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# Towards an Integrative Taxonomy of the Genus *Alstroemeria* (Alstroemeriaceae) in Chile: A Comprehensive Review

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Additional information is available at the end of the chapter

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## Abstract

The genus *Alstroemeria* encompasses approximately 80 species endemic to South America, with 2 centers of diversity (Chile and Brazil). In Chile, *Alstroemeria* represents one of the most diverse genera of vascular monocotyledons, comprising more than 50 recognized or accepted taxa (36 species, 11 subspecies and 10 varieties) from which ca. 82% are endemic to the Mediterranean zone of central Chile, one of the world's diversity hotspots. The taxonomy of the genus is very difficult due to the great variability of the vegetative and floral traits. Moreover, a number of taxa have been recently described and several nomenclatural changes have been proposed. In order to elucidate the taxonomy of some Chilean complexes of *Alstroemeria*, an integrative approach including morphology, colorimetry, cytogenetic, multivariate statistical analyses of morphological variation and DNA-molecular studies have been conducted. In this chapter, we review the literature concerning these approaches; a checklist of the species growing in Chile is provided including all published names, references to the original protologues, accepted names, synonyms and the biogeographic status (endemic or native) of the accepted taxa; maps illustrating the diversity of the genus in South America and its distribution in Chile were constructed.

**Keywords:** checklist, Chilean hotspot, cytogenetic, endemism, geographical distribution, South America, taxonomy

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## 1. Introduction

The family Alstroemeriaceae Dumort. *nom. Cons.*, belongs to the monocotyledon angiosperm clade (Subclass: Liliopsida, Order: Liliales) [1, 2]. It is distributed in Central and South America [3],

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and comprises about 200 species distributed in the genera *Alstroemeria* L., *Bomarea* Mirb., *Leontochir* Phil. and *Schickendantzia* Pax [4]. Some authors recognized *Taltalia* Ehr. Bayer as an independent genus [5, 6] while others included *Taltalia* and *Schickendantzia* in *Alstroemeria* [7]. Genera have been classified in two subfamilies: (a) Subfamily: Luzuriagoideae with *Drymophila* R. Br. and *Luzuriaga* Ruiz & Pav. and (b) Subfamily: Alstroemerioideae with *Alstroemeria* and *Bomarea* (incl. *Leontochir*) [3, 8] or treated Luzuriagoideae as a separate family Luzuriagaceae [3]. *Alstroemeria* comprises about 80 species endemic to South America (southern South America and Eastern Brazil); *Bomarea* includes 120 species in Central and South America; *Luzuriaga* comprises 4 species (3 species in Chile, 1 in New Zealand) and *Drymophila* 1 species from Australia and Tasmania [8]. Phylogenetic studies using morphology and DNA sequences (*rps16*, *rbcL*) recognized *Alstroemeria* as monophyletic and certainly different from *Leontochir* and *Bomarea*; moreover, three subclades of *Alstroemeria* have been recognized that correspond to northern Chile, central Chile and Brazil [9]. *Alstroemeria* was established by Linnaeus in 1762 in honor to the Swedish botanist Claus von Alströmer [10]. It has its boreal distribution in Venezuela (3°N) and its austral limit in the Patagonia of Chile and Argentina, with two main distribution centers in the continent: Brazil (and adjacent areas of Paraguay and Argentina) and Chile (and the adjacent countries Peru, Bolivia and Argentina) [11–15]. In Chile, *Alstroemeria* represents 1 of the most diverse genera of vascular monocotyledons, comprising more than 50 recognized or accepted taxa (36 species, 11 subspecies and 10 varieties) from which about ca. 82% are endemic to the Mediterranean zone of central Chile [14]. Due to the beauty of their flowers, Chilean species of *Alstroemeria*, locally known as “astromelias or lirios del campo” are appreciated all over the world as ornamental plants [16–18]. Many hybrids and cultivars have been developed in several countries, such as, The Netherlands, England, United States and Japan [14]. The taxonomy of the genus is very complex due to the great variability both in vegetative and floral characters [19]. Moreover, several taxa have been recently described (e.g., *A. werdermannii* var. *flavicans* [20], *A. philippi* var. *albicans* [14], *A. philippi* subsp. *adrianae* [21], *A. hookeri* subsp. *sansebastiana* [22], *A. martcorenae* [19], *A. traudliae* [23]) or nomenclatural changes have been made, affecting the rank status of many taxa. Due to its geographical isolation, Chile contains a unique flora which includes an extraordinary number of endemic plants. Furthermore, the area between the Regions of Atacama and Biobío comprises about 60% of the vascular species of the Chilean flora, with nearly 50% endemic to Chile [24]. In this area, identified as a hotspot of biodiversity [25], lives most of the Chilean species of *Alstroemeria*. This area harbors most of the Chilean population, and is characterized by a strong disturbance triggered mainly by agriculture, industry and forestry. In this chapter, we reviewed the taxonomic literature to make an updated checklist of the species growing in Chile and their synonyms. In addition, we construct distribution maps based on the literature as well as on the database of the Herbarium of the University of Concepción (CONC). Recent studies integrating different source of evidence, such as morphometry, cytogenetic, colorimetry and molecular data for better taxonomic species delimitation are discussed.

## 2. Methods

The database of the Herbarium of the University of Concepción (CONC) was used to construct preliminary lists of species and the geographic distribution of each taxon. This database contains the following fields: (1) Taxon name; (2) Collector's name; (3) Collector's number; (4) Latitude; (5) Longitude; (6) Elevation; (7) Administrative region; (8) Locality; (9) Collection

date (month); (10) Collection date (Year); (11) Herbarium and (12) Herbarium number. A total of 714 specimens were included in the CONC-DB. In addition to historical specimens, plants were collected and photographed in the field and kept in CONC. A checklist is provided including all published combinations, references to original publication, accepted names and biogeographic status (endemic or native). Maps illustrating the diversity of the genus in South America and distribution in Chile were constructed based on data taken from the CONC-DB and literature [14, 15, 23], using the software DIVA-GIS 7.5.0.

### 3. Taxonomy and distribution of the genus *Alstroemeria* in Chile

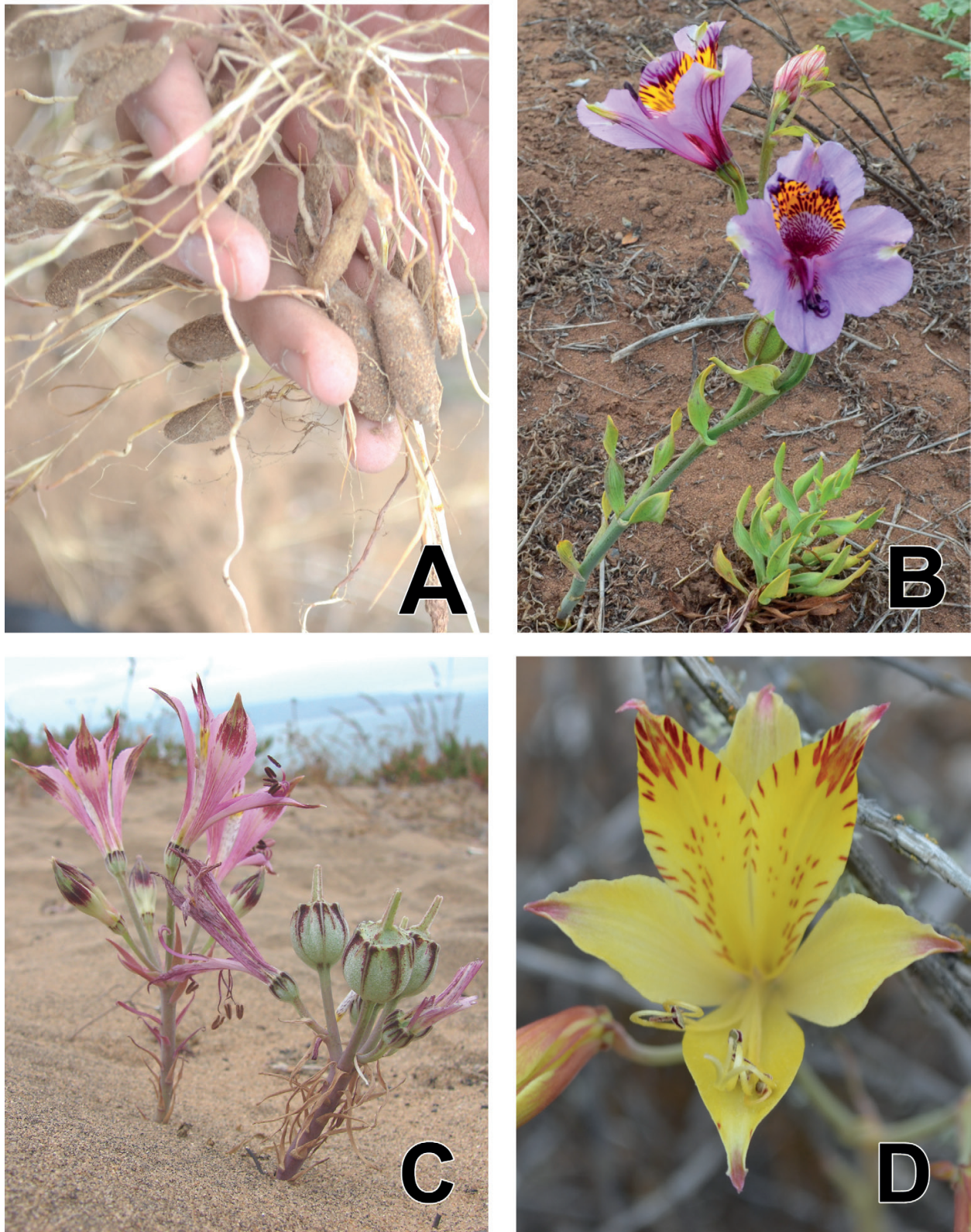
#### 3.1. General morphology

*Alstroemeria* comprises mostly perennial species. In 1998, Bayer [5] established the monotypic genus *Taltalia* to separate the annual *A. graminea* Phil., endemic to northern Chile, from *Alstroemeria*. Perennial species have cylindrical rhizomes, from which two kinds of roots born: thin roots and thick roots which contain starch (**Figure 1A**); *A. ligtu* (locally known as “liuto”) was used by indigenous people (Mapuches or Araucanos) to produce starch from the thick roots. According to Molina [26], the farmers made from the roots of this plant “a white, light, nutritious and so healthy flour that they usually gave it to the sick persons...” [26]. Aerial stems are erect or decumbent. The leaves are often resupinated, that is, twisted from the petiole or the leaf blade so the lower surface becomes functionally the upper surface; sometimes the leaves form basal rosettes; leaf blades thin or thick, sometimes with papillae; the blade varies in shape from linear to elliptic or ovate; fertile stems usually have reduced leaves but sterile stems have well developed leaves (**Figure 1B**). The flowers are slightly zygomorphic (**Figure 1C-D**), with six free tepals in two verticils; the three outer tepals are similar in shape and color; the inner three tepals are differentiated in two upper inner tepals and one lower inner tepal. Upper inner tepals with colored lines (nectar guides) on a lighter background (**Figure 1D**). Stamens 3: the ovary is inferior, 3-carpellate, 3-loculate. The fruit is a six-ribbed loculicidal capsule (**Figure 1C**) with explosive dehiscence, with numerous globose seeds (**Figure 2**).

#### 3.2. Colorimetric studies in Chilean *Alstroemeria*

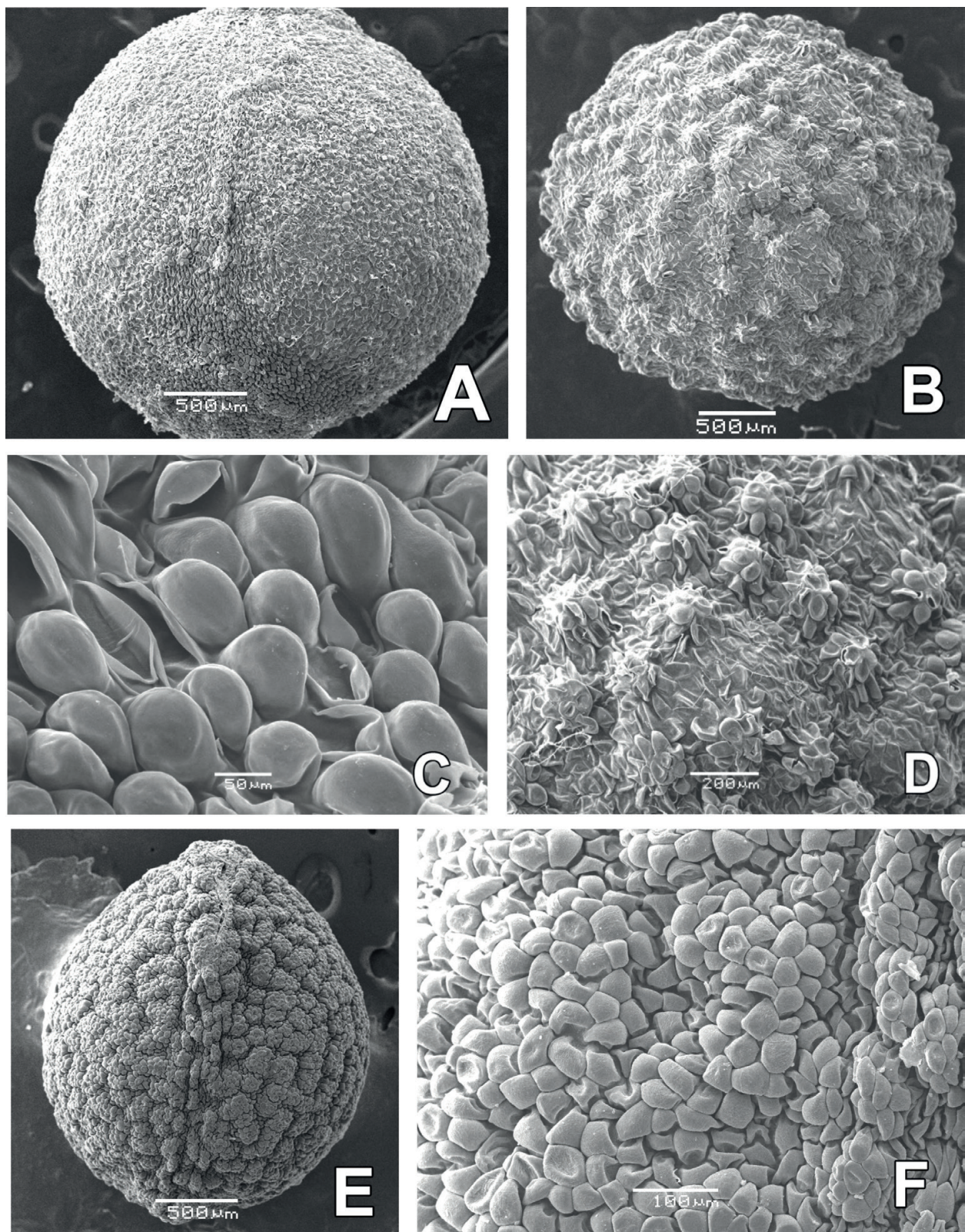
In *Alstroemeria*, the flowers varies in color from white to yellow, pink, red, purple and violet according to the species [11, 14]; color is regulated by several pigments including anthocyanin-like 6-hydroxydelphinidine 3-rutinoside, 6-hydroxycyanidin 3-rutinoside, delphinidin 3-malonylglucoside among others, carotenoids and flavonoids [27]. In some groups of plants, as occurs in *Alstroemeria*, it is possible that the taxonomic characters traditionally used do not have sufficient discriminant power to differentiate very close species or varieties within a species complex. In such cases, it may be useful to have characteristics that pose a new perspective on the problem. It has been shown that the color of the corolla, objectively measured, had high taxonomic value when the traditional characters were less informative to distinguish cryptic taxa [28]. In *Alstroemeria*, the color of the flower has often been used in keys and descriptions [11, 14, 15, 22, 23], however, most of the time, the described color corresponds to a subjective perception of the same by the human eye. The color of the flowers is taxonomically significant in *Alstroemeria* [14, 29, 30]; the





**Figure 1.** Morphology of the roots, rhizomes, leaves, flowers and fruits of *Alstroemeria*. (A) Roots and rhizomes of *A. x chrysantha*; (B) sterile leaves in fertile stems and basal rosettes of *A. magenta*; (C) fruits (capsules) of *A. hookeri* subsp. *recumbens*; (D) flower of *A. x chrysantha*. Photos A and D by V.L. Finot; photos B and C by C.M. Baeza.





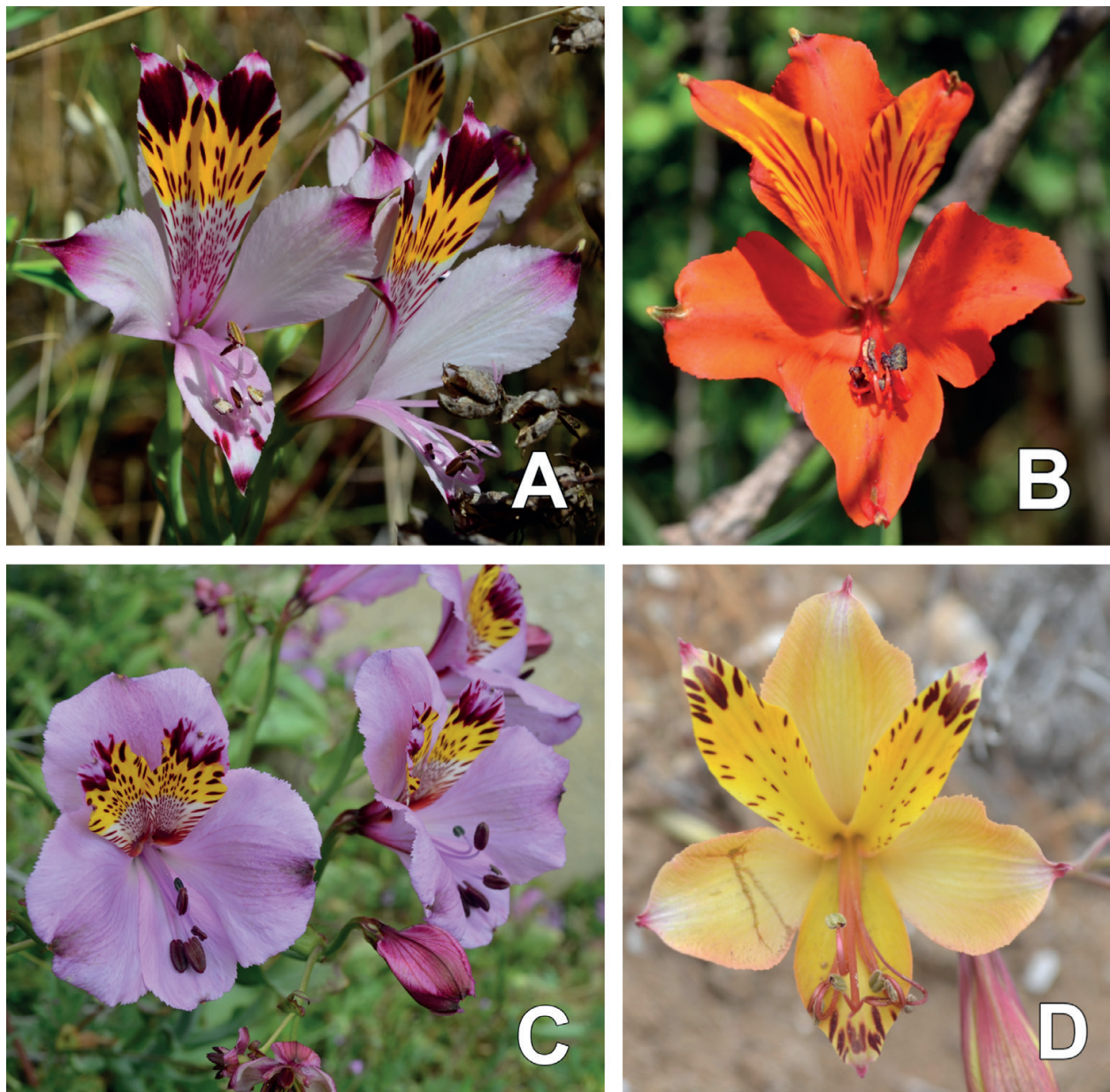
**Figure 2.** Seeds of *Alstroemeria* as seen with scanning electron microscope (SEM). (A) *Alstroemeria presliana* subsp. *australis*. (B) *Alstroemeria magenta*. (C) *Alstroemeria ligtu* subsp. *simsii*. (D). *Alstroemeria magenta*, surface details. (E) and (F) *Alstroemeria x chrysantha*.



outer tepals and the lower inner tepals are similar in shape and color but the upper internal tepals are different, showing unique patterns of maculae (actually nectar guides) that are species specific; however, some species showed variability in the background color [30], because it depends on several ecological factors such as temperature and pH [31]. In order to describe objectively the color (mainly the background color) of the different tepals (external, upper internal and lower internal), the CIElab system [32] has been used in some species complexes of Chilean *Alstroemeria* [29, 30] (**Figure 3**). The CIE (Commission Internationale de l'Eclairage) color system uses three coordinates to locate a given color in the color space. The spectrophotometer registers the reflected wavelengths as numerical values (spectral curve) from which the coordinates that place a given color in the color space are calculated. The color expressed in the CIElab scale uses the Cartesian coordinates  $L^*$ ,  $a^*$  and  $b^*$ .  $L^*$  expresses the luminosity,  $a^*$  denotes the green/red value and  $b^*$  the blue/yellow value. The degree of luminosity of  $L^*$  determines that a color appears lighter or darker and is expressed in a scale from 0 (black or total absorption) to 100 (white). The axis  $a^*$  moves from negative values (green) to positive values (red) while axis  $b^*$  moves from blue (negative values) to yellow (positive values). The color expressed in the CIELCh scale uses polar coordinates ( $L^*$ ,  $C^*$ ,  $h^\circ$ ), derived from the CIElab scale.  $C^*$  denotes chroma (saturation, intensity) and  $h^\circ$  denotes hue, expressed as angular measures. Chroma is the distance of the color from the axes  $a^*$  and  $b^*$  of  $L^*$ , calculated as  $(a^{*2} + b^{*2})^{1/2}$  and represents the color saturation; the hue,  $h^\circ$  is calculated as  $\arctg(b^*/a^*)$ . In *A. magnifica* complex, the colorimetric study of the flower helped to elucidate the taxonomic position of *A. pulchra* var. *maxima*. This taxon, originally described by Philippi in 1864 [33], was transferred by Bayer in 1987 to *A. magnifica* with the subspecific rank (*A. magnifica* subsp. *maxima*) [11].

The colorimetric differences between *A. magnifica* and *A. pulchra* as shown in the reflectance spectra were due mainly to the parameters  $a^*$  and  $b^*$  indicating that *A. magnifica* have tepals comparatively more intense violet than those of *A. pulchra* var. *maxima*. Our results suggest that the color of the flowers can be used as a new taxonomic character in *Alstroemeria* and that var. *maxima* probably belongs to *A. pulchra* as originally proposed and not to *A. magnifica* [29]. Colorimetric studies were carried out also in *A. presliana* [30]. This species comprises two subspecies: subsp. *presliana* and subsp. *australis*. *Alstroemeria presliana* subsp. *presliana* grows in Chile (Regions of Maule and Biobío) and Argentina (Neuquén) [34]; subsp. *australis* is endemic to Chile (Regions of Biobío and Araucanía) [11, 14].

Although the color of the flowers is one of the most important characters to distinguish the subspecies [11], there is a huge variability in color in the flowers of both subspecies. Differences in the spectral reflectance curves were detected between 440 and 540 nm and between 660 and 700 nm in the outer and lower inner tepals. Upper internal tepals differ mainly between 640 and 700 nm. The color measured in the CIElab space is related to the content of anthocyanins so that the flowers containing delphinidin-3-glucosides take on a more blue hue than those containing exclusively cyanidin-3-glucosides [35]. The presence of delphinidin-3-glucosides detected in subsp. *presliana* but not in subsp. *australis* [27] could explain the bluer hue observed in subsp. *presliana* in comparison with subsp. *australis* and the difference observed in the parameter  $b^*$ , which takes negative values in subsp. *presliana* and positive values in subsp. *australis* both in outer and lower inner tepals. On the other hand, in the upper inner tepals,  $b^*$  was positive (yellow), reaching higher values in subsp. *australis* and therefore denoting a more intense yellow color in subsp. *australis* than in subsp. *presliana* [30].

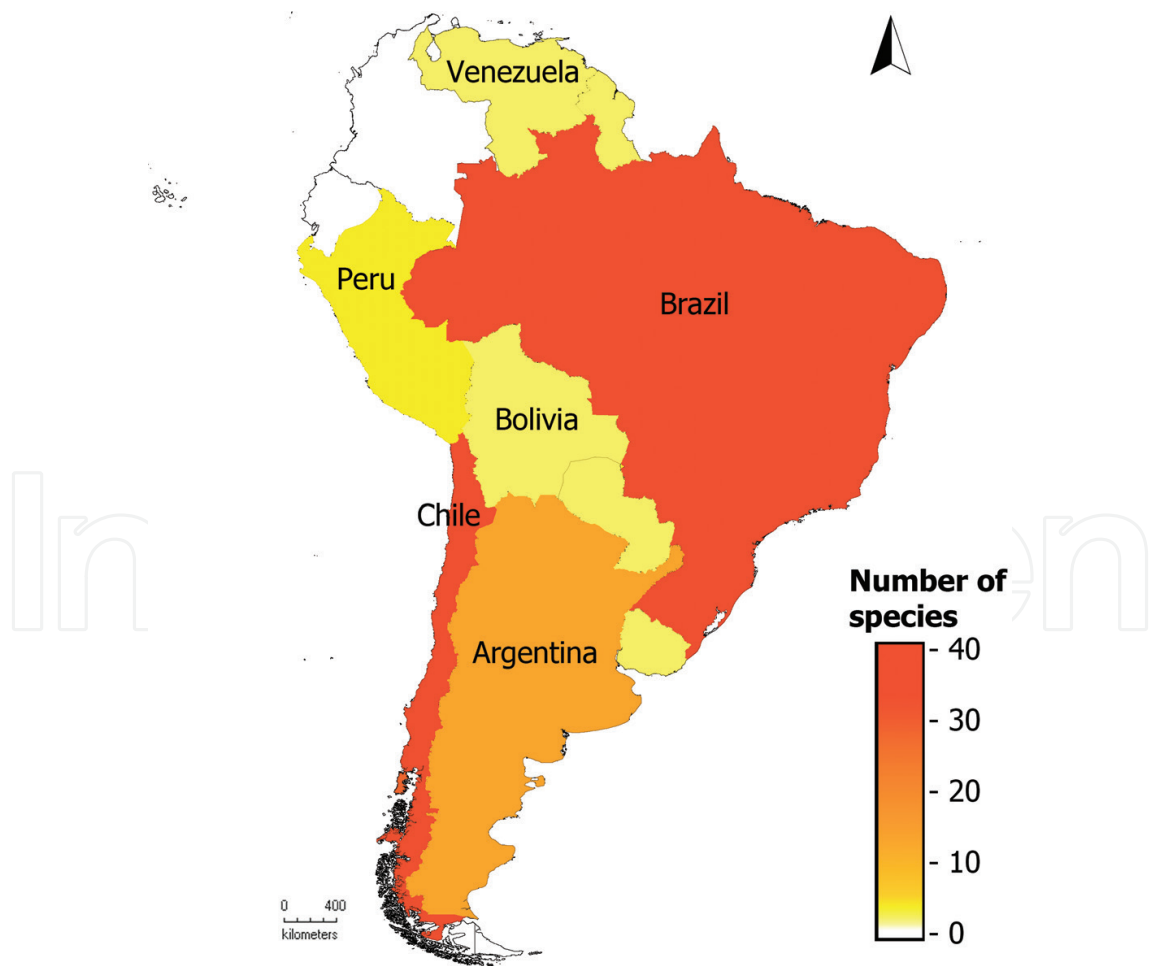


**Figure 3.** Flowers of some species of Chilean *Alstroemeria*. (A) *Alstroemeria pulchra*, Maule region, Talca, Río Claro (Baeza 4393). (B) *Alstroemeria ligtu* subsp. *simsii*, Maule region, Talca, Río Claro (Baeza 4395). (C) *Alstroemeria magnifica* var. *sierrae*, Coquimbo region, Caleta Hornos (Baeza 4375). (D) *Alstroemeria x chrysantha*, Coquimbo region, Huanaqueros (Baeza 4376). Photos A and B by C. Baeza; C and D by V. Finot.

### 3.3. Geographical distribution

In Chile, there are 38 species of *Alstroemeria* and 16 infraspecific taxa (8 subspecies and 8 varieties) and 1 nothospecies (*A. x chrysantha*) [23]. Nevertheless, more than 116 species have been described, most of which are considered synonyms or are names of uncertain application because there is no original material (types) in herbaria (see Checklist below). The description of such high number of taxa can be explained by the extent of morphological variation, especially of the flowers, which harbors most of the characters useful to taxonomy,

and because microevolutionary processes are still active so that species are not yet completely separated. Chile shares only few taxa with its neighboring countries (Argentina, Bolivia and Peru). In Peru, five species have been mentioned [14, 36, 37], one of which is also present in Chile: *A. violacea*. In Bolivia, three species are found, one of which growth in Chile: *A. aurea* ([38], under *A. aurantiaca*). In Argentina, there are 10 species [34], 5 shared with Chile: *A. andina* var. *venustula*, *A. aurea*, *A. patagonica*, *A. presliana* subsp. *presliana*, *A. pseudospathulata*. Thus, more than 88% of the genus is represented by taxa endemic to Chile (**Figure 4**). In Chile, *Alstroemeria* spreads from 20°S (Tarapacá Region) to 53°S (Magallanes Region) [14, 23]. Most taxa have a very restricted distribution in Chile (**Table 1**). The vast majority of the species are distributed in north (Tarapacá-Coquimbo) and central (Valparaíso-Biobío) Chile (**Figure 5**); only six species growth in southern Chile (Araucanía-Magallanes). The most boreal taxa are *A. lutea* and *A. violacea* that reach the Region of Tarapacá (20°S) in northern Chile. *Alstroemeria lutea* is restricted to the coast of the Tarapacá Region (Iquique) whereas *A. violacea* extends southern to 28°S in the Atacama Region; this species if known also from Peru (Arequipa) [14, 23, 37]. The regions with the largest number of taxa are Atacama (14 taxa), Coquimbo (26), Valparaíso (19) and Metropolitan (14) (**Figure 6**). The number of taxa decreases abruptly southern the Maule Region where 12 taxa are found; in Los Ríos and Los Lagos, only one



**Figure 4.** Species diversity of *Alstroemeria* in South America.



| No. | Taxa                                            | AYP | TAR | ANT | ATA | COQ | VAL | RME | LBO | MAU | NUB | BIO | ARA | LRI | LLA | AYS | MAG |
|-----|-------------------------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1   | <i>A. achirae</i>                               |     |     |     |     |     |     |     |     | x   |     |     |     |     |     |     |     |
| 2a  | <i>A. andina</i> var. <i>andina</i>             |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |     |     |
| 2b  | <i>A. andina</i> var. <i>venustula</i>          |     |     |     |     | x   |     |     |     |     |     |     |     |     |     |     |     |
| 3a  | <i>A. angustifolia</i> var. <i>angustifolia</i> |     |     |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |
| 3b  | <i>A. angustifolia</i> var. <i>velutina</i>     |     |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |     |
| 4   | <i>A. aurea</i>                                 |     |     |     |     |     |     |     | x   | x   | x   | x   | x   | x   | x   | x   | x   |
| 5   | <i>A. citrina</i>                               |     |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |     |
| 6   | <i>A. crispata</i>                              |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |     |     |
| 7   | <i>A. cummingiana</i>                           |     |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |     |
| 8   | <i>A. diluta</i>                                |     |     |     |     |     | x   | x   | x   | x   |     |     |     |     |     |     |     |
| 9   | <i>A. exerens</i>                               |     |     |     |     |     |     | x   | x   | x   |     |     |     |     |     |     |     |
| 10  | <i>A. garaventa</i>                             |     |     |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |
| 11  | <i>A. graminea</i>                              |     |     | x   | x   |     |     |     |     |     |     |     |     |     |     |     |     |
| 12a | <i>A. hookeri</i> subsp. <i>hookeri</i>         |     |     |     |     |     |     |     |     | x   | x   | x   |     |     |     |     |     |
| 12b | <i>A. hookeri</i> subsp. <i>maculata</i>        |     |     |     |     | x   |     |     |     |     |     |     |     |     |     |     |     |
| 12c | <i>A. hookeri</i> subsp. <i>recumbens</i>       |     |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |     |
| 12d | <i>A. hookeri</i> subsp. <i>sansebastianae</i>  |     |     |     |     |     |     |     |     |     |     | x   |     |     |     |     |     |
| 13  | <i>A. kingii</i>                                |     |     |     | x   |     |     |     |     |     |     |     |     |     |     |     |     |
| 14  | <i>A. leporina</i>                              |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |     |     |
| 15a | <i>A. ligtu</i> subsp. <i>ligtu</i>             |     |     |     |     |     |     |     |     | x   | x   | x   |     |     |     |     |     |
| 15b | <i>A. ligtu</i> subsp. <i>simsii</i>            |     |     |     |     |     | x   | x   | x   | x   |     |     |     |     |     |     |     |
| 15c | <i>A. ligtu</i> subsp. <i>splendens</i>         |     |     |     |     |     |     |     | x   | x   |     |     |     |     |     |     |     |
| 16  | <i>A. lutea</i>                                 |     | x   |     |     |     |     |     |     |     |     |     |     |     |     |     |     |



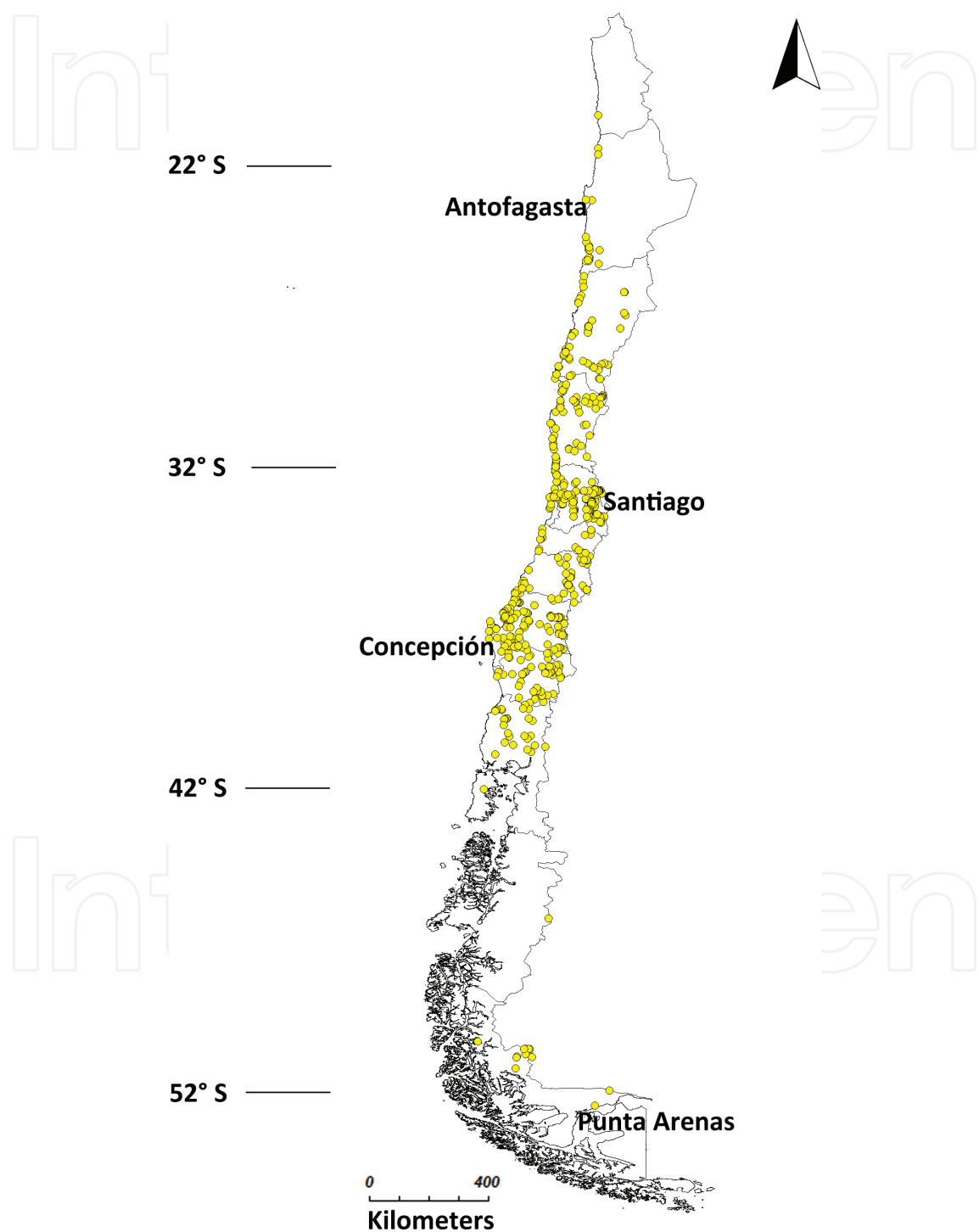


| No. | Taxa                                              | AYP | TAR | ANT | ATA | COQ | VAL | RME | LBO | MAU | NUB | BIO | ARA | LRI | LLA | AYS | MAG |
|-----|---------------------------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 32  | <i>A. spathulata</i>                              |     |     |     |     | x   | x   | x   |     |     |     |     |     |     |     |     |     |
| 33  | <i>A. traudliae</i>                               |     |     |     |     | x   |     |     |     |     |     |     |     |     |     |     |     |
| 34  | <i>A. umbellata</i>                               |     |     |     |     |     |     | x   | x   |     |     |     |     |     |     |     |     |
| 35  | <i>A. versicolor</i>                              |     |     |     |     |     |     | x   | x   | x   | x   | x   | x   |     |     |     |     |
| 36  | <i>A. violacea</i>                                |     | x   | x   | x   |     |     |     |     |     |     |     |     |     |     |     |     |
| 37a | <i>A. werdermannii</i> subsp. <i>flavicans</i>    |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |     |     |
| 37b | <i>A. werdermannii</i> subsp. <i>werdermannii</i> |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |     |     |
| 38  | <i>A. x chrysantha</i>                            |     |     |     | x   | x   | x   |     |     |     |     |     |     |     |     |     |     |
| 39  | <i>A. zoellneri</i>                               |     |     |     |     |     | x   | x   |     |     |     |     |     |     |     |     |     |

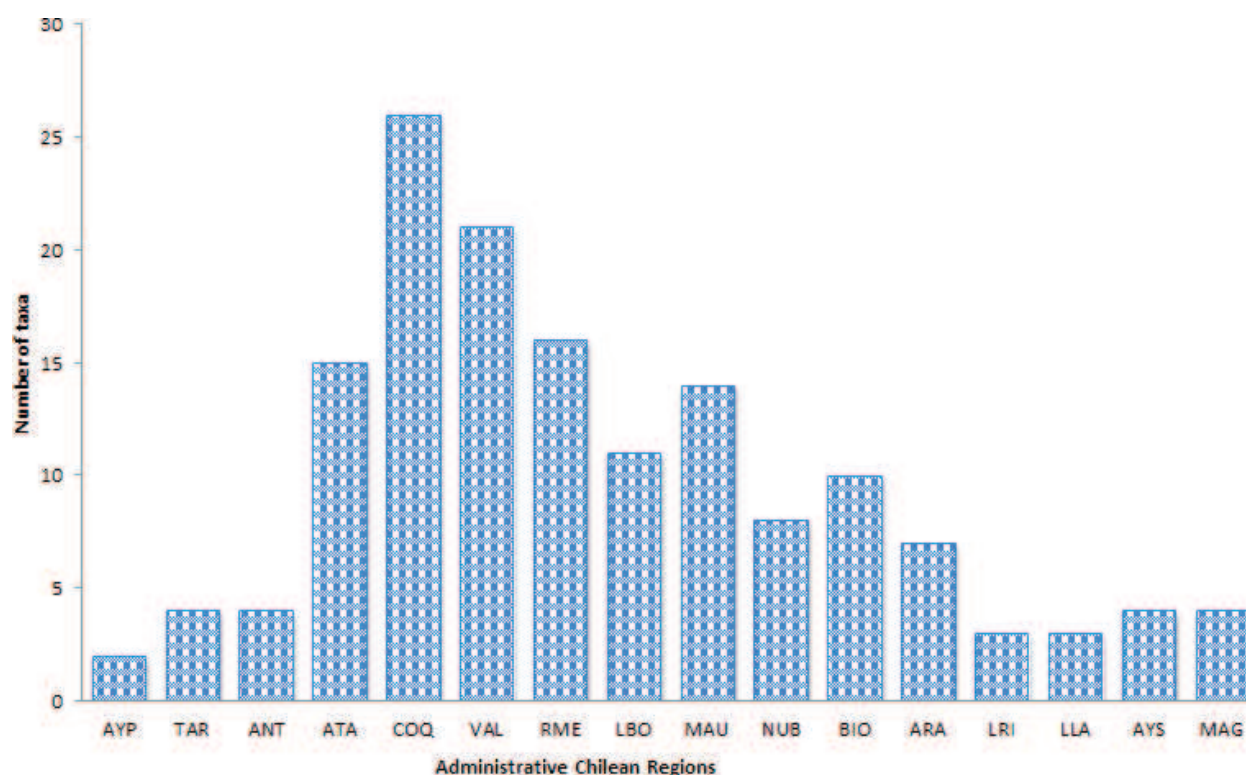
AYP = Arica-Parinacota Region; TAR = Tarapacá Region; ANT = Antofagasta Region; ATA = Atacama Region; COQ = Coquimbo Region; VAL = Valparaíso Region; RME = Metropolitan Region; LBO = O'Higgins Region; MAU = Maule Region; NUB = Ñuble Region; BIO = Biobío Region; ARA = Araucanía Region; LRI = Los Ríos Region; LLA = Los Lagos Region; AYS = Aysén Region; MAG = Magallanes and Antártica Chilena Region.

**Table 1.** Presence (x) of the accepted species of *Alstroemeria* in the administrative political regions of Chile.

species has been collected (*A. aurea*) and *A. patagonica* is found in Aysén and Magallanes being the most austral species of the genus *Alstroemeria* in the world. The latter species grow from 46°30'S to 52°45'S [14] and also in Argentina (Neuquén to Tierra del Fuego) [14, 34]. *Alstroemeria aurea* is the species with the widest distribution in Chile (this species spreads over



**Figure 5.** Distribution of the genus *Alstroemeria* in Chile. Each point represents at least one collection housed in the herbarium of the University of Concepción, Chile (CONC).



**Figure 6.** Number of taxa in the 16 administrative regions of Chile. For regions names see **Table 1**.

10 regions, from the O'Higgins Region, 34°12'S to Torres del Paine National Park, Magallanes Region, 51°21'S). *Alstroemeria revoluta*, the second widely distributed species, spreads from Valparaíso (La Campana National Park, 32°57'S) to Araucanía Region (Traiguén-Galvarino, 38°16'S) and *A. versicolor* ranges from the Metropolitan Region (Rio Clarillo National Reserve, 33°40'S) to Araucanía (Malleco, Renaico, 37°48'S). With these exceptions, most species show very narrow distribution, some of them being confined to a single region, such as *A. lutea* (Tarapacá Region), *A. kingii*, *A. philippi* var. *albicans* and *A. polyphylla* (Atacama Region), *A. andina* var. *venustula*, *A. hookeri* subsp. *maculata*, *A. magnifica*, *A. schizanthoides* var. *alba* and *A. mollensis*, *A. traudliae* (Coquimbo Region), *A. martcorenae* (Valparaíso Region), *A. achirae* (Maule Region), *A. hookeri* subsp. *sansebastiana* (Biobío Region), *A. presliana* subsp. *australis* (Araucanía Region, Nahuelbuta National Park). For the latitudinal distribution of each species, see reference ([14], **Figure 5**). Altitudinally, the genus *Alstroemeria* spreads from the sea level to nearly 4000 m.a.s.l. although most species are found below 2000 m.a.s.l. *Alstroemeria andina*, *A. crispata*, *A. exerens*, *A. pallida*, *A. parvula*, *A. spathulata* and *A. umbellata* can be found above 3000 m of elevation.

#### 4. Cytogenetic studies in Chilean *Alstroemeria*

Cytogenetic studies in *Alstroemeria* have proved to be useful in delimiting species, since each studied taxon has a unique karyotype. These studies have contributed to the delimitation of



the different taxa, as well as to the understanding of the chromosomal processes that determine the divergence among them [39]. Recent studies at the infraspecific level, in taxonomic complexes of the genus, have also been shown to be useful in the recognition of these taxa, either due to differences in the chromosomal architecture or in the asymmetry indexes of the chromosomes [40, 41]. Strasburger [42] was the first researcher to perform chromosome studies in *Alstroemeria* and until 1989 the number of cytological published papers involved no more than 10 different species [43]. In the last 25 years, a wide variety of cytogenetic studies have been carried out in the genus, including physical location of repetitive DNA sequences in *A. aurea* [16, 44, 45], meiosis and mitosis [46], karyology [47–49], variation and size of the genome [50], fluorescent *in situ* hybridization [39, 51, 52] and cytotaxonomy [40, 41, 52–58]. In 15 geographically isolated populations of five species of *Alstroemeria* (*A. aurea*, *A. hookeri*, *A. ligtu*, *A. pelegrina* and *A. presliana*) collected in Chile, karyotypes and variation of RAPD markers have been investigated. Tandemly repeated DNA sequences—5S and 18/25S rDNA genes and the sequence A001-1 were used to characterize karyotypes by fluorescence *in situ* hybridization (FISH). Ten somatic metaphases per population were used for measurement of chromosome length. Differences in RAPD marker bands were used for characterization of populations, creating a similarity index. FISH with all three DNA probes shows a high degree of polymorphism among and sometimes also within accessions of *A. aurea*, *A. hookeri* and *A. ligtu*. The number of chromosome pairs showing 5S rDNA signals is more different for the investigated species *A. aurea*, *A. hookeri*, *A. ligtu*, *A. pelegrina* and *A. presliana* with 5, 7, 5, 3 and 7, respectively, than the number of 18/25S rDNA signals in this succession with 7, 7, 6, 5 and 7 chromosome pairs, showing a high evolutionary dynamics within the genus. Furthermore, among the four populations of *A. hookeri*, accession 4181 was different in arm length of chromosome 3. RAPD markers (index of similarity) also showed a greater genetic distance of accession 4181 from the other three accessions of *A. hookeri* [39].

The study of the chromosomes in *Alstroemeria* has already helped to clarify a number of taxonomic issues within the genus. For example, study of karyotypes in the *A. hookeri* complex permitted change a subspecies to the species rank (*A. cummingiana*), the recognition of a new subspecies (*A. hookeri* subsp. *sansebastiana*) and description of a new species (*A. marticorenae*) [19, 22, 40, 41]. Similar situation occurred in the *A. presliana* complex, where after completing a comparative karyotypic study in 11 populations, it was suggested that *A. presliana* subsp. *australis*, endemic to the cordillera of Nahuelbuta, should be raised to species rank [18].

A number of cytological studies have been completed in the *Alstroemeria ligtu* complex. Buitendijk and Ramanna [16] and Buitendijk et al. [50] found variation in the DNA content and polymorphism of C bands in the chromosomes of subsp. *ligtu*, subsp. *simsii* and subsp. *splendens*. Zhou et al. [51], utilizing FISH, completed the characterization of the genomic DNA of eight highly repetitive sequences in subsp. *ligtu* and *simsii*, showing detailed karyotypes with localization of specific DNA sequences. DAPI staining and acetic orcein, completed a comparative karyotype study of five populations of subsp. *ligtu* from the Region of Biobío and one population of subsp. *simsii* from the Region of Valparaíso [39]. The six populations studied revealed an asymmetric karyotype with  $2n = 2x = 16$  chromosomes. The populations of subsp. *ligtu* have a haploid formula of four metacentric chromosomes (chromosomes 1 and 2 with microsatellites), one submetacentric with a microsatellite and three telocentric

with microsatellites. The population of subsp. *simsii* is characterized by having five metacentric chromosomes (chromosome 2 with a microsatellite and 6 with a secondary constriction) and three telocentric chromosomes with satellites. Baeza et al. [39] analyzed four populations of subsp. *ligtu*, defining localization on the chromosomes of the ribosomal genes 5S and 18-45S. Low polymorphic hybridization sites were detected in the populations, and only chromosome 1 presented a polymorphic site of 5S and 18/25S rDNA in the proximal and distal positions, respectively. Three subspecies are recognized within *A. ligtu* complex: subsp. *ligtu*, subsp. *splendens* and subsp. *simsii*. Fourteen populations were collected throughout its distributional range. Chromosome number, karyotype formulae, karyotypes, ideograms, intrachromosomal asymmetry index  $M_{CA}$ , and interchromosomal asymmetry index  $CV_{CL}$  were calculated [57, 58]. All studied populations showed  $2n = 2x = 16$  chromosomes. Subspecies *ligtu* and *simsii* are clearly differentiated from each other in  $M_{CA}$  and together from subsp. *splendens* with  $CV_{CL}$ . Intrachromosomal asymmetry index revealed two population groups within subsp. *splendens*. These populations also differ in karyotype formulae, habitat, soil type and distribution. We concluded that a fourth subspecies should be described from populations located in the lower part of the cordillera de los Andes in the Region of Maule. Populations of higher elevations correspond to those already described as subsp. *splendens* [57]. A comparative karyotype study was carried out among four populations of *A. diluta* subsp. *diluta* and three populations of *A. diluta* subsp. *chrysantha*. The seven populations presented an asymmetric karyotype, with  $2n = 2x = 16$  chromosomes, and with same karyotype formulae:  $3m + 1sm + 1st + 3t$ . The architecture of the karyotype between the subspecies is the same. The scatter plot among  $M_{CA}$  versus  $CV_{CL}$  shows different groupings between populations of the two subspecies, and the total chromosomes length (TCL) is highest in the populations of subsp. *chrysantha*. According to the results obtained, the populations growing in Valparaíso Region should be considered belong to subsp. *diluta* [58]. We analyzed the karyotypes of 10 populations of *A. magnifica* complex along its natural distribution. All the populations showed an asymmetric karyotype, with  $2n = 16$  chromosomes but with 3 different karyotype formulae. *Alstroemeria magnifica* var. *magnifica* and *A. magnifica* var. *sierrae* presented the same karyotype formula, and *A. magnifica* var. *magenta* and *A. magnifica* var. *tofoensis* each had a different formula. The scatter plot among  $CV_{CL}$  versus  $M_{CA}$  shows different groupings between populations of the four varieties. Based on these results it is possible to consider raising *Alstroemeria magnifica* var. *magenta* to species rank and *A. magnifica* var. *tofoensis* to subspecies; *A. magnifica* var. *magnifica* and *A. magnifica* var. *sierrae* should each remain as varieties. Nevertheless, these taxonomic changes should be considered tentative, as additional sources of evidence become available.

## 5. Molecular studies in *Alstroemeria*

During recent years, an increasing accessibility to molecular data and the development of a vast range of bioinformatics analysis has favored the successful implementation of genetic tools in the identification and conservation of biological diversity [59]. Dominant molecular markers based on random fragment alleles e.g. Inter Simple Sequence Repeat (ISSR), Random Amplified Polymorphic DNA (RAPD) and Amplified Fragment Length Polymorphism (AFLP) have

been used for characterizing genetic diversity in *Alstroemeria* [60–62], becoming the marker of choice for the identification of cultivar varieties with ornamental value [63–65] and conducting population genetic analyses [66, 67]. The use of DNA sequences has been more related to the construction of phylogenetic hypotheses and establishment of biogeographic patterns [8, 9]. Interestingly, near 30% of the Chilean species of *Alstroemeria* form species complexes, comprising from two to four infraspecific taxa each. This pattern is likely explained by adaptation to a wide range of environmental heterogeneity present in Chile [68], which is possibly driving processes of microevolutionary divergence [14]. Given the complexity of interpreting the integrity within and among these species complexes, we started several initiatives for applied genetic studies with the purpose of disentangling the discernibility of intraspecific patterns of divergence, especially in groups highly regarded for their ornamental and conservation value.

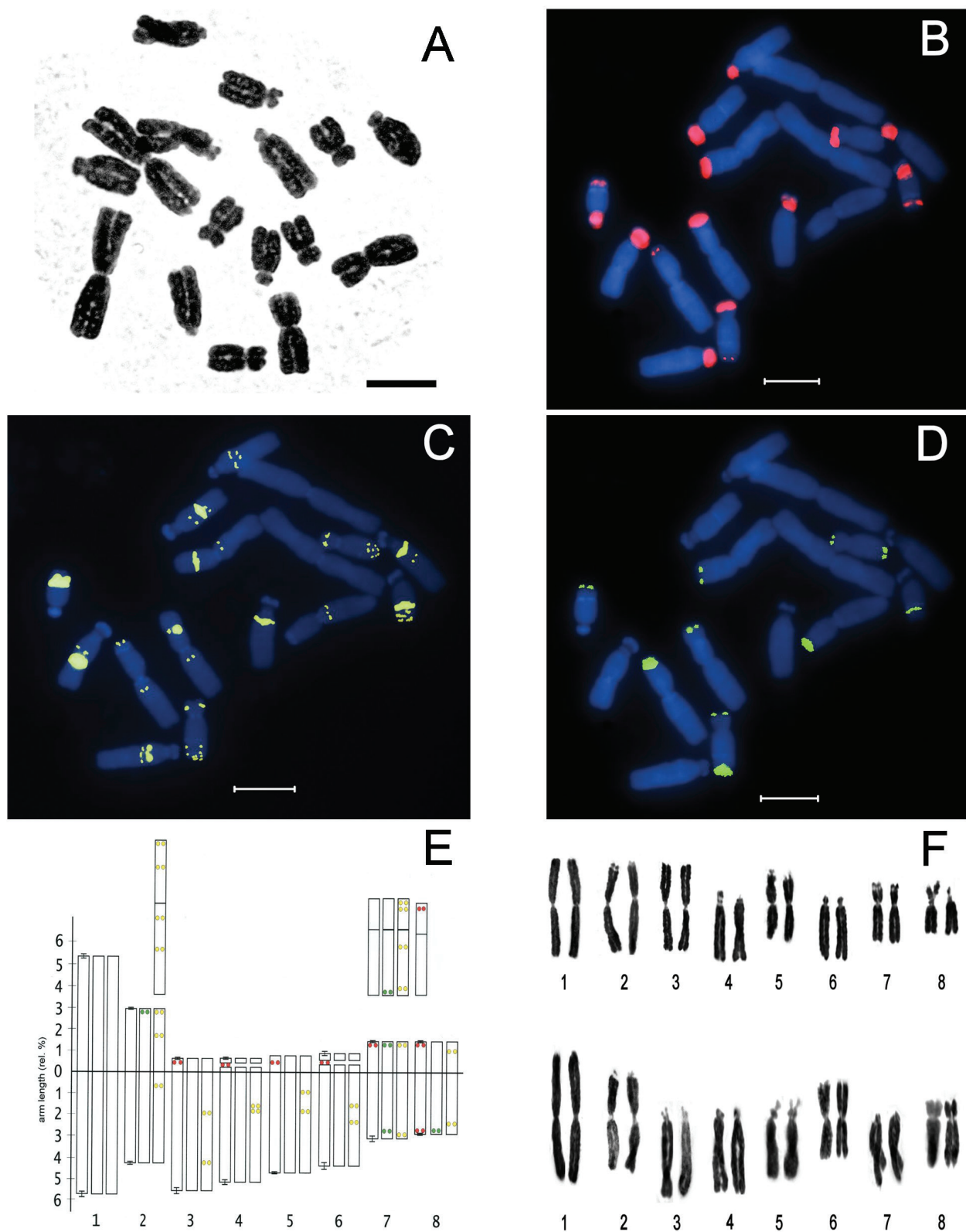
### 5.1. Molecular markers in assessing genetic diversity for conservation in *Alstroemeria*

A priority goal in conservation is to evaluate levels of apportionment of genetic diversity in targeted species, given the association between population genetic diversity and their potential for local adaptation and evolutionary resilience. Genetic variability is the result of the dynamics of gene flow, for which a homogeneous distribution of allelic frequencies is expected under high levels of gene flow among populations [69]. Interestingly, this situation is rarely found in nature, since the strong effect that geographic isolation and selection represents for local populations of plants. As a result, it is not surprising that peripheral populations tend to increase gene differentiation and population structure levels; hence, contributing to the local isolation that eventually could result in different isolated species (**Figure 7**) [69].

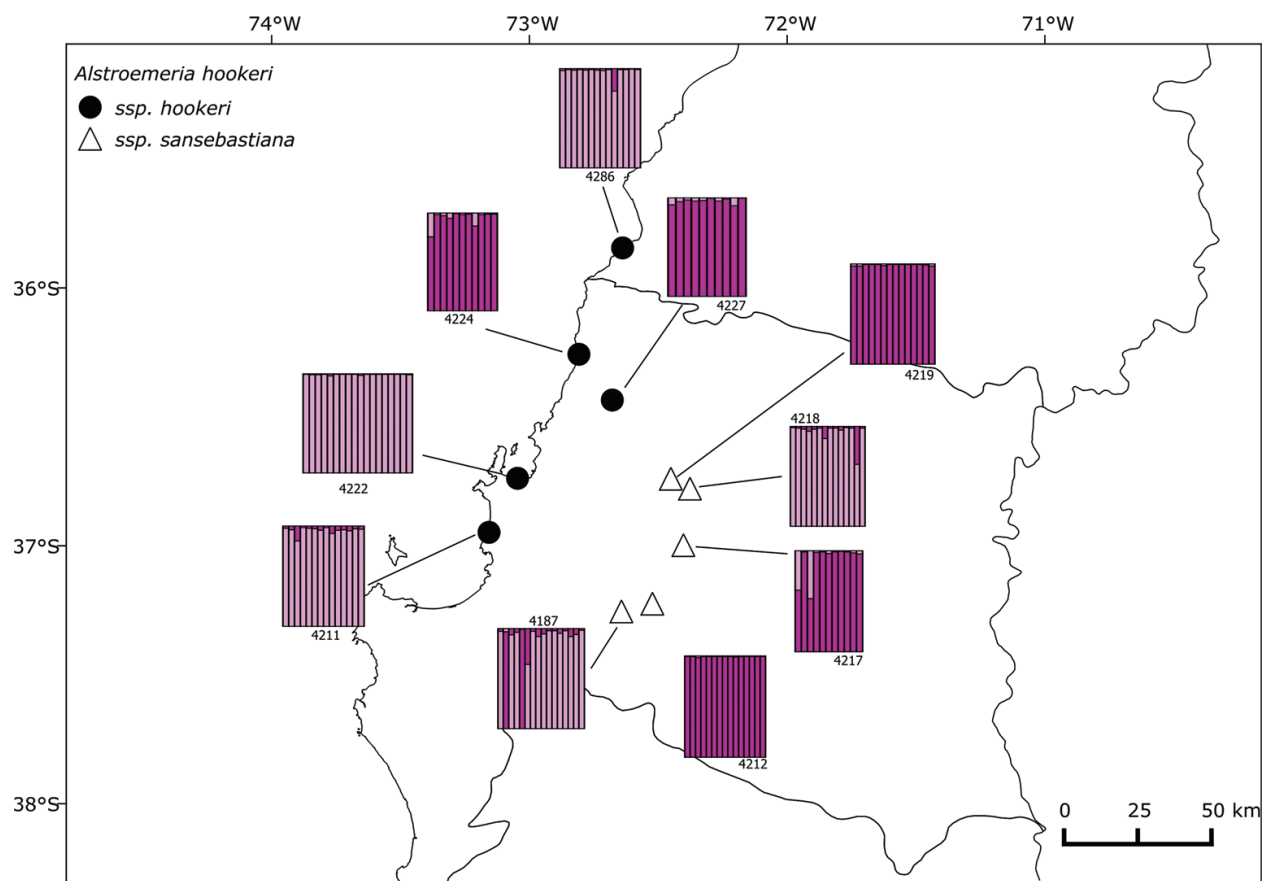
Such patterns of isolation and divergence are no exception in *Alstroemeria*, for which high levels of structuration are documented. For example, *Alstroemeria hookeri* represents a species complex that comprises four subspecies, two of them (subspecies *recumbens* and *maculata*) distributed in North-Central of Chile and two (subspecies *hookeri* and *sansebastianiana*) in southern Chile. Based on ISSR (Inter Simple Sequence Repeat) markers, high levels of population structure were found among southern subspecies (**Figure 8, Table 2**); also concomitant with previous findings found with allozymes markers [67]. Similarly, high levels of within population diversity was found in *A. presliana* complex using AFLP markers (**Table 2**), exhibiting significant levels of among population variability and moderate levels of genetic population structure (**Table 2**). This complex comprises of two varieties (var. *presliana* and var. *australis*), both separately distributed across Coastal and Andean mountain ranges in Chile (**Figure 9**). The results from both complexes showed the existence of two heterogeneous genetic groups with no evident spatial congruence suggesting genetic differentiation among varieties or subspecies. Interestingly, several populations are individually differentiated in their genetic profiles, despite of occurring closely enough with other neighbored populations to sustain substantial levels of gene flow (**Figure 9**).

Among explanations of the observed patterns of genetic diversity found in *Alstroemeria*, strategies of reproduction and dispersal become plausible enough to be considered. *Alstroemeria* species have a restricted capacity of seed and pollen dispersal [66], which in combination with their vegetative reproduction by rhizomes [14, 67], could contribute to maintaining restricted levels of gene flow and sustaining high levels of genetic structure





**Figure 7.** Cytogenetic studies in Chilean *Alstroemeria*. (A) Mitotic metaphase of *Alstroemeria hookeri* Ssp. *hookeri*. (B) Mitotic metaphase of *Alstroemeria hookeri* ssp. *hookeri* using 5S genes. (C) Mitotic metaphase of *Alstroemeria hookeri* ssp. *hookeri* using 18-25S genes. (D) Mitotic metaphase of *Alstroemeria hookeri* ssp. *hookeri* using A001 genes. (E) Ideogram of *Alstroemeria hookeri* ssp. *hookeri* showing genes 5S, 18-25S, and A001 (FISH). (F) Karyotypes of *Alstroemeria presliana*: above, *A. presliana* ssp. *presliana*; below, *A. presliana* ssp. *australis*.

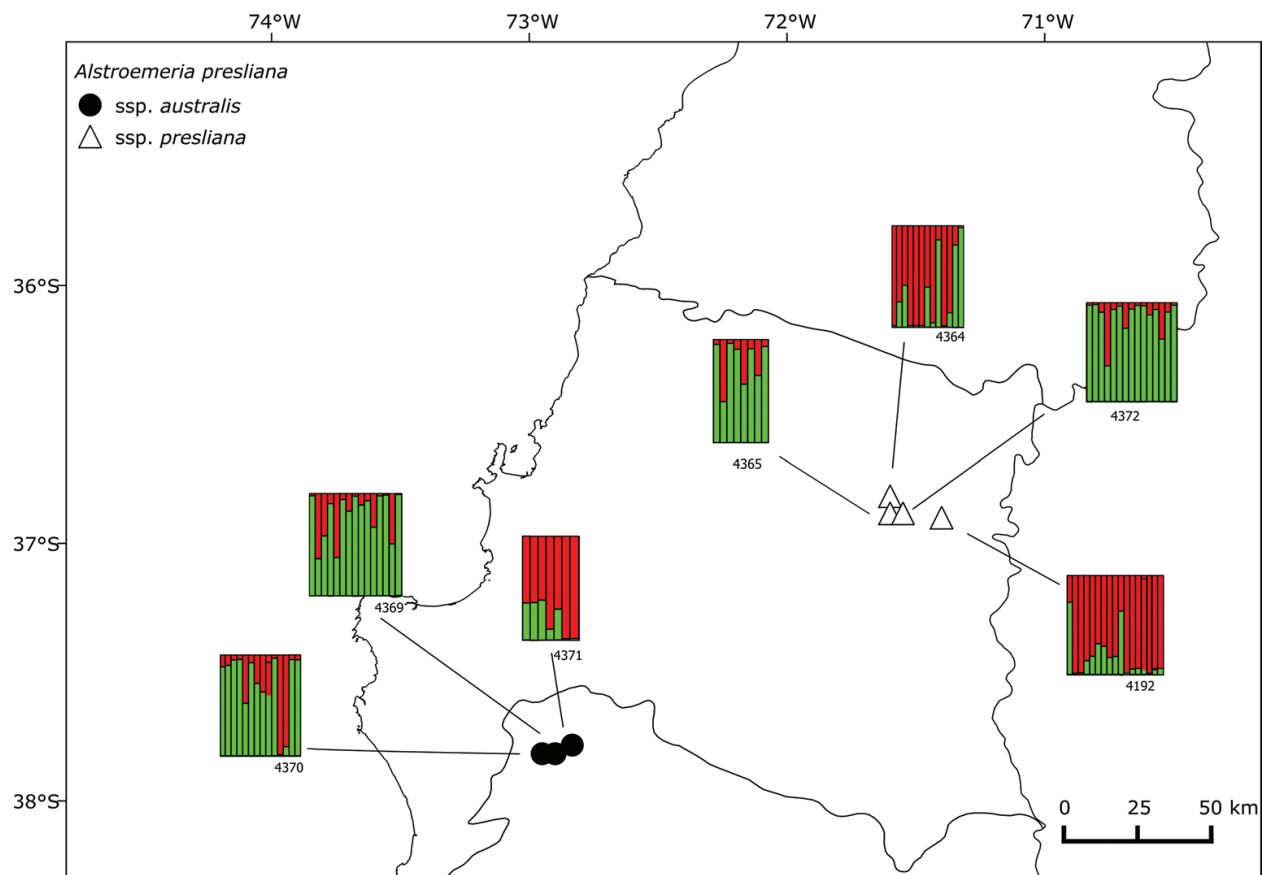


**Figure 8.** Population structure inferred with ISSR in the *A. hookeri* complex. Bar plots colors represent levels of genetic membership ( $k = 2$ ) in each individual per sampled population, as inferred under Bayesian admixture inference criterion with the program STRUCTURE [70].

among populations [67]. The sum of these factors implies that local populations could be subject to strong geographic and ecological isolation, which would explain the diversity of infraspecific taxa found in this and other species complexes [67]. In general, moderate to high levels of among population genetic diversity were detected in the studied *Alstroemeria* species complexes. From a conservation perspective, this pattern suggests that protection

| Species             | Subspecies           | He    | Fst   | AMOVA (%)   |            | Marker/source              |
|---------------------|----------------------|-------|-------|-------------|------------|----------------------------|
|                     |                      |       |       | Within pop. | Among pop. |                            |
| <i>A. hookeri</i>   | <i>hookeri</i>       | 0.052 | 0.582 | 41.71       | 58.28      | Allozymes/Ruiz et al. [67] |
|                     | <i>hookeri</i>       | 0.248 | 0.415 | 58.47       | 41.53      | ISSR/unpublished           |
|                     | <i>sansebastiana</i> | 0.246 | 0.36  | 63.99       | 36.01      | ISSR/unpublished           |
| <i>A. presliana</i> | <i>presliana</i>     | 0.200 | 0.171 | 82.91       | 17.0       | AFLP/unpublished           |
|                     | <i>australis</i>     | 0.198 | 0.179 | 82.10       | 17.9       | AFLP/unpublished           |

**Table 2.** Genetic diversity values obtained with allozymes and DNA markers (fragments analyses), for *A. hookeri* and *A. presliana* complexes.



**Figure 9.** Population structure inferred with AFLP in the *A. presliana* Complex. Bar plots colors represent levels of genetic membership ( $k = 2$ ) in each individual per sampled population, as inferred under Bayesian admixture inference criterion with the program STRUCTURE [70].

initiatives should consider as many populations as possible, in order to preserve the largest proportion of total species genetic diversity.

## 5.2. Molecular phylogenetic studies in *Alstroemeria*

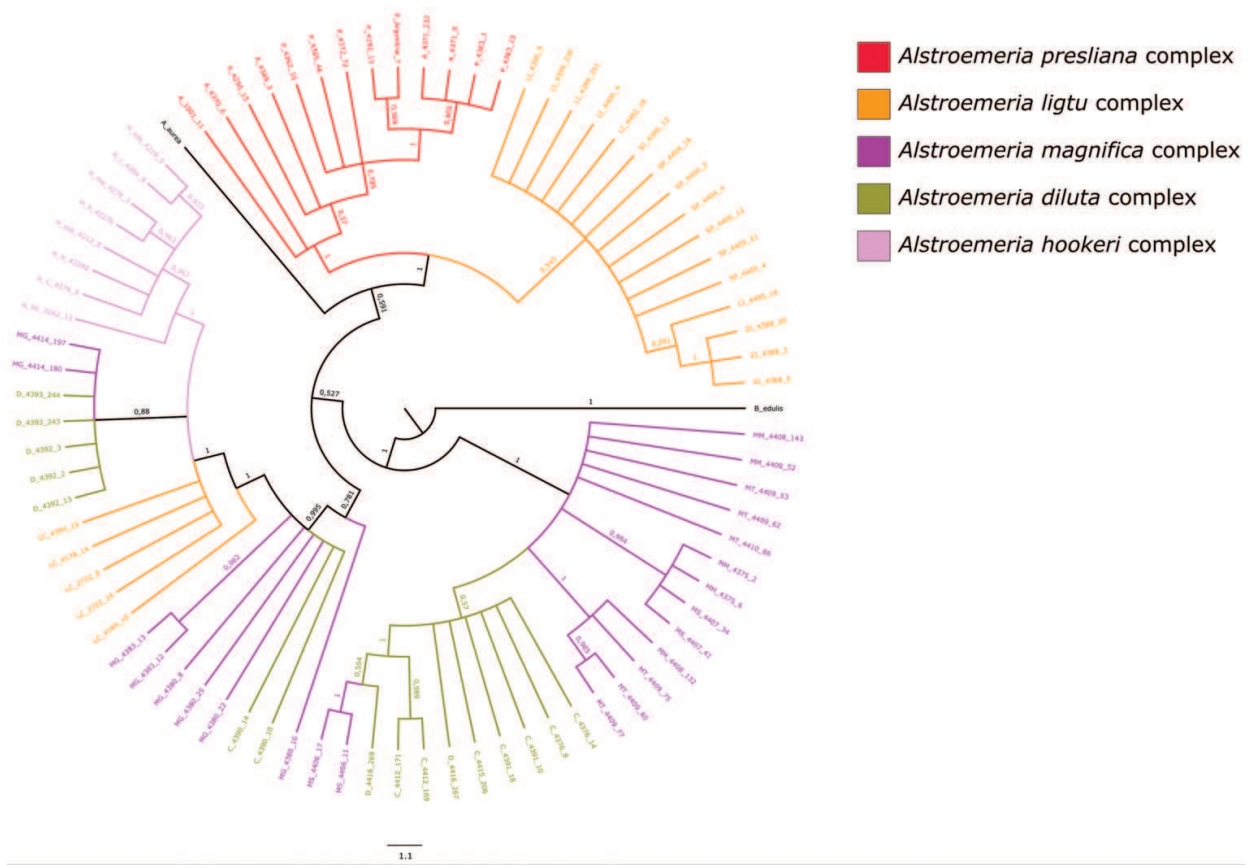
Phylogenetic studies provide a theoretical framework to understand the relationships among populations and species. It is desirable that taxa must represent monophyletic lineages, thus reflecting the genetic, evolutionary and biogeographical integrity of lineages and species. Under such premise, several phylogenetic studies in *Alstroemeria* have been conducted integrating a diverse array of molecular, morphological and cytological data [8, 9]. Chacón et al. [8] conducted the most recent and comprehensive phylogenetic studies in genus *Alstroemeria*, based on DNA sequences and cytological data. From taxonomic and evolutionary perspective, three are the most relevant results: (1) Samples belonging to the same species were retrieved as monophyletic; (2) a biogeographic break exists between Brazilian and Chilean species groups and (3) a relatively recent divergence has occurred with the most species of the genus, being diverged during the last 8 millions of years. Interestingly, some of these results have been confirmed from previous initiatives, especially those reflecting the monophyly of the Brazilian species group with alternative molecular markers (i.e., AFLP) [61].



Despite the promising of these results, species from the Chilean group were mostly under-represented, making difficult to obtain relevant evidence of local patterns of diversification, particularly to those depicting evolutionary trends or taxonomic integrity in species complexes. Nonetheless, while some progress has been achieved scrutinizing chloroplast sequences (*rpl32-trnI*), discordant results challenge the hypothesis integrity previously stated in several of these groups. While *Alstroemeria hookeri* and *A. presliana* complexes are retrieved as monophyletic clades, other groups like *A. magnifica* and *A. ligtu* are retrieved as paraphyletic (**Figure 10**).

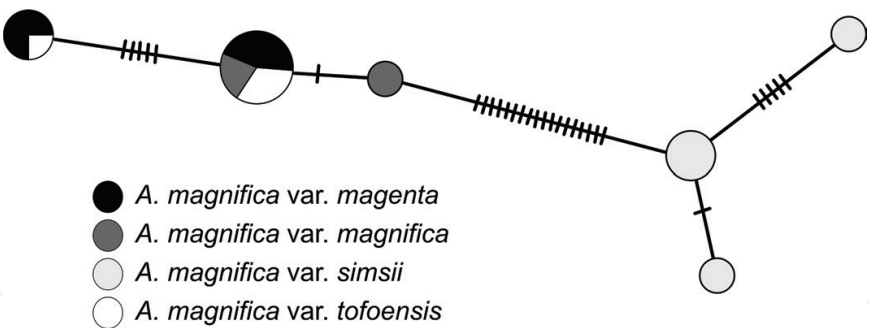
5.3. Molecular markers in eliciting taxonomic status in *Alstroemeria* species complex

The delimitation of species is a fundamental step for conducting natural and applied sciences, as they represent the main study unit for most areas of research (global evaluations of biodiversity, assessment and initiatives for biological conservation, etc.) [72]. In this sense, molecular approaches in taxonomy have been used under the assumption that observed



**Figure 10.** Maximum clade credibility tree (MCCT) inferred with the combination of chloroplast regions (*trnL-S*, *rpl32-trnL*, *petA*) for five species complexes of *Alstroemeria*, calculated with Bayesian inference criterion inferred with Mr. Bayes 3.2 [71]. Each tip represents an individual sampled per population and labels on branches depict posterior probabilities for each clade.

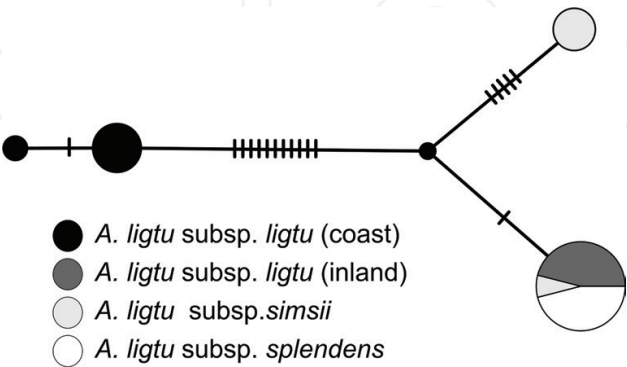
divergent patterns of genetic variation are the direct result of breaks in gene flow, leading to phenotypic and genotypic differences that sustain isolated and differentiated species and populations [69]. The simultaneous use of multiple molecular markers and criteria of delimitation has improved the taxonomic work, particularly helping to contextualize the role of microevolutionary processes in the species generation. As previously stated, species of *Alstroemeria* share attributes that could heavily influence patterns of micro evolutionary isolation and divergence, such as restricted seed and pollen dispersal and vegetative reproduction by rhizomes. Therefore, the wide distribution of taxonomic complexes in areas with contrasting topography and climatic conditions implies the existence of restrictions for gene flow, where substantial effects of ecogeographic isolation and divergence are expected in local diversification patterns [67]. Hence, micro evolutionary processes are currently underway and active [14], probably producing decoupled or unnoticeable patterns of divergence. Traditional taxonomic treatment in *Alstroemeria* has heavily relied on the interpretation of floral diversity and vegetative attributes, which has resulted in an important number of recognized taxa and species complexes described [14]. Nonetheless, because active of micro-evolutionary divergence may not ensure congruence among the diverse phenotypic and genotypic characters, it is likely that an under or overrepresentation of taxa is currently occurring in *Alstroemeria*. Therefore, given that molecular data could reflect patterns of divergence more accordingly to the dynamic of local gene flow, an interesting approach is to evaluate taxonomic boundaries integrating both molecular and phenotypic data as potential taxonomic characters. Recent molecular and phenotypic integrated studies conducted in *Alstroemeria* complexes resulted beneficial when multiple sources of evidence are placed to solve questions about the integrity or the validity of previous taxonomic treatments. For example, when morphometric, cytogenetic and molecular data were employed in *A. hookeri* complex taxa [41, 67], all analyzed characters were partially consistent with the recognition of the new subspecies *Alstroemeria hookeri* subsp. *sansebastianana* [22], and supported the hypothesis of Muñoz & Moreira [14] of elevating *Alstroemeria hookeri* ssp. *cunningiana* to species level. Subsequent investigations were also conducted in other three complexes (*A. ligtu*, *A. magnifica* and *A. presliana*), eliciting similar evidence with significant taxonomic impact. In the *A. magnifica* complex, evidence from morphology, colorimetry and cytology support the change of the taxonomic status of *A. magnifica* var. *magenta*. Preliminary analyses based on chloroplast sequences (*rpl32-trnL*) also supported this observation, validating the separation of var. *magenta* from the other *A. magnifica* varieties (**Figure 11**). In the *A. ligtu* complex, a new entity was discovered based on cytogenetic data, and its taxonomic status was redefined [57, 58]. The molecular data, based on chloroplast DNA (*rpl32-trnL* region) support the separation of Coastal populations of *A. ligtu* subsp. *ligtu* from populations of the inland distribution range (**Figure 12**). Finally, in *A. presliana*, same chloroplast markers also confirm the lack of structure observed with AFLP data; nonetheless, both of them seem not concordant with previous studies conducted with phenotypic data [18, 30]. It is likely that different sources of divergence are shaping idiosyncratic processes of differentiation among species complexes of *Alstroemeria*, suggesting that a case by case evaluation might be required before reaching a consensus for a more genus-wide taxonomic perspective.



**Figure 11.** Haplotype network inferred with trnL-F chloroplast spacer for individuals sampled from population of *A. magnifica* species complex. Network was constructed under parsimony criteria with TCS [73], as implemented in PopART [74].

5.4. Perspectives and future work

Previous studies have demonstrated that a consensus about the integrity of the taxa of *Alstroemeria* is far from being reached, as different patterns of differentiation may difficult to be elicited separately. In this sense, molecular markers have provided a natural framework to contextualize their evolutionary process, reconciling discordance observed from different character sources. Nonetheless, despite of their utility, molecular markers are not exempt of limitations that should be addressed in subsequent studies. One of the main limitations to reach a robust taxonomic hypothesis is the recurrent difficulty to obtain consistent molecular markers adaptable enough for interspecific and intraspecific analyses. These difficulties arise from the extraordinary large and complex genomic architecture of *Alstroemeria*, which is likely comprised of a large proportion of repetitive DNA (18–34 pg.) [17]. Our experience suggests that most nuclear markers tend to recurrently fail to retrieve single and readable copies through recurrent Sanger sequencing techniques, especially for the Internal Transcribed Spacer or ITS. Similarly, fragment analyses also exhibit levels of difficulties for consistent scoring, since the effect that



**Figure 12.** Haplotype network inferred with trnL-F chloroplast spacer for individuals sampled from population of *A. ligtu* species complex. Network was constructed under parsimony criteria with TCS [73], as implemented in PopART.



repetitive DNA has in the proportion of cut sites with restriction enzymes [17]. Since a more widespread consensus exist about the necessity of integrating different sources of molecular evidence and methodologies in species delimitation analyses [75], further work is required in the design of reliable and stable molecular markers for the study of natural species of *Alstroemeria*.

With the onset of new and more accessible technologies for genome sequencing (Next Generation Sequencing or NGS), new possibilities have opened for the generation of more representative analyses of genetic diversity [76, 77]. Unfortunately, such techniques have been not widely implemented in *Alstroemeria*, except important breakthroughs like the sequencing and the annotation of the chloroplast genome in *A. aurea* [78]. The generation of single nuclear polymorphisms (SNP) in non-model organisms has been the approach of choice for high-throughput genome sequencing, adding improved genome representation and resolution for inter and intraspecific levels relationships [79]. The implementation of SNPs might result in a significant improvement in the estimation of genetic diversity and species limits in *Alstroemeria*, as SNPs represent codominant markers capable of providing a higher statistical power and an easier species comparability considering the available genomic resources compared to AFLP [80]. For taxonomic purposes, SNP could greatly improve the use of DNA barcodes to identify species through the use of specific DNA regions, especially when traditional approaches of taxonomy fail [81]. Obviously, the use of NGS and SNP techniques in *Alstroemeria* requires adjustments to overcome the limitations imposed by genome size and complexity, for which recent alternatives have been shown from the study of other equally complex organisms [82]. As such, the perspective of solving the taxonomic problems with molecular techniques in *Alstroemeria* remains promising, yet keeping in perspective its own limitations and challenges to reach the require tools to finally approach the inherent dynamics of macro and micro evolutionary patterns in this group.

## 6. Concluding remarks

Genetic divergence and population structure estimated with AFLPs and ISSR, have demonstrated the importance of molecular markers for conservation purposes in *Alstroemeria*. Integrative use of molecular data with other source of evidence (morphology, cytology and morphometry) give a best interpretation of lineage divergence with better argumentation for taxonomic delimitation in species complexes of *Alstroemeria*. Due to the high proportion of species complex in genus *Alstroemeria* in Chile, is necessary to carry out phylogenetic studies including the most infraspecific taxa and more representative sampling, in addition with a major representation of the genome in the analyses. More efforts are needed in producing more stable molecular markers, in order to further implement integrative analyses. In this sense, it is likely that NGS will play a pivotal role helping to overcome present limitations of molecular work in *Alstroemeria*.

## Acknowledgements

We gratefully acknowledge the Curators and Director of the Herbarium CONC for providing access to the studied specimens. This work was supported by the projects Fondecyt 1130349 “Morphological, molecular and cytogenetic overview of some species complexes of the genus *Alstroemeria* in Chile” and VRID-ENLACE 217.111.063-1.0 “Integrative taxonomy in the genus *Alstroemeria* L. (Alstroemeriaceae): The use of morphological, colorimetric, cytological and molecular approaches on several Chilean complexes”. We acknowledge Nicolás Villalobos for technical support.

## A. Appendix

### Checklist of the Chilean species of *Alstroemeria*

Accepted names were written in **bold**, synonyms in *italics*. Names written in normal fonts corresponds to those whose acceptance or status has not yet been clarified. (E) = Endemic to Chile. (N) = Native.

1. ***Alstroemeria achirae*** Muñoz-Schick & Brink, Gayana, Bot. 57(1): 56. 2000 (E)
2. *Alstroemeria albiflora* C. Presl, Reliq. Haenk. 1(2): 121. 1827 = ***Alstroemeria pallida*** Graham
3. *Alstroemeria amoena* Salisb., Prodr. Stirp. Chap. Allerton 248. 1796 = *Alstroemeria pelegrina* L.
4. ***Alstroemeria andina*** Phil., Linnaea 29: 69. 1858.
  - a. subsp. *venustula* (Phil.) Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 74. 1987 = ***Alstroemeria andina*** Phil. var. ***venustula*** (Phil.) Muñoz-Schick, Not. Mens. Mus. Nac. Hist. Nat. 352: 22. 2003.
  - b. var. ***andina*** (E)
  - c. var. ***venustula*** (Phil.) Muñoz-Schick, Not. Mens. Mus. Nac. Hist. Nat. 352: 22. 2003. (N)
5. ***Alstroemeria angustifolia*** Herb., Amaryllidaceae 96. 1837.
  - a. subsp. *velutina* Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 165. 1987.
  - b. var. *acuminata* Herb., Amaryllidaceae 97. 1837 = ***Alstroemeria angustifolia*** var. ***angustifolia***
  - c. var. ***angustifolia*** (E)
  - d. var. *conferta* Herb., Amaryllidaceae 97. 1837 = ***Alstroemeria angustifolia*** var. ***angustifolia***
  - e. var. *intermedia* Herb., Amaryllidaceae 97. 1837 = ***Alstroemeria angustifolia*** var. ***angustifolia***

- f. var. *solliana* Herb., Amaryllidaceae 97. 1837 = **Alstroemeria angustifolia** var. **angustifolia**
- g. var. **velutina** (Ehr. Bayer) Muñoz-Schick, Mitt. Bot. Staatssamml. München 24: 165. 1987. (E)
6. *Alstroemeria aulica* Ravenna, Onira 4(10): 41. 2000.
7. *Alstroemeria aurantiaca* D. Don, Brit. Fl. Gard., ser. 2, t. 205. 1835 = *Alstroemeria aurea* Graham
8. *Alstroemeria araucana* Phil., Anales Univ. Chile 43: 547. 1873 = *Alstroemeria aurea* Graham
9. *Alstroemeria aurea* Graham, Edinburgh Philos. J. 181. 1833. (N)
  - a. var. *valparadisiaca* Herb., Amaryllidaceae 98. 1837 = **Alstroemeria ligtu** L. subsp. **simsii** (Spreng.) Ehr. Bayer
10. *Alstroemeria aurea* Meyen, Reise Erde 1: 311. 1834, hom. Illeg. = **Alstroemeria ligtu** L. subsp. **simsii** (Spreng.) Ehr. Bayer
11. *Alstroemeria bicolor* Hook., Exot. Fl. 2(9): t. 95. 1824 = **Alstroemeria pulchra** Sims subsp. **pulchra**
12. *Alstroemeria bilabiata* Ravenna, Phytologia 64(4): 282. 1988.
13. *Alstroemeria cantillanica* Ravenna, Phytologia 64(4): 285. 1988.
14. *Alstroemeria chilensis* Lem., Fl. Serres 1(5): 98. 1845 = **Alstroemeria ligtu** L. subsp. **ligtu**
15. *Alstroemeria chillanensis* Grau & Ehr. Bayer, Mitt. Bot. Staatssamml. München 18: 220. 1982 = **Alstroemeria presliana** Herb. subsp. **presliana**
16. *Alstroemeria chiloensis* Phil., Linnaea 29: 71. 1858 = *Alstroemeria aurea* Graham
17. *Alstroemeria ciliata* Poepp., Fragm. Syn. Pl. 6. 1833 = **Alstroemeria ligtu** L. subsp. **simsii** (Spreng.) Ehr. Bayer
18. **Alstroemeria citrina** Phil., Linnaea 22: 264. 1864 (E)
19. *Alstroemeria concolor* Steud., Berberid. Amer. Austr. 53. 1857
20. **Alstroemeria x chrysantha** (Ehr. Bayer) J.M. Watson & A.R. Flores, Fl. Silvtr. Chile 1: 90. 2015.(E)
21. **Alstroemeria crispata** Phil., Linnaea 29: 70. 1858 (E)
22. *Alstroemeria crocea* Phil., Linnaea 33: 262. 1864, non Ruiz & Pav. 1802 = **Alstroemeria pseudospathulata** Ehr. Bayer
23. **Alstroemeria cummingiana** Herb., Amaryllidaceae 96. 183 (E)
24. *Alstroemeria decora* Ravenna, Onira 4(10): 42. 2000.
25. *Alstroemeria dentata* Klotzsch ex Kunth, Enum. Pl. 5: 780. 1850, nom. Nud. = **Alstroemeria ligtu** L. subsp. **simsii** (Spreng.) Ehr. Bayer
26. *Alstroemeria diazii* Phil., Linnaea 33: 261. 1864 = **Alstroemeria exerens** Meyen

27. *Alstroemeria diazii* auct. Non Phil., Fl. Patagonica 2: 162. 1969 = **Alstroemeria presliana** Herb. subsp. **presliana**
28. **Alstroemeria diluta** Ehr. Bayer, Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 178. 1987
  - a. subsp. *chrysantha* Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 178. 1987 (E) = **Alstroemeria x chrysantha** (Ehr. Bayer) J.M. Watson & A.R. Flores
  - b. subsp. **diluta** (E)
29. *Alstroemeria discolor* Ravenna, Onira 4(10): 44. 2000.
30. *Alstroemeria epulauquensis* Ravenna, Phytologia 64(4): 283. 1988 = **Alstroemeria presliana** Herb. subsp. **presliana**
31. **Alstroemeria exserens** Meyen, Reise Erde 1: 34. 1834 (E)
32. *Alstroemeria exserens* Meyen, Reise Erde 1: 34. 1834 = **Alstroemeria exserens** Meyen
33. *Alstroemeria flava* Phil., Linnaea 33: 263. 1864 = **Alstroemeria ligtu** subsp. **ligtu**
34. *Alstroemeria flos-martini* Ker Gawl., Bot. Reg. 9: t. 731. 1823 = **Alstroemeria pulchra** Sims subsp. **pulchra**
35. **Alstroemeria garaventae** Ehr. Bayer, Gattung Alstroemeria in Chile 60. 1987 (E)
36. *Alstroemeria gayana* Phil., Linnaea 29: 71. 1857 = **Alstroemeria magnifica** Herb. var. **magnifica**
37. **Alstroemeria graminea** Phil., Anales Univ. Chile 93: 161. 1896 (E)
38. *Alstroemeria haemantha* Ruiz & Pav., Fl. Peruv. 3: 60. 1802 = **Alstroemeria ligtu** L.
  - a. var. *haemantha* = **Alstroemeria ligtu** L. subsp. **ligtu**
  - b. var. *pilosa* Herb., Amaryllidaceae 100. 1837 = **Alstroemeria ligtu** L. subsp. **simsii** (Spreng.) Ehr. Bayer
  - c. var. *simsiana* Herb., Amaryllidaceae 99. 1837 = **Alstroemeria ligtu** L. subsp. **simsii** (Spreng.) Ehr. Bayer
39. *Alstroemeria haemantha* auct. Non Ruiz & Pav. = **Alstroemeria ligtu** L. subsp. **simsii** (Spreng.) Ehr. Bayer
40. *Alstroemeria herbertiana* M. Roem., Fam. Nat. Syn. Monogr. 250. 1847 = **Alstroemeria revoluta** Ruiz & Pav.
41. *Alstroemeria hirtella* Phil., Linnaea 29: 70. 1858, hom. Illeg. = **Alstroemeria leporina** Ehr. Bayer & Grau
42. **Alstroemeria hookeri** Lodd., Bot. Cab. 13: t. 1272. 1827
  - a. subsp. *cunningiana* (Herb.) Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 157. 1987 = **Alstroemeria cunningiana** Herb.
  - b. subsp. **hookeri** (E)



- c. subsp. **maculata** Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 153. 1987 (E)
- d. subsp. **recumbens** (Herb.) Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 149. 1987 (E)
- e. subsp. **sansebastianana** C.M. Baeza & E. Ruiz, Gayana, Bot. 68(2): 313. 2011 (E)
- 43. *Alstroemeria hookeriana* Schult., Syst. Veg. 7(1): 733. 1829 = **Alstroemeria hookeri** Lodd. subsp. **hookeri**
- 44. *Alstroemeria huemulina* Ravenna, Phytologia 64(4): 285. 1988
- 45. *Alstroemeria inconspicua* Phil., Anales Univ. Chile 43: 546. 1783 = **Alstroemeria revoluta** Ruiz & Pav.
- 46. *Alstroemeria jocunda* Ravenna, Phytologia 64(4): 284. 1988
- 47. **Alstroemeria kingii** Phil., Anales Univ. Chile 43: 548. 1873 (E)
- 48. *Alstroemeria lacrima-solis* Ravenna, Phytologia 64(4): 283. 1988 = **Alstroemeria pseudospathulata** Ehr. Bayer
- 49. **Alstroemeria leporina** Ehr. Bayer & Grau, Mitt. Bot. Staatssamml. München 18: 222. 1982 (E)
- 50. **Alstroemeria ligtu** L., Pl. Alströmeria 10. 1762.
  - a. *Fma. pulchra* (Sims) Voss, Bot. Mag. 50: t. 2421. 1823[1822] = **Alstroemeria pulchra** Sims subsp. **pulchra**
  - b. subsp. *incarnata* Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 131. 1987, nom. Illeg. = **Alstroemeria ligtu** L. subsp. **splendens** Muñoz-Schick
  - c. subsp. **ligtu** (E)
  - d. subsp. **simsii** (Spreng.) Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 122. 1987 (E)
  - e. subsp. **splendens** Muñoz-Schick, Notic. Mens. Mus. Nac. Hist. Nat. 352: 22. 2003 (E)
  - f. var. *andina* Phil., Linnaea 33: 261. 1864 = **Alstroemeria pallida** Graham
  - g. var. *pulchra* (Sims) Baker, Handb. Amaryllideae: 139. 1888 = **Alstroemeria pulchra** Sims subsp. **pulchra**
- 51. *Alstroemeria ligtu* auct. Non L., Trab. Inst. Bot. Farmacol. 33: 26. 1915 = *Alstroemeria aurea* Graham
- 52. *Alstroemeria lothiana* Utinet. J. Jardins Jahrgang 1841: 348. = **Alstroemeria ligtu** subsp. **ligtu**
- 53. **Alstroemeria lutea** Muñoz-Schick, Gayana, Bot. 57(1): 55. 2000 (E)
- 54. *Alstroemeria macreana* Herb., Amaryllidaceae 90. 1837 = **Alstroemeria ligtu** L. subsp. **simsii** (Spreng.) Ehr. Bayer
- 55. **Alstroemeria magenta** Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 191. 1987 = *Alstroemeria magnifica* Herb. var. *magenta* (Ehr. Bayer) Muñoz-Schick

56. **Alstroemeria magnifica** Herb., Bot. Reg. 29: 64. 1843
  - a. subsp. *gayana* (Phil.) Ehr. Bayer, Gatt. Alstroemeria Chile 252. 1987[1986] = **Alstroemeria magnifica** Herb. var. **magnifica**
  - b. var. **magnifica** (E)
  - c. var. *magenta* (Ehr. Bayer) Muñoz-Schick, Notic. Mens. Mus. Nac. Hist. Nat. 352: 22. 2003 = **Alstroemeria magenta** Ehr. Bayer
  - d. var. *sierrae* (Muñoz) Muñoz-Schick, Notic. Mens. Mus. Nac. Hist. Nat. 352: 22. 2003 (E)
  - e. var. *tofoensis* Muñoz-Schick, Notic. Mens. Mus. Nac. Hist. Nat. 352: 22. 2003 (E)
57. **Alstroemeria magenta** Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 191. 1987 (E)
58. *Alstroemeria magna* Ravenna, Phytologia 64(4): 284. 1988
59. **Alstroemeria marticorenae** Negritto & C.M. Baeza, Syst. Bot. 40(1): 70. 2015 (E)
60. *Alstroemeria meyeniana* Schauer, Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. Suppl. 1: 440. 1843 = **Alstroemeria versicolor** Ruiz & Pav.
61. **Alstroemeria mollensis** Muñoz-Schick & Brinck, Gayana, Bot. 60(2): 102. 2003 (E)
62. *Alstroemeria monantha* Ravenna, Phytologia 64(4): 286. 1988
63. *Alstroemeria mutabilis* Kunze, Enum. Pl. 5: 777. 1850 = *Alstroemeria aurea* Graham
64. *Alstroemeria nana* Rendle, J. Bot. 42: 325. 1904 = **Alstroemeria patagonica** Phil.
65. *Alstroemeria nidularis* Ravenna, Phytologia 64(4): 282. 1988
66. *Alstroemeria nivalis* Phil., Linnaea 29: 69. 1858, hom. Illeg. = **Alstroemeria pallida** Graham
67. *Alstroemeria nubigena* Phil., Linnaea 29: 69. 1858 = **Alstroemeria pallida** Graham
68. *Alstroemeria oxyphylla* Ravenna, Phytologia 64(4): 286. 1988, nom. Superfl. = **Alstroemeria pseudospathulata** Ehr. Bayer
69. *Alstroemeria pallens* Phil., Linnaea 33: 265. 1864 = **Alstroemeria exerens** Meyen
70. **Alstroemeria pallida** Graham, Edinburgh New Philos. J. 344. 1829 (E)
71. **Alstroemeria parvula** Phil., Linnaea 33: 261. 1864 (E)
72. **Alstroemeria patagonica** Phil., Anales Univ. Chile 84: 160. 1894 (N)
  - a. fma. *Biflora* Ravenna, Sellowia 19: 34. 1967 = **Alstroemeria patagonica** Phil.
73. *Alstroemeria paupercula* Phil., Fl. Atacam. 51. = **Alstroemeria violacea** Phil.
74. *Alstroemeria pelegrina* L., Sp. Pl. (ed. 2) 1: 461. 1762 (E)
  - a. var. *albescens* Herb. Amaryllidaceae 91. 1837. = *Alstroemeria pelegrina* L.
75. **Alstroemeria philippii** Baker, Handb. Amaryllidaceae 140. 1888

- a. subsp. **adrianae** J.M. Watson & A.R. Flores, *Herbertia* 63: 102. 2009[2010] (E)
- b. subsp. **philippii** (E)
- c. var. **albicans** Muñoz-Schick, *Alstroemerias Chile* 41. 2003 (E)
- d. var. **philippii** (E)
76. *Alstroemeria poetica* Ravenna, *Phytologia* 64(4): 285. 1988
77. *Alstroemeria polpaicana* Ravenna, *Phytologia* 64(4): 283. 1988
78. *Alstroemeria polyphylla* Phil., *Anales Univ. Chile* 93: 160. 1896 (E)
79. *Alstroemeria presliana* Herb., *Enum. Pl.* 5: 773. 1850
  - a. subsp. **presliana** (N)
  - b. subsp. **australis** Ehr. Bayer, *Gatt. Alstroemeria Chile* 122. 1987 (E)
80. *Alstroemeria pseudospathulata* Ehr. Bayer, *Mitt. Bot. Staatssamml. München* 24: 49. 1987 (N)
81. *Alstroemeria pulchella* auct. Non L.f. = **Alstroemeria ligtu** subsp. **simsii** (Spreng.) Ehr. Bayer
82. *Alstroemeria pulchella* L.f. var. *pilosa* Lindl., *Edwards's Bot. Reg.* 17: t. 1410. 1831 = **Alstroemeria ligtu** subsp. **simsii** (Spreng.) Ehr. Bayer
83. *Alstroemeria pulchra* Sims, *Bot. Mag.* 50, t. 2421. 1823[1822]
  - a. subsp. **lavandulacea** Ehr. Bayer, *Mitt. Bot. Staatssamml. München* 24: 187. 1987 (E)
  - b. subsp. **maxima** (Phil.) Ehr. Bayer, *Mitt. Bot. Staatssamml. München* 24: 202 t.14, 18. 1987 (E)
  - c. subsp. **pulchra** (E)
  - d. var. **maxima** Phil., *Linnaea* 33: 266. 1864–65 (E)
84. *Alstroemeria pygmaea* auct. Non Herb., *Svenska Exped. Magell.* 3(5): 205. 1901 = **Alstroemeria patagonica** Phil.
85. *Alstroemeria quillotensis* Herb., *Amaryllidaceae* 97, t.2., f.2, 1837 = **Alstroemeria ligtu** L. subsp. **simsii** (Spreng.) Ehr. Bayer
86. *Alstroemeria recumbens* Herb., *Amaryllidaceae* 97, t.3. 1837 = **Alstroemeria hookeri** Lodd. subsp. **recumbens** (Herb.) Ehr. Bayer
87. *Alstroemeria reflexa* M. Roem., *Fam. Nat. Syn. Monogr.* 4: 252. 1847 = **Alstroemeria revoluta** Ruiz & Pav.
88. **Alstroemeria revoluta** Ruiz & Pav., *Fl. Peruv.* 3: 59. 1802 (E)
89. *Alstroemeria rosea* Hook., *Exot. Fl.* 3(27): t.181. 1825 = **Alstroemeria hookeri** Lodd. subsp. **hookeri**

90. *Alstroemeria rosea* Phil., Sert. Mendoc. Alt. 43. 1871 = **Alstroemeria pallida** Graham
91. *Alstroemeria sabulosa* Ravenna, Phytologia 64(4): 281. 1988
92. **Alstroemeria schizanthoides** Grau, Ehr. Bayer, Mitt. Bot. Staatssamml. München 18: 213. 1982
  - a. var. **alba** Muñoz-Schick, Notic. Mens. Mus. Nac. Hist. Nat. 352: 22. 2003 (E)
  - b. var. **schizanthoides** (E)
93. *Alstroemeria sericantha* Schauer, Nov. Actorum Acad. Caes. Nat. Cut. 19(Suppl. 1): 441. 1843 = **Alstroemeria umbellata** Meyen
94. *Alstroemeria sierrae* Muñoz, Fl. Silvestr. Chile: 64. 1966 = **Alstroemeria magnifica** Herb. var. **sierrae** (Muñoz) Muñoz-Schick
95. *Alstroemeria simsii* Spreng., Syst. Veg. [Sprengel] 2: 80. 1825 = **Alstroemeria ligtu** L. subsp. **simsii** (Spreng.) Ehr. Bayer
96. *Alstroemeria sotoana* Phil., Anales Univ. Chile 93: 159. 1896 = **Alstroemeria versicolor** Ruiz & Pav.
97. **Alstroemeria spathulata** C. Presl, Reliq. Haenk. 1(2): 122, t.22, f.2., 1827 (E)
98. *Alstroemeria spathulata* auct. Non C. Presl, Fl. Patag. 2: 162. 1969 = **Alstroemeria pseudospathulata** Ehr. Bayer
99. *Alstroemeria spectabilis* Ravenna, Phytologia 64(4): 284. 1988
100. *Alstroemeria stenopetala* Phil., Anales Univ. Chile 43: 547. 1873 = *Alstroemeria aurea* Graham
101. *Alstroemeria timida* Ravenna, Phytologia 64(4): 281. 1988
102. *Alstroemeria tigrina* Phil., Linnaea 29: 68. 1857 = **Alstroemeria versicolor** Ruiz & Pav.
103. **Alstroemeria traudliae** J.M. Watson & A.R. Flores, Fl. Sylvestr. Chil. 1: 118. 2015 (E)
104. *Alstroemeria tricolor* Hook., Exot. Fl. 1(5): t. 65. 1823 = **Alstroemeria pulchra** Sims subsp. **pulchra**
105. **Alstroemeria umbellata** Meyen, Reise Erde 1: 356. 1835 (E)
106. *Alstroemeria venusta* Ravenna, Phytologia 64(4): 282. 1988
107. *Alstroemeria venustula* Phil., Linnaea 33: 260. 1864 = **Alstroemeria andina** Phil. var. **venustula** (Phil.) Muñoz-Schick
108. **Alstroemeria versicolor** Ruiz & Pav., Fl. Peruv. 3: 59. 1802 (E)
109. **Alstroemeria violacea** Phil., Fl. Atacam. 51. 1860 (N)
110. *Alstroemeria violacea* Knight & Perry, nom. Nud. = **Alstroemeria violacea** Phil.
111. **Alstroemeria werdermannii** Ehr. Bayer, Gatt. Alstroemeria Chile 87. 1986[1987]



- a. var. **werdermannii** (E)
- b. var. *flavicans* Muñoz-Schick, Gayana, Bot. 57(1): 57, f.3. 2000 = **A. werdermannii** Ehr. Bayer subsp. **flavicans** (Muñoz-Schick) J.M. Watson & A.R. Flores (E)
- c. subsp. **flavicans** (Muñoz-Schick) J.M. Watson & A.R. Flores, Fl. Silvestr. Chile 1: 122. 2015.
- 112. *Alstroemeria xanthina* Phil., Anales Univ. Chile 43: 546. 1873 = **Alstroemeria versicolor** Ruiz & Pav.
- 113. *Alstroemeria yaelae* Ravenna, Phytologia 64(4): 282. 1988
- 114. **Alstroemeria zoellneri** Ehr. Bayer, Mitt. Bot. Staatssamml. München 24: 245, t. 143–144. 1987(E)
- 115. *Taltalia graminea* (Phil.) Ehr. Bayer, Sendtnera 5: 7, f. 1–4. 1998 = **Alstroemeria graminea** Phil.

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