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Along urbanization sprawl, exotic plants distort native bee (Hymenoptera: Apoidea) assemblages in high elevation Andes ecosystem

Patricia Henríquez-Piskulich ^{Corresp., 1}, Alejandro Vera ², Gino Sandoval ³, Cristian Villagra ¹

¹ Instituto de Entomología, Universidad Metropolitana de Ciencias de la Educación, Santiago, Región Metropolitana, Chile

² Departamento de Biología, Universidad Metropolitana de Ciencias de la Educación, Santiago, Región Metropolitana, Chile

³ Departamento de Historia y Geografía, Universidad Metropolitana de Ciencias de la Educación, Santiago, Región Metropolitana, Chile

Corresponding Author: Patricia Henríquez-Piskulich

Email address: patricia.henriquez@mayor.cl

Native bees contribute with a considerable portion of pollination services for endemic as well as economically important plant species. Their decline has been attributed to several human-derived influences including global warming as well as the reduction, alteration and loss of bees' habitat. Moreover, together with human expansion comes along the introduction of exotic plant species with negative impacts over native ecosystems. Anthropogenic effects may have even a deeper impact on communities adapted to extreme environments, such as high elevation habitats, where abiotic stressors alone are a natural limitation to biodiversity. In these, human-borne alterations, such as the introduction of exotic plants and urbanization, may have a greater influence on native communities. In this work we explored such problem, studying the relationship between landscape and its effect over richness and abundance of native bees from the subandean belt in the Andes mountain chain. Furthermore, we investigated the effects of exotic plant abundance on this high-altitude bee assemblage. Despite landscape did not show an effect over bee richness and abundance, exotic plants did have a significant influence over native bee assemblage. The abundance of exotic plants was associated with a relative increase in the proportion of small and medium bee species. Moreover, Halictidae was the only family that appeared to be favored by an increase in the abundance of exotic plant species. We discuss these results and the urgent need for further research of high-altitude environments due to their vulnerability and high endemism.

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2 **Along urbanization sprawl, exotic plants distort native bee (Hymenoptera: Apoidea)**
3 **assemblages in high elevation Andes ecosystem.**

4

5 Patricia A. Henríquez-Piskulich¹, Alejandro A. Vera², Gino S. Sandoval³, Cristian A. Villagra¹

6 ¹ Instituto de Entomología, Universidad Metropolitana de Ciencias de la Educación, Av. José
7 Pedro Alessandri 174, Santiago, Chile

8 ² Departamento de Biología, Universidad Metropolitana de Ciencias de la Educación, Av. José
9 Pedro Alessandri 174, Santiago, Chile

10 ³ Departamento de Historia y Geografía, Facultad de Historia, Geografía y Letras, Universidad
11 Metropolitana de Ciencias de la Educación, Av. José Pedro Alessandri 174, Santiago, Chile

12

13 Corresponding Author: Patricia Henríquez-Piskulich, patricia.henriquez@mayor.cl

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20 Abstract

21 Native bees contribute with a considerable portion of pollination services for endemic as well as
22 economically important plant species. Their decline has been attributed to several human-derived
23 influences including global warming as well as the reduction, alteration and loss of bees' habitat.
24 Moreover, together with human expansion comes along the introduction of exotic plant species
25 with negative impacts over native ecosystems. Anthropogenic effects may have even a deeper impact
26 on communities adapted to extreme environments, such as high elevation habitats, where abiotic
27 stressors alone are a natural limitation to biodiversity. In these, human-borne alterations, such as
28 the introduction of exotic plants and urbanization, may have a greater influence on native
29 communities. In this work we explored such problem, studying the relationship between landscape
30 and its effect over richness and abundance of native bees from the subandean belt in the Andes
31 mountain chain. Furthermore, we investigated the effects of exotic plant abundance on this high-
32 altitude bee assemblage. Despite landscape did not show an effect over bee richness and
33 abundance, exotic plants did have a significant influence over native bee assemblage. The
34 abundance of exotic plants was associated with a relative increase in the proportion of small and
35 medium bee species. Moreover, Halictidae was the only family that appeared to be favored by an
36 increase in the abundance of exotic plant species. We discuss these results and the urgent need for
37 further research of high-altitude environments due to their vulnerability and high endemism.

38 **Keywords:** Apoidea; exotic plant species; montane ecosystems; native bee assemblage;
39 pollinators; urbanization.

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42 Introduction

43 Native bee species are not only important as native plant pollinators, but also 15-30% of productive
44 crops require their pollination services (McGregor 1976). Declines of these insects have been
45 reported at a global scale (Biesmeijer et al. 2006; Fitzpatrick et al. 2007; Cameron et al. 2011).
46 Human activities are the main drivers of native bee's downturn through: fragmentation, biotic
47 homogenization with the introduction of invasive organisms (McKinney & Lockwood 1999), as
48 well as insect's habitat quality degradation and, ultimately, destruction (Foley et al. 2005; Potts et
49 al. 2010). Furthermore, climate change has also been listed among the explanations for native bee
50 declines (Potts et al. 2010). This would not only be detrimental for the perpetuation and
51 maintenance of world's ecosystems, but for the welfare of humanity as well. Among the
52 consequences of pollinator declines are changes in the structure of biotic communities, degradation
53 of biodiversity, and reduction of food production (Allen-Wardell et al. 1998). Mainly, by affecting
54 native flowers and crops of economic importance that greatly depend on pollinators to achieve
55 reproduction (Potts et al. 2010). A decline that may not be easy to recover from if it keeps
56 progressing, giving the continuous pressure over pollinators (Allen-Wardell et al. 1998; Winfree
57 et al. 2009).

58 This situation could be even more critical for native insects adapted to extreme environments,
59 including bees. At a local scale, insects may be especially sensitive to human impact in habitats
60 with extreme climate fluctuations (Boggs & Murphy 1997; Haslett 1997a). This could be the case
61 of high elevation environments, such as montane ecosystems, also recognized as hotspots of
62 biological diversity (Lomolino 2001). Under these conditions, in addition to overcoming current
63 human impacts, native bees must face extreme environmental variation such as severe changes in
64 temperature, elevated levels of ultraviolet radiation, less partial pressure of atmospheric gases,

65 drastic oscillations in the amount of precipitations, strong wind speed, among others (Hodkinson
66 2005). All these abiotic factors have been associated to comparatively reduced diversity and
67 specialized insects in high-altitude habitats (Pellissier et al. 2012; Classen et al. 2015). In general,
68 studies have found lower richness and abundance of insects as altitude increases (Hägvar 1976;
69 Wolda 1987; Lefebvre et al. 2018), and, regarding native bee species, the same pattern has been
70 reported (Arroyo et al. 1982; Hoiss et al. 2012).

71 Together with economic development, often goes along the increase of environment degradation
72 in favor of urbanization, especially in countries with unsustainable development policies (Romero
73 & Ordenes 2004). This problem may also impact high-altitude ecosystems (Baiping et al. 2004;
74 Romero & Ordenes 2004). Regarding the consequences of urbanization on native bee habitats, it
75 has been demonstrated that this affects bee richness and evenness, and also, delays peak abundance
76 during the bee season and decreases temporal turnover (Winfree et al. 2011; Hung et al. 2017).
77 Also, landscape modifications have been found to affect bee assemblages due to species-specific
78 responses such as: body size, nesting habits, feeding behavior and sociality level, among others
79 (Bishop & Ambruster 1999; Williams et al. 2010; Hopfenmüller et al. 2014; Marshall et al. 2015).
80 Considering this, there could be an array of different responses: Some species could respond
81 positively while others could be under threat of disappearing from an ecosystem (Hinnens et al.
82 2012; Fortel et al. 2014). Bees with feeding specializations (also called “oligolectic”) gather
83 resources on floral species of one family or genera of plants, and therefore, are less flexible to
84 changes in their habitats due to human-derived modifications (Steffan-Dewenter et al. 2006;
85 Hernandez et al. 2009). For instance, changes in landscape decrease the proportion of parasitic
86 (Steffan-Dewenter et al. 2006), solitary and also larger-sized native bee species (Hinnens et al.
87 2012). Contrastingly, urbanization may favor cavity-nesting species (Fortel et al. 2014) probably

88 due to the higher nesting resources for these species in urbanized areas (Hernandez et al. 2009).
89 Therefore, knowledge of the pollinator's resources and life-history traits is required to correctly
90 assess the most likely pollination responses under the effects of human activities (Cane et al. 2006).
91 The impact of exotic plants over native bee species has been poorly studied (Corbet et al. 2001;
92 Goulson 2003; Liu & Pemberton 2008). Moreover, to the best of our knowledge, the effects of
93 exotic plant species on mountain native bee assemblages it is yet to be revealed. Their influence
94 could be particularly relevant if they are capable of modifying landscapes and native plant
95 communities, due to cascading effects on different trophic levels (Morón et al. 2009; Fenesi et al.
96 2015). In high elevation environments it has been suggested that exotic plants may jeopardize
97 native pollination services (Miller et al. 2018) and potentially affect native bee populations through
98 modifying the relative abundance and the diversity of native plant species (Stout & Morales 2009).
99 In previous studies it has been found a negative relationship between the presence of exotic plants
100 and the abundance, species richness and evenness of native bees (Morón et al. 2009; Fenesi et al.
101 2015). However, contrary to general trend in landscape studies, and to the best of our knowledge,
102 there are no works on the effect of exotic plants over the species-specific response of native bees
103 due to the threats previously mentioned. If exotic plant species could alter mountain bee
104 assemblages, this may have significant effects on pollination of native plant species. Since their
105 effect could vary depending on which bee species is considered, some native bee species could
106 benefit from the introduction of exotic plants, as providers of additional resources (Tepedino et al.
107 2008; Drossart et al. 2017). Nonetheless, it has been recently demonstrated that the introduction
108 of exotic plants could be even more problematic than changes in landscape, affecting not only
109 insect assemblages but also complete plant-pollinator networks (Hansen et al. 2017). If exotic
110 plants replace the majority of native plant species, not only bees would face the consequences of

111 this introduction, but also the whole ecosystem services may be hampered due to alterations to the
112 biota (Wilde et al. 2015).

113 Despite above-mentioned problems, we found no published studies that focus on the response of
114 native bee assemblages towards the effects of landscapes changes and the introduction of exotic
115 flora in high elevation ecosystems. These dimensions could be essential for the understanding of
116 bee declines, and preventing further losses not only on these insects, but also the rest of pollinating
117 animals (Aguirre-Gutiérrez et al. 2015). In this work, we evaluated if urbanization could have an
118 effect on native bee species richness and abundance. In addition, we focused on the influence of
119 the abundance of exotic plant species and the response of native bee assemblages in order to
120 evaluate specie-specific responses. In general, there is still much to explore from montane biomes
121 (Lomolino 2001). In this context, previous works have listed nearly 50 species of native bees for
122 the subandean belt of central Chile (Arroyo et al. 1982; Camousseight & Barrera 1998; Monckton
123 2016). An area that, unfortunately, is under constant alteration due to the replacement of natural
124 habitats by urban expansion. In particular, we tested the hypothesis that urbanization mediates
125 changes in diversity, and also, that the introduction of exotic flora, that comes along with this,
126 could also play a role in changing the assemblage due to the close relationship between bees and
127 their floral resources. Our objectives were to assess the effect of urbanization over high-altitude
128 native bee diversity and, on the other hand, to test the effects of exotic floral abundance over the
129 assemblage.

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133 **Materials & Methods**

134 **Study Site**

135 We carried out our study in the town of Farellones and its surroundings (33°20'59''S,
136 70°18'34''O), located at 2,360 m.a.s.l in the subandean vegetational belt of Andes mountains of
137 central Chile. A zone characterized by long, snow free-periods of 5-8 months, and annual
138 precipitations of 400-800 mm falling mostly as snow during winter (Arroyo et al. 1981). This
139 correspond to a settlement started around 1930s as a winter sport center and presently the larger
140 ski destination in Chile, with an ongoing expansion of urban areas (Junta de Vecinos de Farellones,
141 2018). Moreover, as in other urbanized high elevation sites along Andes mountain chain, it is
142 possible to find livestock seasonal foraging activities as well as mining exploitation routes (Bahre
143 1979; SERPLAC 1980).

144 In this locality, vegetation is represented by subandean scrub, mainly composed by the Asteraceae
145 family, accompanied by perennial herbs, geophytes, and annual herbs (Arroyo et al. 1982). It has
146 been described that 54% of its vascular flora is native and 29% endemic (Muñoz-Schick et al.
147 2000).

148 We selected eight sites for this study of 80 x 80 m (Fig. S1), criteria for this selection were: (i) the
149 vegetation was unmanaged; (ii) sites were exposed to human activities; and (iii) safe enough to
150 sample, considering that the area presented cliffs and sharp edge precipices. Data was collected
151 from the sites once a month for two seasons: the first in December 2016, January and February
152 2017 (season 1: 2016/2017), and the second in November and December 2017, January and
153 February 2018 (season 2: 2017/2018). Weather with abundant snow precipitation did not permit
154 us to sample in November 2016. Minimal and maximal distances between sites were 380 m and
155 4.4 Km, respectively (Normandin et al. 2017).

156 Plants

157 In order to determine native and exotic floral abundance for each month sampled, we defined
158 transects of 80 m long x 2 meters wide, covering approximately 10% of the total site area. In these
159 transects all flowers of blooming species encountered within one meter on either side was counted.
160 Later, we calculated total density of native and exotic plant for each month using the formula:

$$161 \text{Density (D}_i\text{)} = \text{A}_i/\text{Area}$$

162 In this calculation, “A_i” correspond to the total number of individuals collected along the transect
163 (Baxter, 2014). For each season, we obtained an average of native and exotic floral abundance per
164 month sampled for every site. In addition, in each site we calculated the percentage covered by
165 urban landscape through the analysis of aerial photographs taken with a DJI Spark drone, with
166 ArcGIS v 10.5 to avoid bias caused by the possible effect of other factors associated with human
167 activities. Proximity of each site to urban settlements and roads measured in meters was also
168 considered a factor of human impact. Furthermore, since our study was done in a high mountain
169 environment, altitude of each site was registered to avoid bias caused by site differences.

170 Bee Sampling

171 We sampled bees on sunny days, with temperatures over 15 °C and winds below 15 Km/h
172 (following Fortel et al. 2014). Pan traps and insect nets were used to assess bee assemblages
173 (Nielsen et al. 2011). Pan traps corresponded to plastic bowls painted with yellow, blue or white
174 fluorescent paint (Rocol Top, France) (Normandin et al. 2017). For these samplings, we defined
175 three triplets of pan traps per site. In each triplet we considered one of every color used. These
176 recipients were filled with 400 mL of water and a drop of detergent. Pan traps were separated from
177 each other by 20 to 40 m forming a three meters side equilateral triangle that we left to work at
178 each site from 9 am to 17 pm (Westphal et al. 2008).

179 Complementarily, active net sampling took place one hour during the morning (9 am – 12 pm) and
180 one hour during the afternoon (15 pm – 17 pm), in order to cover for the majority of bee activity
181 for this mountain habitat (LeBuhn et al. 2003). Specimens collected were first stored in 70%
182 ethanol (w/w), and later washed, processed, pinned and identified to the lowest taxonomic level
183 using several keys and specialized taxonomist assistance (Chiappa et al. 1990; Toro & Rodríguez
184 1998; Toro 1999; Monckton 2016). For *Bombus dahlbomii* Guérin-Méneville, 1835
185 (Hymenoptera: Apidae), an endangered (Morales et al. 2016) and conspicuous species, we only
186 collected them to take into account the relative abundance in each sampled site and after the 1-
187 hour sampling period they were all released. Introduced species, such as *Apis mellifera* and
188 *Bombus terrestris*, were not collected in this study.

189 **Data analysis**

190 We computed the parameters separately for the two sampled seasons. Species diversity was
191 characterized by species richness in EstimateS (version 9.1.0, Colwell, Connecticut, U.S.A.). We
192 computed the observed cumulative species richness curve and the total expected species richness
193 with a bootstrapping of 1,000 random iterations of sampling order. In regards to total expected
194 species richness, we used Chao2 since it is the least biased estimator (Gwinn et al. 2016). The
195 proportions of singletons (species represented by a single specimen) was compared for each season
196 by means of Chi-square tests in SPSS (version 23, IBM, New York, U.S.A.).

197 Regarding native bee diversity, to assess correlation between landscape variables we used
198 Spearman correlation coefficients in SPSS, in order to avoid the effect of outliers and biased
199 correlation results (Suchowski 2001). Later, for each sampled season, we evaluated the effect of
200 landscape variables on native bee richness and abundance through generalized linear models
201 (GLM), using glm function in R. Since the dependent variables of richness and abundance

202 presented over dispersion, we used a negative binomial model to take this into account.
203 Furthermore, the effect of each landscape variable was nested in the season to account for inter-
204 seasonal variation. Considering the results of correlation analyses, we maintained the model with
205 the variable of the correlation set with the lowest AIC (Akaike Information Criterion) value,
206 regarding it as the most parsimonious alternative (Johnson & Omland 2004).

207 For the native bee assemblage of our study, we wanted to relate the functional traits of native bees
208 with the abundance of exotic flora. First, we classified our collected native bee specimens based
209 on different functional traits at species level into: “parasitic” and “non-parasitic”. Afterwards, the
210 “non-parasitic” group was subdivided by feeding behavior into: “oligolectic” or “polylectic”. This
211 was done because adults of parasitic bees forage only for nectar (Roubik 1989; Heard 2016). This
212 classification was based on previous published information (Jaffuel & Piri3n 1926; Ruiz 1944;
213 Rozen 1967; Wagenknecht 1969, 1970; Ehrenfeld & Rozen 1977). If there was no information
214 available of functional traits of a particular bee species, we used the information available from
215 the nearest related species.

216 We used the inter-tegular distance (ITD) as a proxy for body size and the functional trait of
217 foraging distance on every individual collected (Greenleaf et al. 2007). Measures were done with
218 the software tpsDig v 2.32, using photographs of the thorax of every collected specimen taken with
219 a Canon EOS 60D camera and camera lens of the same brand model EF-S 60mm f/2.8 Macro
220 USM (Hoiss et al. 2012; Fortel et al. 2014). For *B. dahlbomii*, we measured the ITD from several
221 specimens from Instituto de Entomolog3a, UMCE collection. Species were then grouped into small
222 (<1.5 mm), medium (1.5–3 mm), and large (>3 mm) size classes (Hinners et al. 2012).

223 To determine how groups of species that shared above-mentioned functional traits responded to
224 exotic floral abundance, in each sampled site we tested for the proportion of each functional trait

225 in regards to the site's exotic floral abundance. We pooled the data from both seasons and used the
226 proportion of the total number of native bee individuals (abundance) and total number of species
227 for each classification group.

228 In addition, we evaluated the possible effect of exotic floral abundance in montane bee's
229 assemblage at the family level. For this purpose, we used multinomial and binomial logistic
230 regression models to evaluate the response of exotic floral abundance over each functional group
231 with JMP (version 14, SAS Institute, North Carolina, U.S.A.) (Hinnners et al. 2012).

232 We applied the three-fold Bonferroni correction (Rice 1989) along the three functional trait
233 categories for these analyses. This considering bee's functional traits and the number of non-
234 independent tests done, and thus, the increasing probability of obtaining significant results due to
235 chance.

236

237 **Results**

238 **Native bee diversity**

239 Considering the two sampling seasons of 2016/2017 and 2017/2018, a total of 1,052 bee specimens
240 were collected, 212 in season 1 and 840 in season 2. In total, this corresponded to 28 genera and
241 46 species (32 in 1 and 40 in 2) with a minimum of nine species and a maximum of 27 species per
242 site (Table S1). They belonged to five families: Andrenidae (7 species), Apidae (13 species),
243 Colletidae (7 species), Halictidae (11 species), and Megachilidae (8 species) (Fig. 1). Nonetheless,
244 after our two-year study, it was still not possible to ensure that we had collected all the potential
245 species from Farellones, which can be confirmed by the species accumulation curve not reaching
246 saturation (Fig. 2). Estimated species richness of both pooled seasons was 52.83, therefore,

247 approximately 87.07% of native bee species present in our study location were collected during
248 our work (Table 1).

249 The proportion of singletons did not differ with statistical significance between the two seasons
250 ($\chi^2=0.003$, $df=1$, $p=0.95$). For both seasons 12 bee species (26.09%) were recorded as singletons
251 and four (8.70%) as doubletons. In regards to singletons, two species (4.35%) were parasitic. In
252 total, five species (10.87%) were parasitic and 41 non-parasitic. Non-parasitic were mostly
253 polylectic (78.05%). From the 46 species collected, 15 represented from 1.14% to 5.80% of the
254 total number of specimens (12 to 61 specimens). The three most abundant species were:
255 *Lasioglossum* sp. (279 specimens; 26.52% of the total), *B. dahlbomii* (121 specimens; 11.50%)
256 and *Caenohalictus iodurus* (117 specimens; 11.12%), all of them are polylectic.

257 Spearman correlation coefficients showed for both season a negative correlation between distance
258 to the nearest town and exotic floral abundance ($r \leq -0.857$, $n=8$, $p \geq 0.002$) (Table S2). For the GLM
259 of dependent variables, native bee richness and abundance, we only maintained distance to nearest
260 town since the models with this variable gave the lowest AIC to explain both. Regarding these
261 analyses, landscape variables showed no significant effect over native bee richness and abundance
262 (Table S3).

263 **Native bee species assemblage**

264 Within the plant species found during our field work and used to evaluate changes in the bee
265 assemblage, we encountered 39 plant species: 24.32% were exotic, 70.27% native and 5.41 %
266 were endemic for Chile (Table S4).

267 In regards to mountain bee assemblage composition, “parasitism” and “feeding behavior” had no
268 significant relationship with abundance of exotic plan species. After Bonferroni correction, the

269 variable “body size” (by abundance) showed a significant relationship with “exotic floral”
270 abundance. As the abundance of the latter increased, the proportion of small and medium native
271 bee species was greater, and the proportion of large individuals decreased ($\chi^2=197.96$, $p<0.0001$)
272 (Fig. 3).

273 Finally, for the native bee families in the assemblage, the proportion of Halictidae increased while
274 the proportions of Apidae, Colletidae and Megachilidae decreased ($\chi^2=229.88$, $p<0.0001$). The
275 family Andrenidae maintained a relatively small proportion in all sampled sites (Fig. 4).

276

277 **Discussion**

278 After our two-year study in the subandean belt of montane Andes, we found that the introduction
279 of exotic plant species did show an association with changes in native bee species assemblages. In
280 sites with higher abundance of exotic plants the composition of native bees changed in regards to
281 their body size (Fig. 3), and also at a taxonomic level (Fig. 4). Conversely, we found no evidence
282 of a possible effect of the landscape variables considered, represented by: distance to nearest town,
283 distance to roads, percentage of urban landscape cover, altitude and native floral abundance, on to
284 native bee richness and abundance (Table S3).

285 Even though our work contemplated two seasons, we weren't able to collect all the potential
286 species present in our location, as showed by the mean species accumulation curve. We found 46
287 species, which represents 87.07% of the predicted native bee species richness of this montane area
288 (Table S1). We sampled each of the eight sites from this high Andean zone for a total of seven
289 times (each survey done every four weeks during the bee season of both years). Regardless of what
290 we consider a large survey, we still obtained 12 species (26.09%) of bees in the form of singletons,

291 which could mean (a) we undersampled; (b) there exist a pattern of rarity in the assemblage; or (c)
292 there are a number of transitory species in the assemblage (Williams et al. 2001). Considering this
293 work was done in a high-altitude system, it becomes difficult to consider the latter (c) because of
294 the complexity and geographical isolation of montane communities (Haslett 1997a; Haslett 1997b;
295 Lomolino 2001). Thus, there could be a high number of rare species present in this native bee
296 assemblage, given the ecosystem in which these insects thrive and develop, one with a rich biota
297 and possibly an important number of endemic species (Lomolino 2001). A hypothesis partly
298 supported by the lack of differences between the proportion of singletons in both of the sampled
299 seasons, though in need of further study.

300 Exotic floral abundance proved to be correlated with the proximity to urban areas, were a higher
301 abundance of introduced plants individuals was found near urban lands. High elevation ecosystem
302 may be very sensitive to human-derived changes such as the introduction of exotic species (Badano
303 et al. 2007). It is possible to suggest that the problem lies in the biotic homogenization that comes
304 along with urbanization, and the consequent replace of native and endemic species by invasive and
305 exotic ones (McKinney & Lockwood 1999). Urbanization also triggers the reduction in native
306 flora and fauna diversity, and at the same time, promotes the reproduction and colonization by
307 exotic plant species (Marzluff 2001; McKinney 2002; Frankie et al. 2005). The latter has proven
308 to have significant effects over many ecological variables, the problem falling in the varying
309 magnitude and direction of these context dependent effects (Vilà et al. 2011). Nonetheless, exotic
310 flora could in some cases decrease richness and abundance of native plant and insect species, and
311 at the same time reduce insect biomass with lower insect productivity as a consequence (Heleno
312 et al. 2009; Cook-Patton & Agrawal 2014; Hengstum et al. 2014). For native bees, it has been
313 found varying responses to exotic plant species, where due to the alteration of composition and

314 structure of plant communities some species could be favored while others wouldn't be able to
315 forage and complete their life cycles because of limitations in their biology (Stout & Morales
316 2009). Therefore, some of them could be especially sensitive to the loss of their habitats (Mckinney
317 1997). A problem, that could be potentially important at this high-altitudes, where Hymenoptera
318 are the dominant flower visitors (Arroyo et al. 1982; Makrodimos et al. 2008). Studies have found
319 a relationship between floral specialization and risk of extinction, were oligolectic species are at a
320 higher risk of being affected by changes in their habitats (Packer et al. 2005; Roberts et al. 2011).
321 Even though most bee species in our study were polylectic, loss of dominant plant species in an
322 ecosystem might adversely affect generalists and specialists in the same manner (Frankie et al.
323 1997). Furthermore, since native plant richness of an ecosystem is negatively correlated with the
324 vulnerability to plant invasions (Knops et al. 1999), mountain environments could be more
325 susceptible to the dispersal of exotic plant species due to the decrease in species richness with
326 altitude (Rahbek 1995). This becomes very relevant not only because of the great endemism of its
327 community (Muñoz-Schick et al. 2000), but also because there is already evidence supporting the
328 classification as endangered for bee species in this habitat, such as the case of *B. dahlbomii*, the
329 largest Apiformes known to date (Morales et al. 2016). A species that could already be threatened
330 by the presence of the introduced bumblebee *B. terrestris* (Montalva et al. 2008; Montalva 2012;
331 Arbetman et al. 2013).

332 For montane Andes, richness and abundance of native bee species didn't show differences
333 associated with landscape variables, but we did find an association between exotic floral
334 abundance increase and the rise in the proportion of small and medium native bee specimens (Fig.
335 3). On the other hand, the proportion of bee specimens of large sizes dropped along the increase
336 of introduced plant species (Fig. 3). In regards of the consequences of exotic flora over the

337 phylogenetic structure of the assemblage, the effect is probably related to body size, since
338 Halictidae specimens present in our study ranged between small or medium sized bee and were
339 the only family that showed a rise in its proportion of total specimens with higher exotic floral
340 abundance (Fig. 4). It has been demonstrated that larger bee species are able to cover longer
341 distances in the search of resources than smaller and medium sized bees (Greenleaf et al. 2007),
342 but their success is still affected by the quality of their habitat, decreasing in sites where urbanization
343 is stronger (Martins et al. 2013). If exotic flora keeps expanding, it is possible there could be
344 changes not only for bees, but also for this entire high-altitude ecosystem. Different bee species
345 may prefer different floral resources during foraging (Hinnert & Hjelmroos-Koski 2009; Harmon-
346 Threatt & Kremen 2015), and they can also have varied responses towards the use of exotic flora
347 over native plant species (Morandin & Kremen 2013). For an optimal larval development, bees
348 need to reach their pollen nutritional requirements (Brodschneider & Crailsheim 2010), therefore,
349 low quality pollen can affect the development and survival of native bees and consequently affect
350 the complete assemblage of this group of insects (Herbert et al. 1970; Peng & Jay 1976; Cane &
351 Roulston 2002; Di Pasquale et al. 2013). Nevertheless, even if the abundance of small and medium
352 native bees increased, the long-term effects of these changes on this native bee assemblage are still
353 unknown and further studies are needed to assess their extent and implications.

354 Based on our results, landscape variables didn't show an effect over native bee richness and
355 abundance. Considering our study was located in a small Andean urban area with a great number
356 of "green spaces" (gardens and town squares) it could be a possibility that connectivity still
357 remains unaffected. Regardless if urbanization results in a higher number of edifications,
358 destruction and fragmentation of natural habitats, loss of areas capable of sustaining wild life
359 (McIntyre et al. 2001; Seto et al. 2012) and thus, habitat loss and permanent disappearance of wild

360 species as a consequence (McKinney 2002), these predictors will depend of the quality of the
361 surrounding landscape (Tscharntke et al. 2005). Therefore, if “green spaces” are large or close
362 from one another, the impact these areas would have in preserving biodiversity in the long-term
363 may buffer the effects of urbanization (Rudd et al. 2002; Goddard et al. 2010).

364 Because of the spatial limitations of our study, we mostly sampled an already disturbed area, and
365 as a consequence, further research is necessary to assess the extent of our findings regarding the
366 effect of exotic flora over high-altitude bee assemblages and plant communities. For instance, this
367 makes necessary to compare our results with more pristine high-altitude environments. Our work
368 shows that native assemblages in high-altitude ecosystems are modified by the introduction of
369 exotic plant species. Such response needs further research on the implications for the pollination
370 network and ecosystem of this mountain environment. Given the response of the functional traits
371 in comparison with native bee richness and abundance alterations due to landscape changes, the
372 use of species-specific traits could be an important tool to detect early changes in native bee
373 assemblages and take appropriate conservation measures. This work contributed to the scarce
374 information regarding the connection between high-altitude pollinators and urbanization effects,
375 especially in regards to the relationship between the introduction of exotic flora and native
376 assemblages. Furthermore, our work stresses the need to elucidate the direct effect of exotic flora
377 can have in native bee ecophysiology and the long-term ecological dynamics. This study also
378 highlights the urgent need to plan urban expansion ahead of time and taking into account the
379 biodiversity that will be affected, so management measures can be also included. For instance, the
380 control of weeds and introduction of exotic ornamental plant species. Furthermore, it is important
381 to stress the need for science education and outreach to generate a common conscience of the value
382 of local biodiversity and the ecosystem services they provide (Wilson et al. 2017). Biotic

383 homogenization has been described as one of the most detrimental human activities on biological
384 diversity (McKinney & Lockwood 1999). This, in addition to the fact of the disconnection of our
385 own species with their native biodiversity, makes it more difficult for humans to empathize with
386 nature and promote its conservation (McKinney 2006). A future goal should be to include
387 management practices that buffer the effects of urbanization over biodiversity.

388 In montane ecosystems, natural habitats are under constant alteration and replacement due to the
389 rapid growth of urban areas, especially those of touristic, mining, and livestock interests (Bahre
390 1979; SERPLAC 1980; Romero & Ordenes 2004). For example, urban planning focus in the
391 search of a good view and clear skies without sustainable development (Romero & Ordenes 2004).
392 Therefore, it becomes paramount to consider the conservation of biodiversity in high-altitude areas
393 and implement an appropriate land use regulation (De Palma et al. 2016). The latter should include
394 large native green spaces close to one another, not only to protect montane bees, but also for other
395 native organisms such as vertebrates and invertebrate that live in this area, and that could fulfill
396 important roles yet to be discovered within ecosystem services.

397

398 **Conclusions**

399 The exotic flora in montane habitats is capable of altering native bee assemblage's composition.
400 Nevertheless, further research is necessary in order to assess the ecological and evolutionary
401 consequences of these invasions. Furthermore, we did not find landscape effect from urbanization
402 variables, we suggest that the occurrence of empty lots with remaining patches of native flora may
403 contribute to habitat connectivity in this high-altitude town, reducing the effect of urbanization
404 itself over native bee species. We propose that the existence of "green spaces", composed by local

405 plant community, and control of exotic plant species may ameliorate the effects of human
406 expansion in high elevation bee habitats.

407

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Figure 1

Specimens from the different Families collected during the study.

(a) *Acamptopoeum submetallicum* (Andrenidae), scale bar 1.5 mm. (b) *Centris nigerrima* (Apidae), scale bar 2 mm. (c) *Xeromelissa* sp. (Colletidae), scale bar 0.5 mm (d) *Caenohalictus iodurus* (Halictidae), scale bar 1 mm. (e) *Anthidium chubuti* (Megachilidae), scale bar 2 mm. Photography: Patricia Henríquez-Piskulich.



Figure 2

Mean species accumulation curve for pooled data from two sampled seasons (1000 randomizations).

The vertical axis corresponds to number of species and the horizontal to sampled sites.

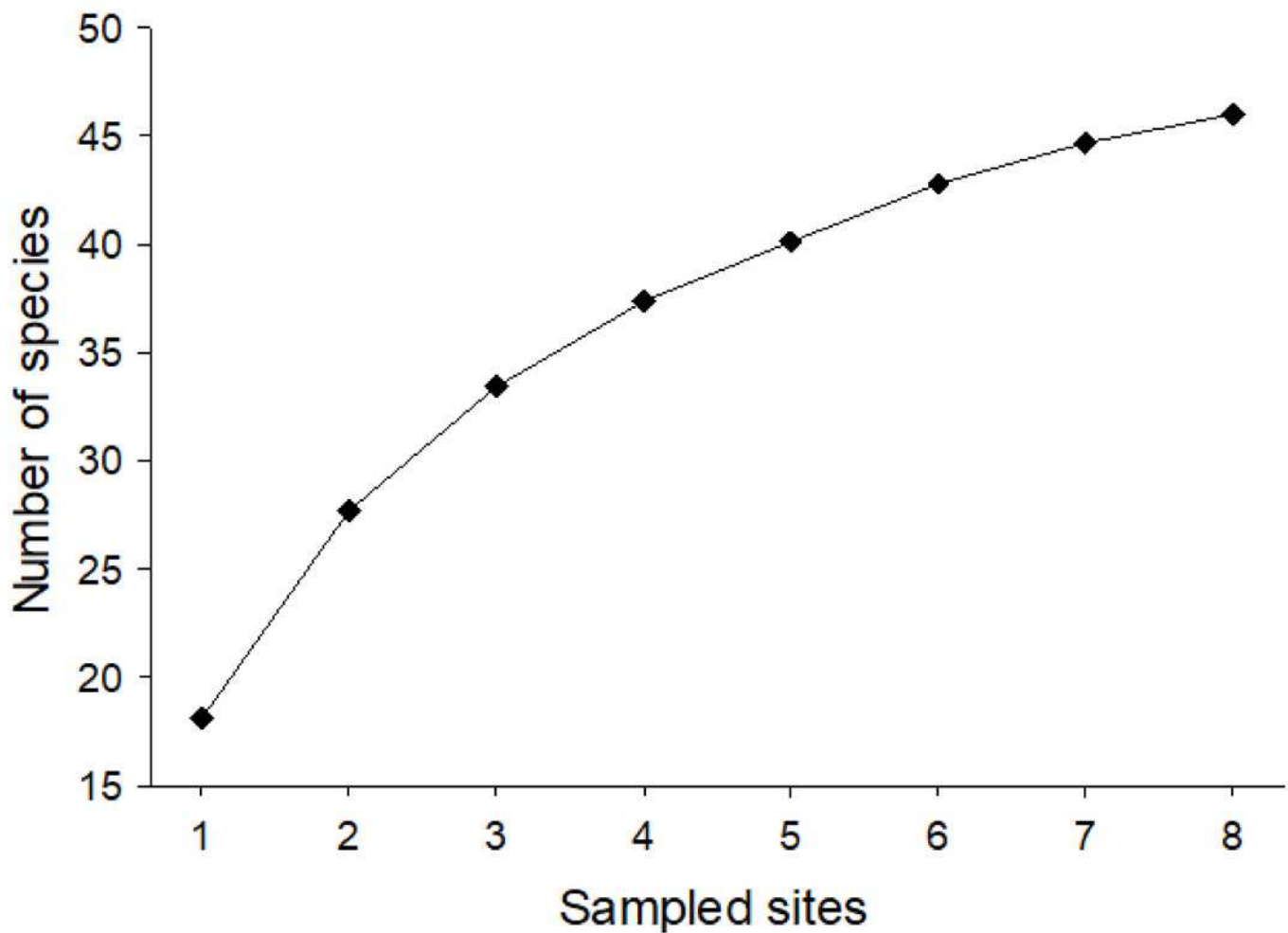


Table 1 (on next page)

Observed and estimated species richness for Mountain habitat at Farellones and its vicinity.

Season	Sobs ^a ±Sd ^b	Chao 2±SD (completeness)
2016-2018	46±9.53	52.83±5.15 (87.07)
2016/2017	32±8.07	43.48±7.98 (73.60)
2017/2018	40±8.29	46.62±5.29 (85.80)

^aSobs=observed specie

^bSd=standard deviator

Figure 3

Relationship between Native bee species grouped by body size range (Small, Medium and Large) versus exotic floral abundance ($\chi^2=197.96$, $p<0.0001$).

The left vertical axis corresponds to the proportion of total specimens and the horizontal to exotic plant abundance proportion. The groups of the right vertical axis correspond to areas between the regression lines.

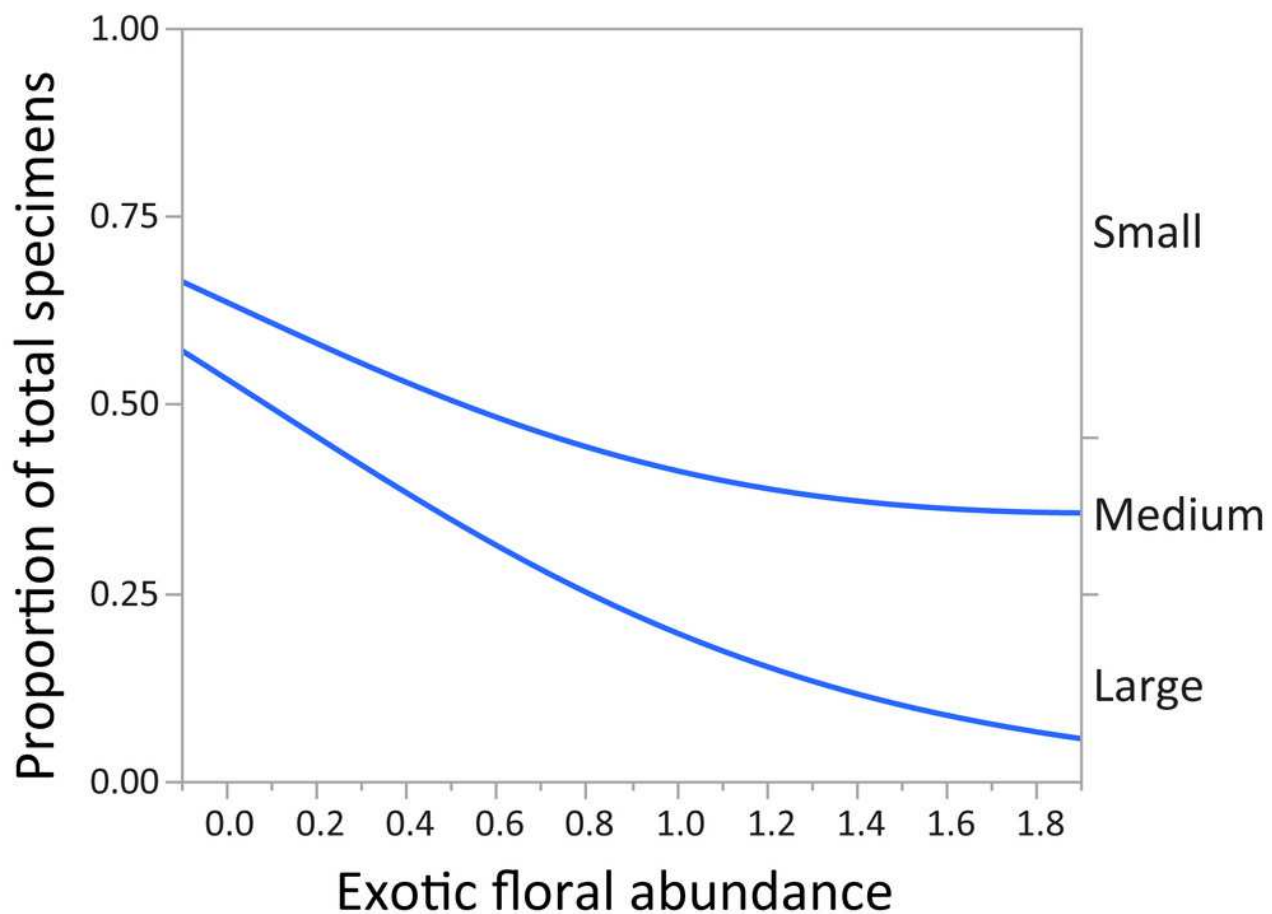


Figure 4

Relationship between native bee family versus exotic floral abundance proportions ($\chi^2=229.88$, $p<0.0001$).

The left vertical axis corresponds to the proportion of total specimens and the horizontal to exotic floral abundance proportion. The groups of the right vertical axis correspond to areas between the regression lines.

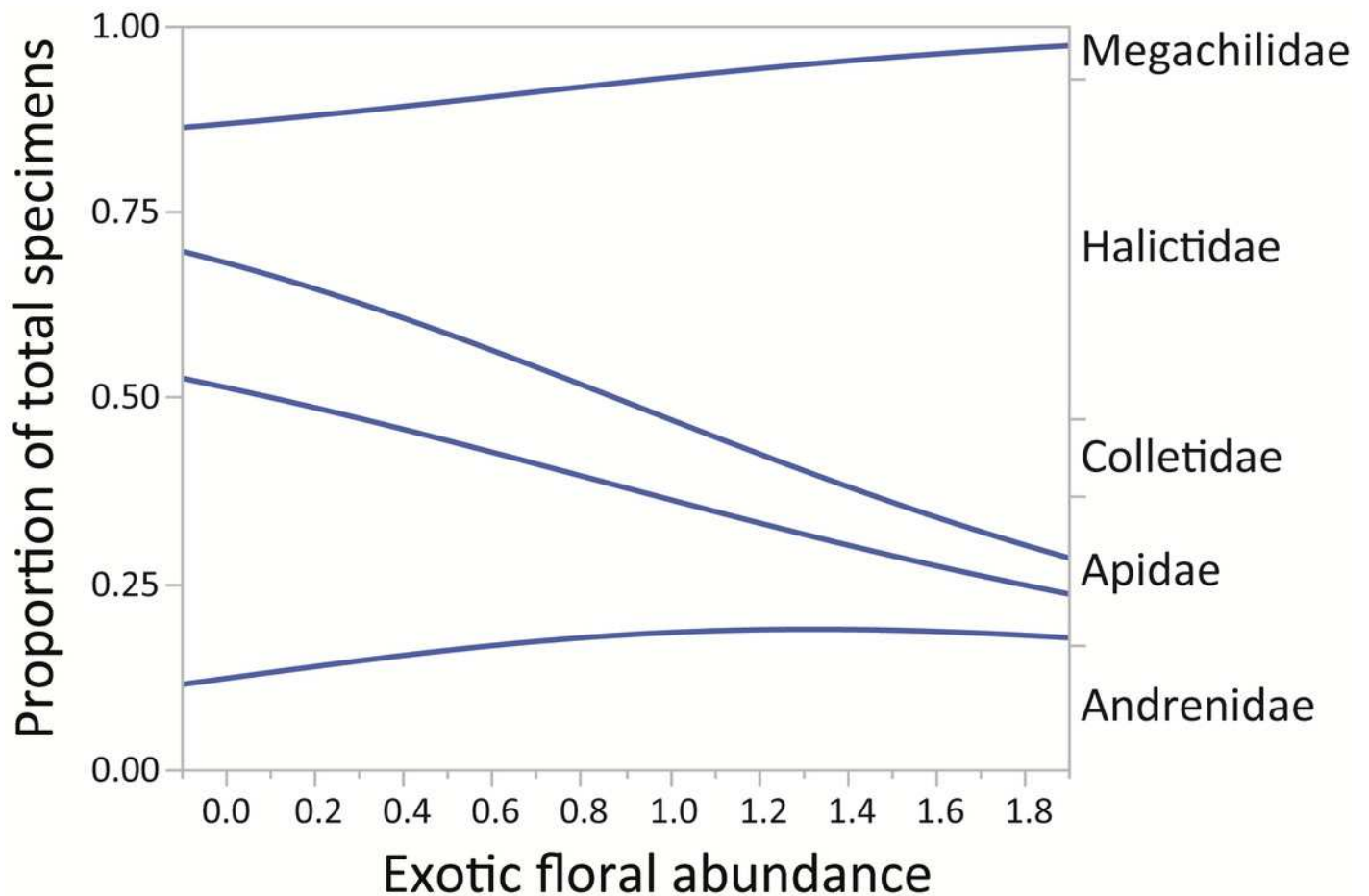


Figure 5

Map of selected sites for the study.

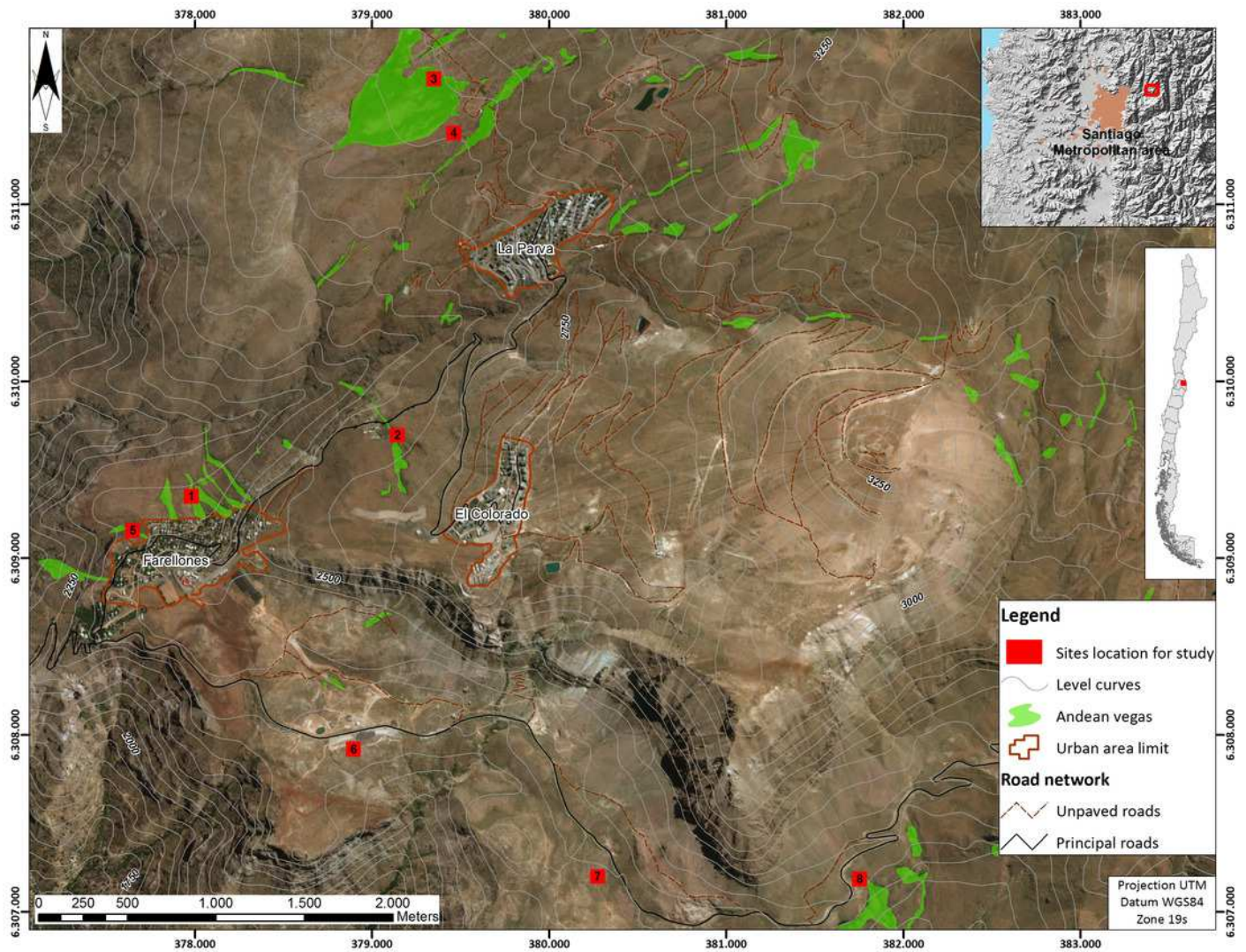


Table 2 (on next page)

List of native bee species collected during field work and their functional traits.

Specie	Family	Number of specimens	Body size	Feeding behavior	Parasitism	Observedfloral associations during the study	References
<i>Acamptopoeum submetallicum</i>	Andrenidae	25	Medium	Polylectic	Non-parasitic	<i>Anthemis cotula</i>	Rozen 1967; Packer et al. 2005
<i>Alloscirtetica gayi</i>	Apidae	5	Large	Polylectic	Non-parasitic	<i>A. cotula</i> <i>Stachys philippiana</i>	Wagenknecht 1970
<i>Alloscirtetica rufitarsis</i>	Apidae	8	Large	Polylectic	Non-parasitic	<i>Adesmia gracilis</i> <i>A. cotula</i> <i>S. philippiana</i>	Wagenknecht 1970
<i>Anthidium chilense</i>	Megachilidae	2	Medium	Polylectic	Non-parasitic		Toro & Rodríguez 1998
<i>Anthidium chubuti</i>	Megachilidae	16	Large	Polylectic	Non-parasitic	<i>Adesmia</i> sp. <i>Chaetanthera pusilla</i>	Toro & Rodríguez 1998
<i>Anthidium espinosai</i>	Megachilidae	1	Large	Polylectic	Non-parasitic		Toro & Rodríguez 1998
<i>Anthophora incerta</i>	Apidae	2	Large	Polylectic	Non-parasitic	<i>A. cotula</i> <i>Chuquiraga oppositifolia</i>	Ruiz 1940
<i>Bombus dahlbomii</i>	Apidae	121	Large	Polylectic	Non-parasitic	<i>Phacelia secunda</i> <i>S. philippiana</i>	Abrahamovich et al. 2001
<i>Cadeguala occidentalis</i>	Colletidae	1	Large	Polylectic	Non-parasitic	<i>S. philippiana</i>	Packer et al. 2005; Montalva et al. 2011

<i>Caenohalictus aplacodes</i>	Halictidae	3	Medium	<i>Polylectic</i>	Non-parasitic	<i>Berberis empetrifolia</i> <i>A. cotula</i>	Michener et al. 1979; Rojas & Toro 2000
<i>Caenohalictus iodurus</i>	Halictidae	117	Small	Polylectic	Non-parasitic	<i>B. empetrifolia</i> <i>Taraxacum officinale</i>	Michener et al. 1979; Rojas & Toro 2000
<i>Caenohalictus rostraticeps</i>	Halictidae	6	Medium	Polylectic	Non-parasitic	<i>Alstromeria pallida</i> <i>Madia sativa</i> <i>S. philippiana</i>	Michener et al. 1979; Rojas & Toro 2000
<i>Callistochlora chloris</i>	Halictidae	61	Medium	Polylectic	Non-parasitic	<i>A. cotula</i> <i>Brassica campestris</i> <i>C. oppositifolia</i> <i>T. officinale</i>	González-Vaquero & Galvani 2016
<i>Callistochlora prothysteres</i>	Halictidae	1	Medium	<i>Polylectic</i>	Non-parasitic	<i>A. cotula</i>	González-Vaquero & Galvani 2016
<i>Caupolicana bicolor</i>	Colletidae	1	Large	<i>Polylectic</i>	Non-parasitic		Ruiz 1938
<i>Centris cineraria</i>	Apidae	14	Large	Polylectic	Non-parasitic	<i>A. gracilis</i> <i>S. philippiana</i> <i>A. pallida</i>	Wagenknecht, 1971; Chiappa et al. 2000
<i>Centris nigerrima</i>	Apidae	22	Large	Polylectic	Non-parasitic	<i>Calceolaria arachnoidea</i> <i>C. oppositifolia</i> <i>S. philippiana</i>	Wagenknecht, 1971; Chiappa et al. 2000
<i>Chalepogenus caeruleus</i>	Apidae	2	Medium	Polylectic	Non-parasitic		Roig-Alsina 1999

<i>Chilicola</i> (<i>Heteroediscelis</i>) <i>curvapeligrosa</i>	Colletidae	34	Small	<i>Polylectic</i>	Non-parasitic		Jaffuel & Piri3n 1926; Gonz3lez & Giraldo 2009
<i>Colletes araucariae</i>	Colletidae	41	Medium	Polylectic	Non-parasitic	<i>A. cotula</i> <i>C. oppositifolia</i> <i>M. sativa</i> <i>P. secunda</i>	Ruiz 1944; Toro 1999
<i>Colletes fulvipes</i>	Colletidae	2	Large	<i>Polylectic</i>	Non-parasitic	<i>Adesmia</i> sp.	Ruiz 1944; Toro 1999
<i>Colletes musculus</i>	Colletidae	18	Medium	Polylectic	Non-parasitic	<i>A. cotula</i> <i>B. empetrifolia</i>	Ruiz 1944; Toro 1999
<i>Diadasia chilensis</i>	Apidae	22	Medium	Polylectic	Non-parasitic	<i>A. cotula</i> <i>Senecio eruciformis</i>	Ruiz 1940; Montalva et al. 2010
<i>Epiclopus gayi</i>	Apidae	1	Large	Polylectic	Parasitic		Wagenknecht 1969
<i>Epiclopus lendlianus</i>	Apidae	5	Large	Polylectic	Parasitic		Wagenknecht 1969
<i>Euherbstia excellens</i>	Andrenidae	1	Large	<i>Polylectic</i>	Non-parasitic	<i>A. cotula</i>	Hurd & Linsley 1976; Rozen 1993
<i>Isepeolus luctuosus</i>	Apidae	1	Medium	Polylectic	Parasitic		Spinola 1851; Montalva et al. 2010
<i>Kelita</i> sp.	Apidae	4	Small	NA	Parasitic		Ehrenfeld & Rozen 1977
<i>Lasioglossum</i> sp.	Halictidae	279	Small	Polylectic	Non-parasitic	<i>A. cotula</i> <i>S. philippiana</i>	Montalva et al. 2010; Polidori et al. 2010
<i>Liphanthus andinus</i>	Andrenidae	50	Small	<i>Oligolectic</i>	Non-parasitic		kozen 1967; Mena & kuz 2003
<i>Liphanthus coquimbensis</i>	Andrenidae	6	Small	<i>Oligolectic</i>	Non-parasitic		kozen 1967; Mena & kuz 2003

<i>Lipanthus sabulosus</i>	Andrenidae	56	Small	Oligolectic	Non-parasitic		Rozen 1967; Mena & Ruz 2003
<i>Megachile (Dasymegachile) distinguenda</i>	Megachilidae	12	Large	Polylectic	Non-parasitic	<i>Trifolium repens</i>	Durante et al. 2006
<i>Megachile pollinosa</i>	Megachilidae	1	Large	Polylectic	Non-parasitic		Raw 2007
<i>Megachile saulcyi</i>	Megachilidae	8	Large	Polylectic	Non-parasitic	<i>A. pallida</i> <i>A. cotula</i> <i>C. oppositifolia</i>	Durante et al. 2006
<i>Megachile semirufa</i>	Megachilidae	35	Large	Polylectic	Non-parasitic	<i>C. oppositifolia</i> <i>P. secunda</i> <i>Solidago chilensis</i> <i>T. repens</i>	Durante et al. 2006; Montalva et al. 2012
<i>Protandrena</i> sp.	Andrenidae	7	Small	Polylectic	Non-parasitic		Gonzalez & Ruz, 2007; Gonzalez et al. 2013
<i>Rhopitulus evansi</i>	Andrenidae	30	Small	Oligolectic	Non-parasitic	<i>S. eruciformis</i> <i>S. chilensis</i>	Ruz & Chiappa, 2004; Rozen 2014
<i>Ruizantheda cerdai</i>	Halictidae	1	Medium	Polylectic	Non-parasitic		Spinola 1851; Jaffuel & Piri6n 1926; Montalva et al. 2010
<i>Ruizantheda mutabilis</i>	Halictidae	5	Medium	Polylectic	Non-parasitic	<i>A. cotula</i>	Spinola 1851; Jaffuel & Piri6n 1926; Montalva et al. 2010

<i>Ruizantheda nigrocaerulea</i>	Halictidae	1	Medium	Polylectic	Non-parasitic	<i>A. cotula</i>	Spinola 1851; Jaffuel & Piri3n 1926; Montalva et al. 2010
<i>Ruizantheda proxima</i>	Halictidae	1	Medium	<i>Polylectic</i>	Non-parasitic	<i>A. cotula</i>	Spinola 1851; Jaffuel & Piri3n 1926; Montalva et al. 2010
<i>Sphecodes rugulosus</i>	Halictidae	3	Small	<i>Polylectic</i>	Parasitic	<i>A. cotula</i>	Montalva et al. 2010; 3zbek et al. 2015
<i>Svastrides melanura</i>	Apidae	4	Large	Polylectic	Non-parasitic	<i>A. cotula</i>	Ruiz 1940; Wagenknecht 1970; Montalva et al.
<i>Trichothurgus herbsti</i>	Megachilidae	1	Large	Polylectic	Non-parasitic		Walter & Sielfeld 1973
<i>Xeromelissa</i> sp.	Colletidae	15	Small	<i>Polylectic</i>	Non-parasitic		Rozen & Wyman 2015

Data in italic represents when information available from the nearest related species was needed.

NA: Not available

Table 3 (on next page)

Spearman correlation coefficients for landscape variables.

2016/2017 Season	Distance to nearest town (p-value)	Distance to roads (p-value)	Infrastructures (p-value)	Altitude (p-value)	Native floral abundance (p-value)
Distance to roads (p-value)	-0.262 (0.531)	-	-	-	-
Urban landscape (p-value)	0.412 (0.310)	-0.247 (0.555)	-	-	-
Altitude (p-value)	-0.333 (0.420)	0.262 (0.531)	-0.577 (0.134)	-	-
Native floral abundance (p-value)	-0.095 (0.823)	0.310 (0.456)	0.412 (0.310)	0.333 (0.420)	-
Exotic floral abundance (p-value)	-0.857 (0.007)	0.095 (0.823)	-0.247 (0.555)	0.167 (0.693)	0.119 (0.779)
2017/2018 Season	Distance to nearest town (p-value)	Distance to roads (p-value)	Infrastructures (p-value)	Altitude (p-value)	Native floral abundance (p-value)
Distance to roads (p-value)	-0.262 (0.531)	-	-	-	-

Urban landscape (p-value)	0.412 (0.310)	-0.247 (0.555)	-	-	-
Altitude (p-value)	-0.333 (0.420)	0.262 (0.531)	-0.577 (0.134)	-	-
Native floral abundance (p-value)	0.071 (0.867)	0.167 (0.693)	0.247 (0.555)	0.476 (0.233)	-
Exotic floral abundance (p-value)	-0.905 (0.002)	0.310 (0.456)	-0.412 (0.310)	0.262 (0.531)	-0.143 (0.736)

Cells with significant p-value are written in bold.

Table 4 (on next page)

GLM results for mountain native bee richness and abundance.

Factor	B	SE	Wald Chi-Square	p-value
GLM: Richness season 2016/2017, Negative binomial distribution, AIC = 130.91				
Distance to nearest town	-0.001	0.0009	0.845	0.358
Distance to roads	-0.001	0.0089	0.026	0.873
Urban landscape	0.003	0.0030	1.081	0.299
Altitude	0.000	0.0032	0.022	0.881
Native floral abundance	0.150	0.3334	0.202	0.653
Factor	B	SE	Wald Chi-Square	p-value
GLM: Abundance season 2016/2017, Negative binomial distribution, AIC = 176.97				

Distance to nearest town	-0.001	0.0009	1.591	0.207
Distance to roads	-0.002	0.0092	0.059	0.809
Urban landscape	0.002	0.0029	0.587	0.444
Altitude	-0.001	0.0031	0.106	0.744
Native floral abundance	0.049	0.3044	0.026	0.871
Factor	B	SE	Wald Chi-Square	p-value
GLM: Richness season 2017/2018, Negative binomial distribution, AIC = 130.91				
Distance to nearest town	-0.001	0.0008	0.604	0.437
Distance to roads	-0.002	0.0081	0.062	0.803
Urban landscape	0.001	0.0027	0.284	0.594
Altitude	0.000	0.0033	0.005	0.943

Factor	B	SE	Wald Chi-Square	p-value
Native floral abundance	-0.067	0.3080	0.047	0.828
GLM: Abundance season 2017/2018, Negative binomial distribution, AIC = 176.97				
Distance to nearest town	-0.001	0.0008	1.597	0.206
Distance to roads	0.003	0.0080	0.175	0.676
Urban landscape	0.002	0.0026	0.448	0.503
Altitude	-0.001	0.0033	0.048	0.827
Native floral abundance	-0.123	0.2985	0.170	0.680

Results of generalized linear models with abundance or species richness as dependent variables and landscape variables as independent variables. The effect of independent variables was nested in the year to account for interannual.

*AIC=Akaike Information Criterion.

Table 5 (on next page)

List of plants registered during field work and their origin.

Species	Family	Origin
<i>Adesmia gracilis</i>	Fabaceae	Native
<i>Adesmia</i> sp.	Fabaceae	Native
<i>Alstroemeria pallida</i>	Alstroemeriaceae	Native
<i>Anthemis cotula</i>	Asteraceae	Exotic
<i>Astragalus looseri</i>	Fabaceae	Native
<i>Berberis empetrifolia</i>	Berberidaceae	Native
<i>Brassica campestris</i>	Brassicaceae	Exotic
<i>Calceolaria arachnoidea</i>	Calceolariaceae	Native
<i>Cardamine vulgaris</i>	Brassicaceae	Native
<i>Calandrinia affinis</i>	Montiaceae	Native
<i>Cerastium arvense</i>	Caryophyllaceae	Exotic
<i>Chaetanthera chilensis</i>	Asteraceae	Native
<i>Chaetanthera linearis</i>	Asteraceae	Native
<i>Chaetanthera pusilla</i>	Asteraceae	Native
<i>Chuquiraga oppositifolia</i>	Asteraceae	Native
<i>Convolvulus arvensis</i>	Convolvulaceae	Exotic
<i>Cynoglossum creticum</i>	Boraginaceae	Exotic
<i>Epilobium nivale</i>	Onagraceae	Native
<i>Gilia crassifolia</i>	Polemoniaceae	Native
<i>Haplopappus diplopappus</i>	Asteraceae	Native
<i>Haplopappus schumannii</i>	Asteraceae	Native
<i>Lobelia oligophylla</i>	Campanulaceae	Native
<i>Madia sativa</i>	Asteraceae	Native
<i>Microsteris gracilis</i>	Polemoniaceae	Native
<i>Mutisia sinuata</i>	Asteraceae	Native
<i>Oenothera acaulis</i>	Onagraceae	Endemic
<i>Olsynium philippii</i>	Iridaceae	Native
<i>Perezia carthamoides</i>	Asteraceae	Native
<i>Phacelia secunda</i>	Boraginaceae	Native
<i>Quinchamalium chilense</i>	Santalaceae	Native
<i>Rhodophiala rhodolirion</i>	Amaryllidaceae	Native
<i>Sanicula graveolens</i>	Apiaceae	Native
<i>Schizanthus hookeri</i>	Solanaceae	Native
<i>Senecio eruciformis</i>	Asteraceae	Native
<i>Solidago chilensis</i>	Asteraceae	Exotic
<i>Stachys philippiana</i>	Lamiaceae	Endemic
<i>Taraxacum officinale</i>	Asteraceae	Exotic
<i>Trifolium repens</i>	Fabaceae	Exotic
<i>Veronica anagallis-aquatica</i>	Plantaginaceae	Exotic