

SHORT REPORT

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Temporal and spatial variation of the pollinator assemblages in *Alstroemeria ligtu* (Alstroemeriaceae)

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Findings

Plant-pollinator interactions have been seen as a co-adaptative process between pollinators and flowers (Johnson and Steiner 2000). Even though specialized pollinator systems do exist, most plants are pollinated by a wide spectrum of pollinators (Ollerton 1996; Waser et al. 1996). Accordingly, the degree of generalization in a plant-pollinator system may vary temporally and spatially in relation to biotic or abiotic environment fluctuations (see Gómez and Perfectti 2009, for review). In general, spatial variation has been invoked as the most important factor in the maintenance of generalization (Herrera 1996; Fenster et al. 2004), and temporal variation has been overlooked (but see Williams et al. 2001; Gómez 2002). In the long run, pollinator variation can be translated into inter-population variation in the degree of generalization, which subsequently can affect the reproductive success of plant species (Suárez et al. 2009; Botto-Mahan et al. 2011).

Alstroemeria ligtu var. *simsii* Sprengel (Alstroemeriaceae) is a perennial herb endemic to central Chile (Muñoz and Moreira 2003). *A. ligtu simsii* is a hermaphroditic self-incompatible subspecies that relies entirely on pollinators for reproduction (Arroyo and Uslar 1993). The zygomorphic flowers are 4 to 6 cm long and arranged in umbels with one to four flowers each. The flowers consist of four red tepals, two distinctive yellow tepals streaked with brownish lines (Figure 1A). The flowering season extends from November to January, following by the fruiting season that ends in February (Arroyo and Uslar 1993; Botto-Mahan et al. 2011).

The study was carried out during two austral spring seasons (2011 and 2012), in six populations that comprise most of the distributional range of *A. ligtu simsii* from central Chile (Figure 1B). The region is characterized by a

Mediterranean-type climate (di Castri and Hajek 1976), where populations were exposed to similar variation of temperature and precipitation (considering maximum and minimum of both abiotic variables in the warmest, coldest, wettest, and driest months), which did not differ significantly among them (temperature: $F_{5,35} = 0.55$, $P = 0.73$; precipitation: $F_{5,35} = 0.30$, $P = 0.90$). In every year, 74 to 200 plants per population were tagged, and pollinator assemblages were characterized in terms of abundance and diversity. Due to floral phenology occurring at the same time in each location (November to December) for both years, each population was sampled in the same week, repeating this procedure for three consecutive weeks until covering the whole flowering period. Only floral visitors that contacted plant reproductive structures were considered as legitimate pollinators. We registered pollinator frequency in 15-min census between 1000 to 1700 hours in a total of 2,157 focal plants. The pollinators were identified at the highest resolution possible and classified at functional groups (Fenster et al. 2004). Then, visit rate (number of visits per plant per hour), species richness (S), and Shannon diversity index (H') were estimated for each population and year in the PAST software version 2.17 (Hammer et al. 2001). Additionally, we compared similarity in the pollinator assemblage composition, based on proportional visitation data, which takes into account both the identity of pollinators and their relative abundance. We used cluster analyses with Euclidean distance in the PAST software. Finally, we correlated pollinator composition matrix (PM) between the two studied seasons with the geographic distance matrix (GM), using Mantel test in the PAST software using 10,000 iterations.

Pollinator assemblages varied both temporally and spatially. First, during the 2011 season, we registered a total of 24 pollinator species and 2,137 visits. Considering all populations together, pollinator assemblages were

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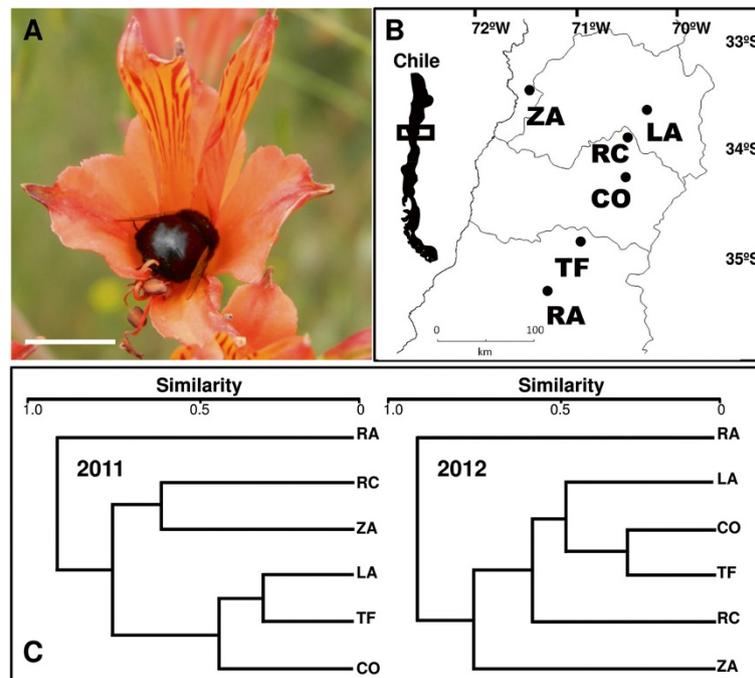


Figure 1 *A. ligtu simsii*, geographical distribution, and dendrogram. (A) *A. ligtu simsii* pollinated by *L. covina*, scale bar = 1.5 cm. (B) Geographical distribution of the studied populations. (C) Dendrogram showing similarity of pollinator assemblage between flowering seasons 2011 and 2012.

composed by three functional groups: Diptera (50.5% of visits), Hymenoptera (39.9% of visits), and Lepidoptera (9.4% of visits, Table 1). However, Hymenoptera was the functional group with the highest richness (Table 1). By contrast, during the 2012 season, 29 pollinator species were registered, but only 1,069 visits with different percentages of representation. Specifically, Hymenoptera increased its contribution (64.2% of visits), whereas Diptera and Lepidoptera decreased their relative importance in the total assemblage with respect to the previous year (33.8% and 2.1% of visits, respectively). Notwithstanding, Hymenoptera remained as the functional group with the highest richness, with *Centris nigerrima* being the only pollinator shared by all populations of *A. ligtu simsii* in both flowering seasons (Table 1). Second, in the 2011 season, the visit rate, species richness, and species diversity differed among populations (Table 1). For example, population TF (see table of population abbreviations) showed the highest visit rate, but ZA population showed the highest richness and LA the highest diversity (H') values. The similarity analyses (Figure 1C) showed that RA was the most dissimilar population. Otherwise, we observed two clusters of population: the first group was composed by LA, TF, and CO, with distance of similitude ranging from 0.20 to 0.44. Populations RC and LA formed the second group with 0.61 of distance of similitude. However, this

similarity did not show a latitudinal pattern (Mantel test: PM_{2011} vs. GM: $r_m = 0.02$, $P = 0.43$). In the same way, for the 2012 season, populations also differed in the pollinator assemblage composition. For example, TF reduced ten times its visitation rate with respect to 2011 (from 20.7 to 1.92, respectively), and the ZA population showed the highest richness, and CO the highest H' values. During 2012, RA remains as the most dissimilar population, even though the rest of the populations belong to one cluster only; the populations LA, TF, and CO maintained their range of similarity (0.27 to 0.50) compared to the other populations (Figure 1C). In this flowering season, no latitudinal pattern was observed in the similarity of pollinator composition (Mantel test: PM_{2012} vs. GM: $r_m = 0.35$, $P = 0.08$).

Overall, our results showed that *A. ligtu simsii* is a generalist plant with 4 to 16 different pollinator species. Consistently, we found that pollinator abundance, richness, and diversity were different among populations and years. This scenario is particularly important if we consider that plants of *A. ligtu simsii* necessarily require a pollinator agent to transport pollen from anthers to stigmas. In this context, temporal and spatial variations in the pollinator assemblages of *A. ligtu simsii* may determine the reproductive success of individuals, populations, and consequently the maintenance of this subspecies.

Table 1 Temporal and spatial variation of pollinator assemblages in *A. ligtu simsii*

Pollinators	Visitation rate (<i>Vr</i> , visits flower ⁻¹ h ⁻¹)											
	2011						2012					
	ZA N = 180	LA N = 180	RC N = 240	CO N = 125	TF N = 74	RT N = 178	ZA N = 200	LA N = 150	RC N = 200	CO N = 200	TF N = 200	RT N = 200
Diptera												
<i>Diptera sp.1</i>	0.09	0	0	0	0	0	0	0	0	0.02	0	0
<i>Diptera sp.2</i>	0	0.56	0	0	0	0	0	0	0	0	0	0
<i>Diptera sp.3</i>	0	0.07	0	0	0	0	0	0	0	0	0	0
<i>Diptera sp.4</i>	0	0.13	0	0	0	0	0	0	0	0	0	0
<i>Lasia aenea</i>	1.71	0.09	0.03	0	0	0	2.04	0	0.04	0	0	0
<i>Lasia corvina</i>	0.73	6.22	0	10.53	10.3	0	0.14	2.61	0	1.56	0.96	0
<i>Mycteromia sp.</i>	0	0.04	0.32	0.58	4.86	0	0	0.03	0	0.30	0	0.18
<i>Vr</i> (Diptera)	2.53	7.11	0.35	11.11	15.1	0	2.18	2.64	0.04	1.88	0.96	0.18
<i>S</i> (Diptera)	3	6	2	2	2	0	2	2	1	3	1	1
<i>H'</i> (Diptera)	0.74	0.52	0.31	0.20	0.63	0	0.24	0.06	0	0.49	0	0
Hymenoptera												
<i>Alloscirtetica gayi</i>	0.22	1.02	1.17	0	2.70	0	0.02	3.17	0.46	0.46	0.14	0.06
<i>Andrenido sp.1</i>	0	0	0	0	0	0	0.22	0	0	0	0.04	0
<i>Apis mellifera</i>	0.67	0.51	0.12	0.51	0	0	0	0	0	0	0	0
<i>Bombus ruderatus</i>	0	0	0	0	0	0	0	0	0	0	0	3.06
<i>Bombus terrestris</i>	0	0	0	0	0	0	0	0	0	0	0	0.06
<i>Caenohalictus sp.</i>	0	0	0	0	0.70	0	0	0	0	0	0	0
<i>Centris nigerrima</i>	1.09	0.60	0.20	0	0.32	1.57	0.46	0.61	0.38	0.32	0.32	0.08
<i>Cerceris gayi</i>	0	0	0	0	0	0	0.02	0	0	0	0	0
<i>Corynura sp.</i>	0	0	0	0.13	0	0	0	0	0	0	0	0
<i>Epiclopus sp.</i>	0	0.76	0	0	0	0	0	0	0	0	0	0
<i>Halictido sp.1</i>	0	0	0.08	0	0	0	0	0	0	0	0	0
<i>Lasioglossum sp.</i>	0	0	0	0	1.19	0.25	0	0	0	0.08	0	0
<i>Manuelia gayi</i>	0.96	0.24	2.37	0.22	0.32	0	0.14	0	0.08	0.18	0	0.18
<i>Megachile sp.</i>	0.11	0	0.22	0.10	0	0.20	0	0	0	0.08	0.02	0.02
<i>Mesonychium gayi</i>	0	0	0.20	0	0	0	0	0.05	0.04	0	0.36	0
<i>Ruizantheda mutabilis</i>	0.13	0.02	0.02	0	0	0	0	0.16	0	0.46	0	0
<i>Ruizantheda proxima</i>	0.22	1.02	1.17	0	2.70	0	0.02	3.17	0.46	0.46	0.14	0.06
<i>Svastrides melanura</i>	0	0	0	0	0	0	0.22	0	0	0	0.04	0
<i>Trichothurgus sp.</i>	0.67	0.51	0.12	0.51	0	0	0	0	0	0	0	0
<i>Vr</i> (Hymenoptera)	3.49	4.62	4.45	0.99	5.41	2.02	1.02	6.96	1.18	1.58	0.96	3.76
<i>S</i> (Hymenoptera)	7	7	9	5	6	3	6	5	6	6	7	7
<i>H'</i> (Hymenoptera)	1.66	1.68	1.38	1.28	1.39	0.68	1.41	1.06	1.47	1.59	1.48	0.76
Lepidoptera												
<i>Elina sp.</i>	0.09	0.69	0	0	0	0	0.02	0.11	0	0	0	0
<i>Nymphalido sp.1</i>	0	0.22	0	0	0	0	0.02	0	0	0	0	0
<i>Phoebis mercedis</i>	3.36	0.04	0	0	0.11	0.02	0.16	0.16	0	0.04	0	0
<i>Vr</i> (Lepidoptera)	3.45	0.96	0	0	0.11	0.02	0.20	0.27	0	0.04	0	0
<i>S</i> (Lepidoptera)	2	3	0	0	1	1	3	2	0	1	0	0
<i>H'</i> (Lepidoptera)	0.11	0.71	0	0	0	0	0.64	0.67	0	0	0	0

Table 1 Temporal and spatial variation of pollinator assemblages in *A. ligtu simsii* (Continued)

Total												
Vr	9.47	12.69	4.80	12.10	20.70	2.04	3.40	9.87	1.22	3.50	1.92	3.94
S	12	16	11	7	9	4	11	9	7	10	8	8
H'	1.94	1.85	1.56	0.57	1.43	0.73	1.43	1.48	1.57	1.73	1.43	0.91

ZA, Zapata; LA, Lagunillas; RC, Río Clarillo; CO, Coya; TF, Termas del Flaco; RT, Radal Siete Tazas; Vr, visitation rate; S, richness; H', Shannon diversity.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

AG conceived of the study, participated in its design, coordination and drafted the manuscript. MM and PR participated in the data analyses and drafted the manuscript. All authors read and approved the final manuscript.

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