. 3.

