

Is the same pollinator species equally effective in different populations of the generalist herb *Alstroemeria ligtu* var. *simsii*?

¿Es la misma especie de polinizador igualmente efectiva en diferentes poblaciones de la hierba generalista *Alstroemeria ligtu* var. *simsii*?

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RESUMEN

En esta investigación estimamos la efectividad de polinización en tres poblaciones de *Alstroemeria ligtu*. Los resultados muestran que *Lasia* es el género de polinizador más frecuente, cuya efectividad varía entre poblaciones. Proponemos que la efectividad de polinización puede responder a condiciones locales que varían en el rango de distribución de la planta y sus polinizadores.

In the last decades, many studies have tried to determine how different floral traits (*e.g.*, color, shape, odor) or pollinator syndromes reflect plant adaptations to particular pollinator species (review Rosas-Guerrero *et al.* 2014, Murúa & Espíndola 2015). Although pollination specialization exists, most of the flowering plant species are visited by a diverse number of pollinator species, which has shown that generalist pollination is a predominant plant-animal interaction in nature (Waser *et al.* 1996, Herrera 2005, Ollerton *et al.* 2006). In those cases, the relative importance of pollinators as selective agents is not necessarily obvious. Since, the action of selection can vary depending on the diversity (species number), abundance (visitation frequency), and effectiveness (pollen carry over by visit) of each pollinator (Aigner 2001, Ne'eman *et al.* 2010, Sahli & Conner 2011). In this respect, Stebbins (1970) proposed "The Most Effective Pollinator Principle", which raises that flower phenotype would be molded by the most frequent and effective pollinator species. So, even if a plant species presents a diverse pollinator assemblage, only some of them would have a greater impact on the reproductive success of the plant (Kay & Sargent 2009).

Alstroemeria ligtu L. var. *simsii* (Spreng.) Ehr. Bayer (Alstroemeriaceae) is a perennial and hermaphroditic self-incompatible herb, which is completely dependent on pollinators for reproduction (Arroyo & Uslar 1993). Along its range of distribution, their populations show a high spatial variation in their pollination assemblages, being visited by

approximately 24 different species of insects belonging to the Diptera, Hymenoptera and Lepidoptera orders (González *et al.* 2014). Despite this, recent investigations have shown that most of the *A. ligtu* populations are mainly visited by the same pollinator species (*e.g.*, *Lasia corvina* Erichson (1840) and *Centris nigerrima* Spinola (1851)), which are consistent among years (González *et al.* 2014, 2015), suggesting that they may engage in a more specialist, rather than generalist, plant-pollinator interaction. However, there is still unknown how effective are these species in transferring pollen to *A. ligtu*. According to this, it is possible to ask whether the same floral visitor could be equally effective in the pollination service provided to these populations. In order to answer this question, here we characterize the pollinator assemblages and determine the pollination effectiveness of the main pollinator species in three *A. ligtu* populations.

The study was conducted during the flowering season of 2014 (November - December) in three populations of central Chile Cuesta Zapata, Río Clarillo and Termas del Flaco, where *A. ligtu* flowers dominated the area (Fig. 1A-B). All populations are characterized by a Mediterranean-type climate with strong rains during wintertime (Di Castri & Hajek 1976). The population Cuesta Zapata (ZA; 33°39'19" S; 70°19'23" W) occurs in Coastal hills at 529 masl, where the site is dominated by *Quillaja saponaria* Molina and different herbs species such as *Alstroemeria pulchra* Sims, *A. angustifolia* Herb., *Carduus pycnocephalus* L., *Sisymbrium officinale* (L.) Scop., *Loasa tricolor* Ker Gawl.,

Clarkia tenella (Cav.) F.H. Lewis & M.E. Lewis, *Oxalis rosea* Jacq., *Eschscholzia californica* Cham., *Calceolaria* sp., *Schizanthus tricolor* Grau & Gronbach, and *Papaver* sp. (pers. obs.). Río Clarillo population (RC; 33°46'80" S; 71°49'72" W) is located in the pre-Andean mountains at 1153 masl, where individuals of *A. ligtu* are inhabiting with a diverse assemblages of trees, scrubs and herbs species like *Cryptocarya alba* (Molina) Looser, *Quillaja saponaria*, *Escallonia pulverulenta* (Ruiz & Pav.) Pers., *A. angustifolia*, *Carduus pycnocephalus*, *Conium maculatum* L., *Leucheria* sp., *Madia chilensis* (Nutt.) Reiche, *Stellaria chilensis* Pedersen, *Geranium bertereanum* Colla, *Sisyrinchium* sp., *Stachys grandidentata* Lindl., *Leucocoryne ixioides* (Hook.) Lindl., *Pasithea caerulea* (Ruiz & Pav.) D. Don, *Loasa tricolor*, *Clarkia tenella*, and *Schizanthus tricolor* (pers. obs.). Whereas the third population occurs on road to Termas del Flaco (TF; 34°60'87" S; 71°49'72" W) at 585 masl, where plants are mainly surrounding by herbs such as *Hypericum perforatum* L., *Sisyrinchium* sp., *Anagallis arvensis* L., *Rubus ulmifolius* Schott and *Calceolaria* sp. (pers. obs.).

In each population, we selected three random patches of plants separated by 3 meters. A total of 482 plants were studied (ZA=200, RC= 200, TF=82). All individuals were tagged and monitored during 2 to 4 days per months. In order to characterize flower size one flower per plant were cut and photographed from a frontal view. Corolla area (mm²) were measured from digitalized photos and analyzed using Image J Laucher program version 1.45 (available online: <https://imagej.nih.gov/ij/>). Pollinator visitation regimens were quantified through focal observations during 15 min per plant, in sunny days between 10:00 and 15:00 hours. Visitation rate was calculated as the number of visits per flower per hour (visits*flower⁻¹*hour⁻¹). In addition, the handling time (*i.e.*, the time speeded in a flower during a single visit) of each pollinator species was recorded. Only the most frequent pollinators were captured and stored in Eppendorf tubes with 1 ml of ethanol. The insects were moved to laboratory for pollen load counting. All captured pollinators were photographed, and their body lengths were measured in ImageJ Laucher program. Pollen was removed from pollinator's body by shaking tubes in a vortex for 1 minute. From each tube, we took one aliquot of 0.3 ml and we put in a Neubauer chamber for quantification. In this way, under microscope we identified and quantified the pollen grains of *A. ligtu* and the other plant species based on the description made by Arredondo-Núñez (2010). This procedure was carried out three times and pollinator pollen load (PL) was estimated as the average number of pollen grains transported. Since the number of pollen grains carried on the body has been related to the pollinator body length (Griffin *et al.* 2009) we standardized our data by dividing the pollen grains by pollinator's total body length (mm).

To identify the main pollinator species of each population

the five species with the highest visitation frequency were selected using the results of an ANOVA test. Once the main pollinator per population was identified, their pollinator effectiveness was estimated as VR*PL (Ne'eman *et al.* 2010). Finally, to determine statistical differences in visitation rate, pollinator effectiveness and handling time of main pollinator species a GLM with Gaussian distribution was performed. All variables were transformed to log (x+1) previously to the analysis in R package (Core Team 2018).

Corolla size measurements for all *A. ligtu* populations are presented in Table 1. The largest corolla areas were observed in plants inhabiting RC, followed by ZA, and the smallest ones were quantified in TF. Respecting to pollinator visitation regimens, a total of 798 visits by 22 pollinator species were registered in approximately 60 h of observation per population (RC: 63.5 h, TF: 69.5 h, ZA: 66.8 h; Appendix 1). Hymenoptera was the order with the highest number of species (12 species), followed by Diptera (8 species) and Lepidoptera (2 species). When only the most frequent pollinators were considered per population, the ANOVA test showed significant differences in the visitation rates of the five species with the highest visitation frequency in each *A. ligtu* populations (Table 2). The species of the dipteran genus *Lasia* were the most frequent pollinators in the three populations. *Lasia corvina* was the most frequent pollinator species in RC and TF, with the 62% and 85% of the total visits, respectively (Fig. 1C). While, *Lasia aenea* Philippi (1865) was the responsible of 50% of the visits in ZA population (Fig. 1D).

L. corvina showed a higher visiting rate in RC than in TF, and *L. aenea* in ZA (Fig. 1E). *L. corniva* showed thirteen times higher effectiveness in RC than in TF, while that *L. aenea* in ZA was also higher than *L. corvina* in TF (Fig. 1F). While, pollinator handling time species was mostly the same in each *A. ligtu* populations (Fig. 1G). Finally, GLM analysis showed significant differences in the visitation rate and pollinator effectiveness, but not in the handling time of main pollinator species among sites (Table 3).

Results of this study reveal that not only the visitation rate, but also the pollinator effectiveness can vary among *A. ligtu* populations, even if the same pollinator genus or species are the responsible of most of the visits in a population. Here, we found that *Lasia corvina* was the main pollinator in two of the three study populations (RC and TF) and *L. aenea* was in the third one (ZA). Where, they showed different visitation frequency and pollinator effectiveness, which seems not to be related to pollinator handling time. Pollinator choices are based on different floral cues which together favored their performance and gain in the foraging process (Waser 1983). In RC population, *L. corvina* visited more frequently and effectively the flowers of *A. ligtu* than those in TF and ZA, but in the later *L. aenea* showed higher pollination effectiveness than *L. corvina* in TF. Pollination foraging behavior and consequently the success of the

pollination process depend on several non-exclusive factors both at the individual and community scale. At the individual level, flower size is an important visual signal in pollinator attraction, where it is known that plants with larger corolla sizes could have a higher chance to be visited than smaller ones (Conner & Rush 1996). In RC, flowers have larger corolla areas than those in TF and ZA (Table 1), which might increase the probability of pollen recollection. In the same way, plants in ZA showed a higher corolla area than

plants in TF, which could explain the higher mean visitation rate of *L. aenea*. At the community scale, an important factor that can also compromise pollination effectiveness is the composition of co-flowering species within a plant community (Hegland & Boeke 2006). Pollination sharing can lead to pollen competition by visitation loss or interspecific pollen transfer, where plant species can steal pollinators reducing visitation frequency and/or they could perform mixed visits increasing pollen exchange between

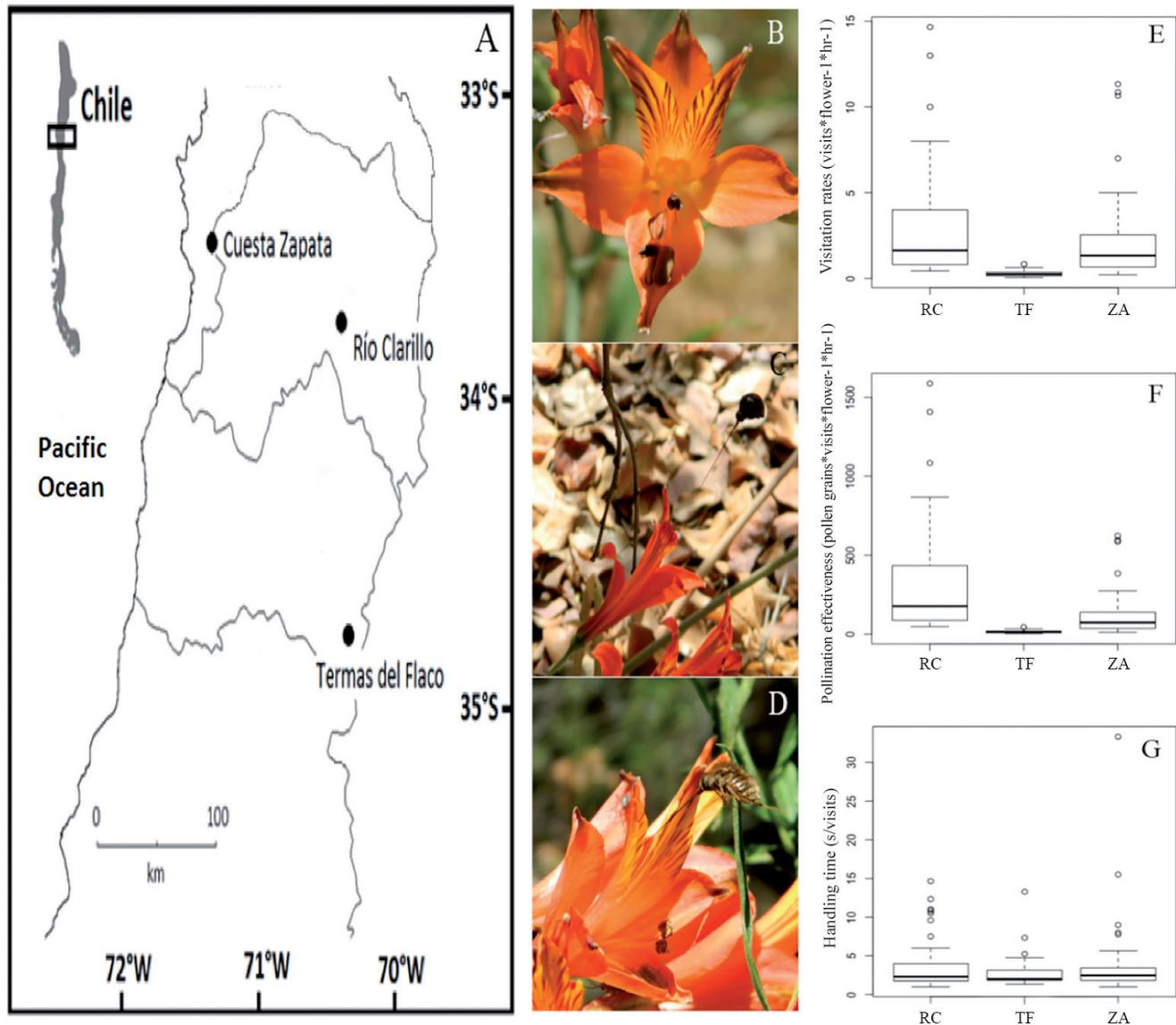


FIGURE 1. Geographical distribution of studied populations, *Alstroemeria ligtu* flower detail, pollinator species and differences in the visitation rate, pollination effectiveness and handling time of the main pollinator species of each *A. ligtu* study populations. A) Populations locations, B) *A. ligtu* flower, C) *Lasia corvina*, D) *L. aenea*, E) Visitation rate, F) Pollination effectiveness, and G) Handling time. / Distribución geográfica de las poblaciones estudiadas, detalle de la flor de *Alstroemeria ligtu*, especies de polinizadores y diferencias en las tasas de visita, efectividad de polinización y tiempo de manipulación del principal polinizador de cada población en estudio de *A. ligtu*. A) Ubicación de las poblaciones, B) Flor de *A. ligtu*, C) *Lasia corvina*, D) *L. aenea*, E) Tasa de visita, F) Efectividad de polinización, y G) Tiempo de manipulación.

plants in the community (Morales & Traveset 2008). Here, we observed that *L. corvina* carried on average a larger amount of *A. ligtu* pollen and less pollen grains of other plant species inhabiting in RC than in TF, and ZA (Table 1), which could explain in part the highest pollination effectiveness estimation. Contrary, *L. aenea* in ZA carried more pollen of others plant species than *L. corvina* in TF, but this pollinator still showed a higher effectiveness (Table 3). This difference could be explaining by individual preferences and the different modes that pollinator species have to interact with the flower. Different species could be explaining the differences in the pollinator effectiveness, however, there is another important factor, and that is how the pollinator interact with the flowers (*i.e.*, pollinator

behavior). *L. corvina* and *L. aenea* showed almost the same average handling time (RC= 3.4 s/visit, ZA=3.5 s/visit) and they have higher pollinator effectiveness respect to the main pollinator of TF, which also showed the lowest HT (TF=2.8 s/visit). The time that pollinators spend in a flower can be tightly related to the amount of pollen grains that they are able to extract from the flower (Ohashi 2002). Therefore, it is expected that the more time the insect spend on the flower; the more pollen it may extract. Nevertheless, this must be explored more carefully in order to determine if this effectively has the any impact on pollinator effectiveness.

In summary, this work has revealed that the same genus and/or pollinator species can have different effectiveness across *A. ligtu* populations. In the light of this evidence,

TABLE 1. Corolla size of *Alstroemeria ligtu*, Principal pollinator species, Pollinator’s proboscis length, Pollen grains of *A. ligtu* and from other plant species carried by the principal pollinator species in each study population. / Tamaño de la corolla de *Alstroemeria ligtu*, Polinizador principal, Largo de la proboscis del polinizador, Granos de polen de *A. ligtu* y de otras especies de plantas acarreados por el polinizador principal en cada población en estudio.

POPULATION	COROLLA AREA (mm ²)	PRINCIPAL POLLINATOR (N)	PROBOSCIDE LENGTH (mm)	POLLEN <i>A. LIGTU</i> (grains/ml)	POLLEN FROM OTHER SPECIES (grains/ml)
Rio Clarillo (RC)	9.1 ± 2.3	<i>Lasia corvina</i> (28)	1.6 ± 0.2	158 ± 139	20 ± 31
Termas del Flaco (TF)	5.8 ± 1.4	<i>Lasia corvina</i> (21)	1.7 ± 0.2	75 ± 111	21 ± 30
Zapata (ZA)	7.1 ± 2	<i>Lasia aenea</i> (12)	1.2 ± 0.06	55 ± 49	39 ± 63

TABLE 2. Visitation rate differences of the five most frequent pollinator species in each *Alstroemeria ligtu* populations after ANOVA analysis. Populations: Río Clarillo (RC), Termas del Flaco (TF) and Cuesta Zapata (ZA). / Diferencias en la tasa de visita de los cinco polinizadores más frecuentes de cada población de *Alstroemeria ligtu* después de un analisis ANDEVA. Poblaciones: Río Clarillo (RC), Termas del Flaco (TF) y Cuesta Zapata (ZA).

POPULATION	Df	SS	MS	F VALUE	P
Zapata (ZA)	1	0.13	0.13	8.45	0.0036
Rio Clarillo (RC)	1	3.05	3.05	115.81	2.2e-16
Termas del Flaco (TF)	1	0.21	0.21	133.88	2.2e-16

TABLE 3. Pollination effectiveness (PE), Visitation rate (VR), and Handling time (HT) difference of the most frequent pollinator species of each *Alstroemeria ligtu* populations after a GLM model with Gaussian distribution. Populations: RC= Río Clarillo, TF= Termas del Flaco and ZA= Cuesta Zapata. / Diferencias en efectividad de polinización (PE), Tasa de visita (VR), y Tiempo de manipulación (HT) de la especie de polinizador más frecuente de cada población de *Alstroemeria ligtu* después de un modelo GLM con distribución gaussiana. Poblaciones: RC= Río Clarillo, TF= Termas del Flaco y ZA= Cuesta Zapata.

	POPULATION	ESTIMATE	STD. ERROR	T VALUE	P
PE	Zapata (ZA)	- 0.32	0.076	- 4.25	2.31e-05
	Termas del Flaco (TF)	- 0.28	0.075	- 3.73	0.0002
VR	Zapata (ZA)	0.0017	0.033	0.052	0.95
	Termas del Flaco (TF)	- 0.031	0.041	- 0.768	0.44
HT	Zapata (ZA)	- 0.06	0.018	- 3.72	0.0002
	Termas del Flaco (TF)	- 0.11	0.017	- 6.39	2.81e-10

future investigations must focus in determining the pollinator efficiency (Schupp *et al.* 2017), that is to say, how the quality of pollination performance by a species (e.g., visitation and pollen extraction) could affect the quantity of pollination (*i.e.*, pollen deposition and seed production), and consequently plant population fitness. Under a scenario of spatial variation of pollinator assemblage and effectiveness in *A. ligtu*, it is possible that local conditions can drive local plant adaptation, which could stimulate the generation of a mosaic of phenotypic plant selection across their range of distribution.

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APPENDIX

APPENDIX 1. Visitation rates of pollination assemblages of each *Alstroemeria ligtu* var. *simsii* population. Populations: Río Clarillo (RC), Termas del Flaco (TF) and Cuesta Zapata (ZA). / Tasa de visita del ensamble de polinizadores en cada población de *Alstroemeria ligtu* var. *simsii*. Poblaciones: Río Clarillo (RC) , Termas del Flaco (TF) y Cuesta Zapata (ZA).

ORDEN	FAMILY	POLLINATOR SPECIES	VISITATION RATE (visits*flower ⁻¹ *h ⁻¹)		
			RÍO CLARILLO (RC)	TERMAS DEL FLACO (TF)	CUESTA ZAPATA (ZA)
Diptera	Bombyliidae	<i>Anthrax</i> sp.	0.024 ± 0.015	-	-
Diptera	Bombyliidae	<i>Bombyliidae</i>	-	0.002 ± 0.001	-
Diptera	Bombyliidae	<i>Bombyliidae</i>	0.032 ± 0.013	-	0.015 ± 0.008
Diptera	Acroceridae	<i>Lasia aenea</i>	-	-	0.496 ± 0.089
Diptera	Acroceridae	<i>Lasia corvina</i>	0.957 ± 0.136	0.145 ± 0.016	0.015 ± 0.008
Diptera	Tabanidae	<i>Tabanidae</i>	-	0.015 ± 0.003	-
Diptera	Tabanidae	<i>Tabanidae</i>	0.006 ± 0.004	-	-
Diptera	Tabanidae	<i>Dasybasis</i> sp.	-	-	0.029 ± 0.021
Hymenoptera	Apidae	<i>Alloscirtetica gayi</i>	0.035 ± 0.018	0.0001 ± 0.0001	0.005 ± 0.003
Hymenoptera	Halictidae	<i>Caenohalictus azarae</i>	0.017 ± 0.010	0.003 ± 0.001	0.039 ± 0.018
Hymenoptera	Apidae	<i>Centris nigerrima</i>	-	-	0.105 ± 0.031
Hymenoptera	Halictidae	<i>Halictidae</i>	0.015 ± 0.009	-	-
Hymenoptera	Halictidae	<i>Lasioglossum</i>	-	0.0001 ± 0.0001	-
Hymenoptera	Apidae	<i>Manuelia gayi</i>	0.262 ± 0.064	-	0.040 ± 0.017
Hymenoptera	Megachilidae	<i>Megachile cinerea</i>	-	0.0005 ± 0.0003	0.009 ± 0.005
Hymenoptera	Megachilidae	<i>Notanthidium steloides</i>	0.053 ± 0.019	-	0.022 ± 0.009
Hymenoptera	Pieridae	<i>Phoebis</i> sp.	0.003 ± 0.003	-	0.111 ± 0.028
Hymenoptera	Halictidae	<i>Ruizantheda mutabilis</i>	0.011 ± 0.007	-	-
Hymenoptera	Apidae	<i>Svastrides melanura</i>	0.120 ± 0.060	0.004 ± 0.001	0.012 ± 0.007
Hymenoptera	Vespidae	<i>Vespula germanica</i>	0.002 ± 0.002	0.0001 ± 0.0001	0.026 ± 0.008
Lepidoptera	Nymphalidae	<i>Nymphalidae</i> sp.	0.007 ± 0.004	-	0.052 ± 0.016
Lepidoptera	Pieridae	<i>Tatochila</i> sp.	-	-	0.013 ± 0.008

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