



REVIEW ARTICLE

Pollination in the Chilean Mediterranean-type ecosystem: a review of current advances and pending tasks

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Chile; Mediterranean-type ecosystem; plant–pollinator interactions; pollination.

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ABSTRACT

We conducted a systematic review of the scientific literature published on plant–pollinator interactions, from both the plant and pollinator perspective, in the Chilean Mediterranean-type ecosystem (MTE hereafter). Our search identified 69 published papers on 235 native plant species from 62 families. Less than 7.9% of the flowering species inhabiting the Chilean Mediterranean have been studied, and most studies were restricted to only one locality and one reproductive season. The geographic location of the studies differed from a random pattern, showing two well-defined areas where most studies were conducted. Likewise, most studies in the Andes Range were performed above 2000 m a.s.l. The number of species of flower visitor per plant species was low (4.25 ± 0.22), which probably results from the historical and biogeographic isolation of Chile. This literature survey shows that studies relating floral traits with pollinator attraction and plant reproduction are the most frequent topics of research, reaching 37.6% of studies, followed by studies that examine pollination in relation to human impact (16.1%), micro- and macroevolution (14.0%), relationships between pollination and other ecological interactions (10.8%), community and network assessments (11.8%), and effects of abiotic variables on pollination interactions (9.7%). Our review highlights a lack of research on the effects of pollination for anthropogenic land use especially as agricultural practice is one of the most salient features of the Chilean MTE. Future directions to increase our understanding of the role of plant–pollinator relationships for biodiversity maintenance should include: to extend the taxonomic and geographic scope of research, to increase the number of spatial and temporal replicates, to increase the number of studies on pollination networks as they provide estimates of community complexity and putative stability, to develop studies that estimate the importance of pollination for plant demographic parameters and conservation, and to conduct studies that estimate the ecological service provided by Chilean native pollinators for crop yield and sustainable agriculture.

THE CHILEAN MEDITERRANEAN

The Chilean Mediterranean-type ecosystem (MTE hereafter) shares this climate type with few regions of the world. The origin of this type of climate in Chile is related to the development of the ‘arid diagonal’ of South America, the rise of the Andes (the final uplift dated 15–8 Ma), and the establishment of the cold Humboldt Current. All these events together led to the aridification of the climate and the evolution of new mechanisms in the local flora to endure these new climatic conditions during the Neogene (Armesto *et al.* 2007). The Mediterranean climate in Chile is characterised by a high seasonality, with most rainfall and low temperatures occurring in winter between June and August (mean total annual rainfall between 100–200 mm), and low rainfall and high temperatures in the summer season, December through February. According to the original descriptions of di Castri (1973) and di Castri & Hajek (1976) this ecosystem occurs below 1500 m a.s.l. between 31°11′ S and

35°51′ S. More recently, the proposal of Luebert & Pliscoff (2006), based on GIS-based information on bioclimatic and floristic variables, extends its geographic boundaries between 23°S on the coast and 28°S in the Andes, to 37°S on the coast and in the Andes, and 39°S in the Central Depression (Fig. 1). Considering the geographic extent of the Chilean MTE, Bannister *et al.* (2012) defined three floristic regions: the north Mediterranean (23–28° S), the central Mediterranean (29–32° S) and the south Mediterranean (33–37° S). The north Mediterranean region presents tropical climate elements, whereas the south Mediterranean region presents temperate climate elements. In terms of floristic composition, north and central Mediterranean regions share a high level of floristic similarity, whereas the south Mediterranean flora has more influence from temperate ecosystems (Bannister *et al.* 2012).

Studies in the Chilean MTE can be traced back at least 40 years, stimulated by the idea of the evolutionary convergence in the biotas of central Chile and California. The

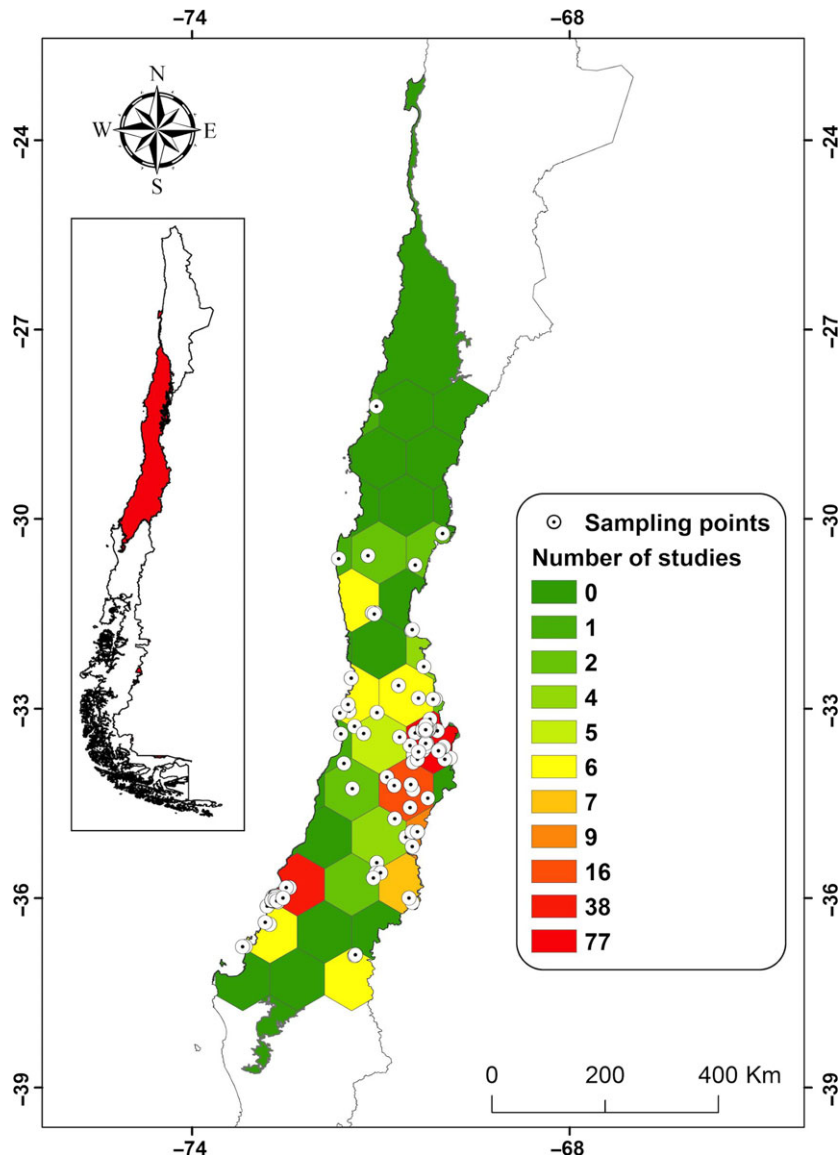


Fig. 1. Spatial distribution of the studies performed in the Chilean MTE. Dark green hexagons depict the areas where a higher number of studies were conducted. The distribution range of the Mediterranean-type ecosystem follows Luebert & Pliscoff (2006).

International Biological Program initiative in the 1970s supported diverse studies on the comparison of the two biotas at various levels of organisation and regarding their relationships to abiotic features (e.g. Cody *et al.* 1977; Mooney 1977; Cody & Mooney 1978). After these seminal studies, several components of the Chilean MTE have been described in detail and compared with Californian counterparts, including vascular plants (e.g. Parsons & Moldenke 1975; Arroyo *et al.* 1995), mammals (e.g. Glanz 1977), birds (e.g. Cody 1970, 1973), reptiles (e.g. Fuentes 1976) and invertebrates (Hunt 1973). Likewise, herbivory, predator–prey interactions, fire frequency, soil nutrient availability and land use have also been studied and suggested as influences on the biodiversity of the Chilean MTE (see review in Fuentes *et al.* 1995). Despite the broad spectrum of taxonomic units and ecological processes examined, there is a scarcity of information on plant–pollinator relationships in the Chilean MTE. This is unfortunate as pollination has been a focus of attention for naturalists for at least 200 years and it is one of the most important ecological interactions. Pollination often contributes to the maintenance of higher trophic levels

and stabilises multispecific sets of interactions (e.g. Bascompte *et al.* 2006; Campbell *et al.* 2011). An estimated of 90% of all flowering plants are pollinated by animals (Ollerton *et al.* 2011) and about 85% of the most important crops rely on animal pollination (Klein *et al.* 2007). These figures indicate that pollinators provide a critical ecological service for wild plants and crops, being vital for biodiversity maintenance and sustainability of the human population. In the context of this review, those studies assessing pollination in the Chilean MTE reviewed were limited to indirectly reference to the importance of pollination as an ecological service, but did not present a formal assessment of this topic. The references estimate the contribution of native and exotic plants as pollen and nectar donors for honey and propolis production (e.g. Montenegro *et al.* 2001, 2003).

QUESTIONS AND PROCEDURE

The aim of this paper is to provide a narrative review of the studies dealing with plant–pollinator interactions in the

Chilean MTE, with special emphasis to ecological characteristics that may contribute to the maintenance of biodiversity. We examined the types of questions asked by researchers and classified studies according to six broad categories of focus related to: (i) geographic distribution, spatial and temporal extent, and effects of abiotic variables on pollination; (ii) studies on variation in flower morphology, colour and floral polymorphisms; (iii) relationship of pollination with other ecological interactions; (iv) studies at the micro- and macroevolution levels; (v) studies at the community and network levels; and (vi) pollination in a human-altered environment. In addition, we compiled a series of characteristics of the plants and pollinators involved as well as variables related to the sites where studies were performed. More specifically, in this review we attempt to answer the following questions: (i) are studies randomly dispersed across the MTE or do they tend to concentrate in some particular areas; (ii) what is the spatial and temporal extent of studies; (iii) what proportion of flowering plant species inhabiting the Chilean MTE have been studied; and (iv) how well represented are general topics of plant–pollinator research in the Chilean MTE? The response to these questions, along with analysis of our categories allows us to identify gaps in knowledge and the areas for future research to better understand the role of plant–pollinator interactions in shaping the biodiversity of Chilean MTE.

We compiled studies on plant–pollinator interactions in the Chilean MTE with the help of Web of Science using the following keywords: ‘Chile’ plus one of the following: ‘pollination’, ‘plant–pollinator’, ‘pollinator’ or ‘flower’. In addition, papers published in local scientific journals not included in Web of Science were also inspected when the indexed papers consulted cited them. From the papers we identified, we selected those with coordinates within the Chilean Mediterranean as defined by Luebert & Pliscoff (2006), and evaluated information on pollination interactions. Only papers presenting some measure of pollination (*e.g.* pollination or visitation rates, reproductive success measures, reproductive system) were included in the database. The resulting database consisted of 69 studies (see Table S1), from which the following variables were extracted: (i) geographic coordinates, (ii) elevation (m a.s.l.), (iii) species, (iv) family, (v) number of spatial replicates (localities), (vi) number of temporal replicates (flowering seasons), (vii) origin of plants (exotic, native, endemic) and (viii) number of pollinators recorded (dataset available upon request).

Study data came from 235 flowering native plants out of the 2976 recorded species in the Chilean MTE (Bannister *et al.* 2012), which represents less than 7.9% of the potential flora. Additionally, 35 exotic plant species from 29 genera and 17 families were reported in the literature reviewed. Examining the data on native species in the next two taxonomic levels, 137 out of the 817 genera (17%) and 62 out of the 168 families (37%) recorded for the Chilean MTE (according to Bannister *et al.* 2012) have been studied. These numbers mean that at least two-thirds of the native flora in the Chilean MTE (and their phylogenetic and evolutionary distinctiveness) lack information on pollination. Moreover, 83% of the 235 species were studied only once (Fig. 2A), indicating that knowledge on plant–pollinator relationships in the Chilean MTE is restricted to an extremely small subset of the potential species involved in these interactions. Most of the studies focused on plant species, giving detailed information on their morphology, range of

distribution and phenology, among other characteristics. Pollinators, in most cases, were only named, and little information was given about them. They are usually identified at the species level, but some studies only report the number of pollinators belonging to a given genus or order. In our literature review, we found that flower visitors described in the Chilean MTE belong to eight different orders from 58 families and 162 genera (Table 1), among which Hymenoptera was the most represented (42.8%), followed by Diptera (31.3%), Lepidoptera (12.5%), Coleoptera (10.1%), Apodiformes (2.1%), Hemiptera (1%), Orthoptera (0.1%) and Psocoptera (0.1%). The mean number of flower visitors recorded per plant species was 4.25 ± 0.22 (mean \pm 1 SE, $N = 518$), a low figure, probably related to the historical and biogeographic isolation of Chile (Moreira-Muñoz 2011). However, this figure should be interpreted with caution, as sampling procedures used by studies were often highly heterogeneous. Regarding invasive species, research on exotic plants represented about 12% of studies, and only two out of 69 publications (3%) focused on invasive pollinators.

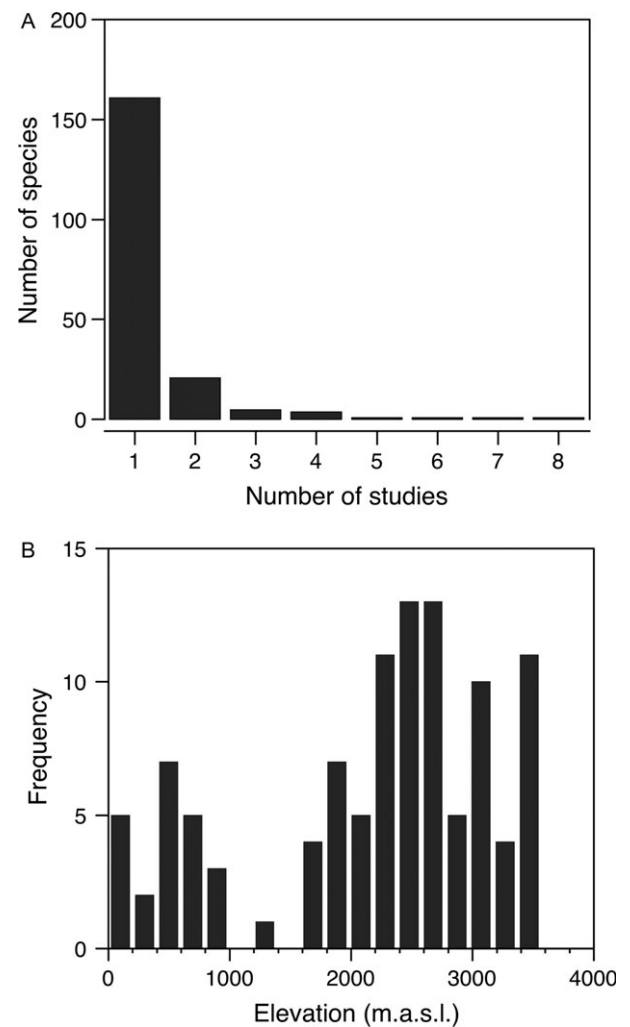


Fig. 2. (A) Distribution of the number of species over the number of studies conducted. (B) Distribution of studies performed in an elevation interval between 200 m and sea level.

Table 1. Orders of flower visitors in the Chilean MTE and the number of families and genera belonging to each order.

Order	No. Families	No. Genera
Apodiformes	1	3
Coleoptera	13	24
Diptera	14	38
Hemiptera	6	6
Hymenoptera	15	59
Lepidoptera	7	30
Orthoptera ^a	1	1
Psocoptera	1	1
	58	162

^aThe order Orthoptera was reported only in one paper, and no information was given related to the number of species, genera or families belonging to that order, so we assumed that it was, at least, one family from one genus.

A REVIEW OF THE EVIDENCE

Geographic distribution

To assess whether the pollination studies conducted in the Chilean MTE were evenly distributed along the potential area or concentrated in particular locations, we used a spatial randomness test. This test revealed that the number of sampling units did not follow a random negative binomial distribution (Negative binomial Chi-squared test, Morisita patchiness = 12.7, $P < 0.001$), indicating that studies in the Chilean MTE tend to be more spatially aggregated than could be expected by chance (Fig. 1). It appears that most researchers tend to study localities selected *a priori*, often on the basis of physiognomy, or natural reserves that ensure isolation from urban areas to avoid human disturbance. Studies are concentrated in two major regions: (i) the Andes foothills to the east of Santiago, probably due to the proximity to the city, and (ii) the western margin of the Coastal Mountain Range about 350–450 km south of Santiago, where remnants of the once continuous Ruil forest are still present in a disturbed and fragmented landscape (Bustamante *et al.* 2005). In addition to climate, topography and anthropogenic disturbance are the major factors that explain the distribution of vegetation in the Chilean MTE (Fuentes *et al.* 1995); these factors probably also explain the distribution of studies. Most were performed above 2000 m a.s.l. in the Andes Range, with a notorious absence of studies at some elevations, particularly evident in the gap for studies between 1000 and 1600 m a.s.l. (Fig. 2B). The relatively low number of pollination studies conducted in lowlands (<1000 m a.s.l.) may be related to the presence of human settlements (urban areas, crops, cattle raising areas), which are associated with large changes in land use and vegetation. Highly disturbed and transformed lands are consistently avoided for research aiming to answer ecological and evolutionary questions about pollination.

Spatial and temporal extent

Even though some studies included spatial replicates across the distribution range of genera and species (e.g. *Alstroemeria*, *Chaetanthera*, *Gomortega*, *Mimulus*, *Oxalis* and *Schizanthus*), 52% of studies were performed in only one locality (Fig. 3A). While this pattern is based on the type of questions posed by

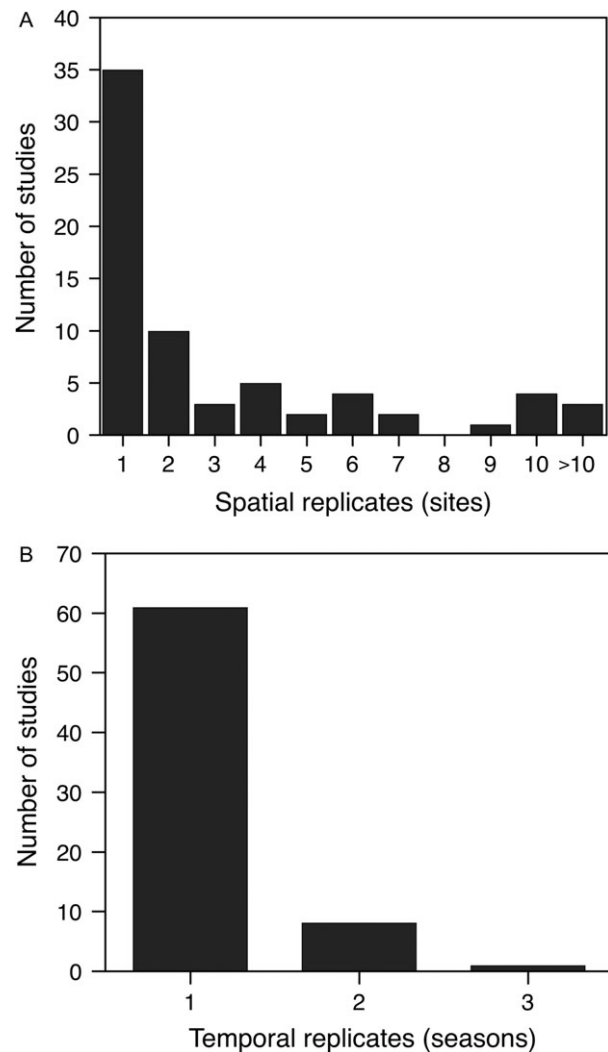


Fig. 3. Distribution of the number of studies based on: (A) the number of spatial replicates (study sites), (B) the number of temporal replicates (reproductive seasons).

researchers, incorporation of edapho-climatic heterogeneity across the Chilean MTE (Fuentes *et al.* 1995) would allow explanation of the spatial variation in plant–pollinator relationships.

Regarding temporal variation, most studies were restricted to one flowering season (Fig. 3B). Only eight out of 69 studies showed temporally replicated observations or experiments covering 2 or more years. Muñoz *et al.* (2005) tested the role of soil nitrogen on flower traits, pollinator visitation and reproductive success of *Chuquiraga oppositifolia* (Asteraceae) during the summers of 2002 and 2004. Carvallo & Medel (2010) recorded pollination visits and estimated inbreeding depression through seed production and seed germination in a population of *Mimulus luteus* (Phrymaceae) in 2005 and 2006. Esterio *et al.* (2013) recorded the visitation rate and pollen transfer effectiveness of bees and bumblebees in a population of *M. luteus* during 2010, 2011 and 2012. González *et al.* (2014) recorded the pollinator assemblage and visitation rate in six populations of *Alstroemeria ligtu* (Alstroemeriaceae) during the springs of 2011 and 2012. Arroyo *et al.* (2006) estimated the

levels of autogamy and pollination of *Chaetanthera euphrasioides* in two consecutive years. Rozzi *et al.* (1997) measured pollen and biotic seed dispersal of *Anarthrophyllum cumingii* in 1987 and 1988. Medan & Montaldo (2005) evaluated the association between the endemic *Colletia ulicina* (Rhamnaceae) and the hummingbird *Sephanoides sephaniodes* in two consecutive years. Finally, Suárez *et al.* (2011) replicated some of their observations on *Madia chilensis* related to floral design, display traits and the relation between floral phenotype and environmental variables in the 2008 and 2009 growing seasons.

Effects of abiotic variables on pollination

One of the most important characteristics of the Chilean MTE is the high spatial variability in abiotic variables. Fuentes *et al.* (1995) hypothesised that similar to other Mediterranean ecosystems, species diversity in the Chilean MTE is associated with habitat diversity locally. Moisture and temperature differences between equatorial- and polar-facing slopes (in Chile, corresponding to north and south, respectively) are one of the most conspicuous characteristics of Mediterranean ecosystems (among other ecosystems worldwide). These differences may contribute substantially to small-scale variation in plant morphology and pollination regimes. These kinds of questions have been addressed in some studies, most of them carried out in the Andes. For example, Rozzi *et al.* (1997) compared the flowering periods and insect visitation rates in *Anarthrophyllum cumingii* (Papilionaceae) on equatorial- and polar-facing slopes, concluding that plants inhabiting different slopes differed in their peak of flowering. Different insect taxa were involved in pollination due to this phenological displacement. A similar result was obtained by Torres-Díaz *et al.* (2007, 2011) addressing the importance of temperature variation between slopes on the pollinator visits in *Chaetanthera apiculata* and *C. lycopodioides* (Asteraceae) and stigma longevity in *C. renifolia*. Equatorial-facing slopes reached higher temperatures than east- and west-facing slopes, which translated into higher visitation rates by lepidopteran and hymenopteran species. Stigma receptivity, in turn, was extremely long in unpollinated plants, suggesting this trait may increase the chance of reproduction for species inhabiting high-elevation ecosystems. On a smaller spatial scale, Suárez *et al.* (2011) noted that small-scale variation in soil moisture associated with slope exposure substantially influenced the flower phenotype in *Madia chilensis* (Asteraceae), and the probability of receiving pollinator visits, where plants on north-facing slopes received more visits. The role of temperature in flower longevity was experimentally examined by Arroyo *et al.* (2013), through exposing flowers of *Oxalis compacta* (Oxalidaceae) to different temperatures in the field. The authors concluded that flowers remain open longer at cool temperatures, probably mitigating lower pollination rates, and close earlier in warmer conditions where pollination tends to be faster, suggesting confounding effects of the stress imposed by temperature on the plant and its pollinators.

The effects of soil nutrients on pollination have also been assessed, particularly in relation to nitrogen content. In this regard, Rundel (1982) compared the efficiency of nitrogen utilisation of Chilean and Californian MTE shrubs. The extent to which plant reproduction is controlled by bottom-up effects related to nitrogen availability and pollen limitation was examined 20 years later by Muñoz *et al.* (2005) and Muñoz &

Arroyo (2006). Nitrogen addition experiments were performed over 3 years on the pollen-limited *Chuquiraga oppositifolia* (Asteraceae). While floral display, pollinator visitation and reproduction did not increase in the first 2 years, there was a significant increase in the third year, suggesting a long-term effect of nitrogen addition on the reproductive success of this plant species.

Variation in flower morphology, colour and floral polymorphism

The importance of flower phenotype in attracting pollinators is the issue that has received most attention (37.6% of studies reviewed). An early paper of Peralta *et al.* (1992) found that *Acacia caven* (Leguminosae) has showy, but nectarless, flowers that attract only coleopterans. Later, Humaña *et al.* (2008) found that four species of *Chloraea* (Orchidaceae) complete rely on pollination for fruit production, but few or no pollinator visits were recorded. Ladd & Arroyo (2009) reported a similar result in two species with contrasting floral morphology: *Nastanthus spathulatus* (Calyceraceae) was visited by only one bee species (*Megachile saulcyi*), whereas no pollinators were recorded on *Rhodophiala rhodolirion* (Amaryllidaceae). Further understanding of the importance of flower morphology has been gained with the use of experimental modifications of flower traits on pollination rate and plant reproductive success. The adaptive value of nectar guides has been experimentally assessed in *Alstroemeria ligtu* (Alstroemeriaceae), finding that the removal of petals without nectar guides had no effect on pollinator rates and plant reproductive success, but the removal of petals with nectar guides significantly reduced both variables (Botto-Mahan & Ojeda-Camacho 2000; Botto-Mahan *et al.* 2011). Likewise, partial or total petal removal in *Loasa tricolor* (Loasaceae) had contrasting effects on pollination rates, indicating a dose-dependent response of pollinators to flower herbivory (Cares-Suárez *et al.* 2011). These results differ from those obtained by Cuartas-Domínguez & Medel (2010), who reported that phenotypic modification of the lateral sepals and the labellar lobe of *Chloraea blettioides* (Orchidaceae) had no effect on male and female fitness functions. Similarly, Espinoza *et al.* (2012) found no effect on reproductive success of petal cutting in *Viola portalesia* (Violaceae), but a significant effect of flower density. Regarding plant density, Cavieres *et al.* (1998) and Molina-Montenegro & Cavieres (2006) found that large-sized flowers of *Alstroemeria pallida* (Alstroemeriaceae) and *Nothoscordum gramineum* (Alliaceae) predict pollinator visits and plant reproductive success only at high flower densities; a similar result was obtained by Arroyo *et al.* (2007) in *Chaetanthera lycopodioides* (Asteraceae). Butterflies visiting this species preferred large floral displays. In contrast, González & Pérez (2010) found that flower size was not associated with pollen limitation in 16 perennial species at the northernmost limit of the Chilean MTE.

Regarding pollination syndromes, Medel *et al.* (2007) found that *M. luteus* populations with large nectar guides are mainly visited by hummingbirds, while populations with large corolla sizes are mainly visited by bees. The consistency of the association between the endemic *Colletia ulicina* (Rhamnaceae) and the hummingbird *Sephanoides sephaniodes* was examined at two sites during two consecutive years (Medan & Montaldo 2005), indicating that this interaction is well established, as the

hummingbird visits were frequent, systematic and occurred at different sites. Despite this consistency, the interaction lacks specialisation, as *C. ulicina* has another important pollinator (*Bombus dahlbomii*) and the hummingbird visits other flowering plants. In more specialised plant–pollinator associations, Murúa & Espíndola (2015) found a significant match between the floral morphology of ten *Calceolaria* species and the morphology of their oil-collecting specialised pollinators, leading to highly specialised associations in some cases (e.g. Murúa *et al.* 2014).

Carvalho & Medel (2005) identified modular units in flower design in *M. luteus* using the conditional independence approach to identify integrated phenotypes (Magwene 2001). They concluded that corolla and nectar guide size form an integrated module related to pollinator attraction, which is consistent with the traits under pollinator-mediated selection in Medel *et al.* (2003). The ecological factors influencing floral integration were examined in *Alstroemeria ligtu* (González *et al.* 2015) and *Schizanthus* spp. (Pérez *et al.* 2007). The pattern of floral integration in *A. ligtu* was associated with the composition of pollinator assemblages, suggesting that pollinator-mediated selection is shaping integration patterns. In *Schizanthus*, floral integration was observed in pollinator-dependent species, but not in species with autonomous selfing, stressing the role of pollinator-mediated selection. These studies as a whole, suggest that high floral integration in Chilean MTE may be a relatively frequent pattern across a large range of species, probably as a consequence of the contribution of few pollinator species to plant reproductive success of many species (e.g. see González *et al.* 2014; Lemaitre *et al.* 2014; but see Galetto *et al.* 1998).

Only three studies have used procedures of geometric morphometrics to characterise flower shape. Medel *et al.* (2003) used elliptic Fourier analysis to examine whether nectar guide outlines in *M. luteus* were under pollinator-mediated selection, revealing disruptive selection on nectar guide size and shape. Botto-Mahan *et al.* (2004) examined whether fluctuating asymmetry (FA) influences pollinator attraction and female fitness in *M. luteus*. Their results did not reveal a significant linear or non-linear relationship between nectar guide FA and fitness. Later, Murúa *et al.* (2010) used a landmark approach to characterise corolla shape in *Viola portalesia* (Violaceae), finding pollinator-mediated selection on the geometric relationship among petals.

Regarding flower colour, Cooley *et al.* (2008) identified anthocyanin pigments, flower morphology and nectar variation of the yellow *Mimulus luteus* var *luteus*, and the red-pigmented *M. luteus* variegatus, *M. naiandinus* and *M. cupreus* in a common garden experiment using seeds collected from different localities of central Chile. By combining phenotypes with field observations, the authors associated pollinator assemblages with phenotypic variants, concluding that flower colour differences are not associated with different pollinator assemblages.

Walter (2010) studied the floral biology of *Echinopsis chiloensis* (Cactaceae), aiming to characterise its pollination syndrome, visitors, visitation rate and their pollination efficiencies. Anthesis was both nocturnal and diurnal and depended on daytime temperature. Even though both nocturnal and diurnal pollinators contributed to fruit set, nocturnal pollination was more efficient. This conclusion contrasts with the findings of Ossa & Medel (2011) in another *E. chiloensis* population. The authors reported that anthesis is strictly diurnal and flowers are visited mainly by hymenopterans and dipterans, fitting a diurnal insect pollination syndrome. These results taken

as whole suggest that both time of anthesis and pollination syndrome are labile conditions that depend on the abiotic characteristics and geographic location of the population under assessment.

Regarding heterostyle polymorphism, the only study conducted on the tristylous *Oxalis* (Oxalidaceae; Marco & Arroyo 1998) found that floral morphs of *Oxalis squamata* are strongly incompatible, but produced similar fruit and seed production. However, intermorph and intramorph cross-pollination experiments in *O. compacta* revealed seed production, suggesting that incomplete incompatibility allows reproduction in a limited pollinator environment (Arroyo *et al.* 2012).

Studies linking pollination with other ecological interactions

Most of these studies examined the relationship between foliar (e.g. Suárez *et al.* 2009; Valdivia *et al.* 2011) or floral (e.g. Pohl *et al.* 2006; Botto-Mahan *et al.* 2011; Cares-Suárez *et al.* 2011) herbivory with another variable related to the pollination process. Explicit tests searching for statistically significant interaction terms and indirect effects in factorial experimental designs were restricted to two studies, which provided mixed results. Pohl *et al.* (2006) examined whether the artificial removal of nectar guides in the landing petal of *M. luteus* influenced pollination by the Andean Hillstar, *Oreotrochilus leucopleurus*. Their results revealed significant non-additive effects, i.e. the effects of flower herbivory showed a statistical interaction with those of hummingbird pollination. In contrast, the flower damage imposed by nectar-robbing ants on *Tristerix aphyllus* (Loranthaceae) did not affect pollination by the hummingbird *Sephanoides sephaniodes*, rejecting the hypothesis of indirect effects between ecological interactions (Caballero *et al.* 2013). A correlational study performed by González-Gómez & Valdivia (2005) suggested a negative indirect interaction between flower damage by the Austral blackbird, *Curaeus curaeus*, and pollination by the giant hummingbird, *Patagona gigas*, in *Puya coerulea* (Bromeliaceae), suggesting the need for future experimental studies.

Suárez *et al.* (2009) examined the influence of foliar herbivory on pollination in *Alstroemeria exerens* (Alstroemeriaceae). Specifically, they provided evidence that artificial foliar damage affects display and floral attraction traits, and that such characteristics are important in pollinator attraction and the duration of visits. By connecting the effects, they concluded that indirect effects between foliar damage and pollination were important in the population.

The only study focusing on the relationship between predation and pollination was that of Muñoz & Arroyo (2004), who studied experimentally the effect of lizards and insectivorous birds on pollinator visitation and seed output in the insect-pollinated shrub *Chuquiraga oppositifolia* (Asteraceae). Their results revealed that plots with lizard removal had higher pollinator visitation rate and seed output than control plots, suggesting that the presence of lizards may modify the foraging behaviour of pollinators, reducing the reproductive success of the focal plant, but insectivorous birds showed no effect.

Studies of micro- and macroevolution

Studies in this category can be classified in three subgroups. First, studies that used quantitative genetics to determine the importance of pollinator-mediated selection acting upon the

floral phenotype. For example, the role of hummingbirds and bees as selective forces acting on corolla and nectar guide traits of *M. luteus* as was examined by Medel *et al.* (2003). Likewise, Cuartas-Domínguez & Medel (2010) detected selective forces acting on the negative correlation between the labellar lobe and flower tube in the orchid *C. bletiodes*, indicating that selection promoted alternative combinations of traits. Valdivia & Niemeyer (2006) examined the presence of correlational selection between inflorescence size and amount of floral scent by estimating experimental interaction effects between traits as surrogate of selection estimates in *Escallonia myrtoidea* (Escalloniaceae). Their results revealed the absence of a significant interaction, suggesting absence of correlational selection between traits.

Cost estimates associated with trait maintenance were examined in two studies. Carvallo & Medel (2010) examined the cost involved in the maintenance of autogamy in *M. luteus*. For example, although correlated with inbreeding depression, the reduction of anther–stigma separation increased seed production, probably through the positive selection of autogamy in environments with high pollinator unpredictability. Celedón-Neghme *et al.* (2007) tested the hypothesis that the maintenance of flower size variation in *Madia sativa* (Asteraceae) within populations results from conflicting selection forces acting upon this trait; large floral ray capitula were visited more often by insect pollinators. However, in the absence of pollinators, large ray capitula had reduced reproductive success through autogamy. These results suggest that the maintenance of intra-population variation in the number of ray florets represents a balance between costs and benefits associated with this floral trait.

The second subgroup consists of studies focused on the detection of genetic variation and consequent inference of gene flow and population differentiation. These studies are scarce in the Chilean MTE. Arroyo *et al.* (2006) reported low genetic variation in populations of *Chaetanthera euphrasioides* (Asteraceae). By combining information on genetic variation and selfing levels in *Schizanthus hookeri* and *Schizanthus grahamii*, Pérez (2011) reported that while populations of *S. hookeri* show low and relatively similar selfing levels, high population differentiation and variable selfing rates are prevalent in populations of *S. grahamii*.

The third subgroup involves studies addressing patterns of phenotypic evolution in an explicit phylogenetic context. This approach has been used to infer the way morphological and reproductive traits have evolved in species of the endemic genus *Schizanthus* (Pérez *et al.* 2006, 2007, 2009). Using a molecular phylogeny and reconstructing ancestral states, the authors examined whether floral traits evolved with changes in floral visitors. Their data showed mixed results; while some lineages evolved morphology in relation to well-defined pollinators, others presented a lack of correspondence between morphology and current pollinator species. Likewise, when floral integration was traced along the phylogeny, high levels of integration were observed in pollinator-dependent species, but not in species showing autonomous selfing, which would act as a reproductive assurance mechanism when species are specialised and subject to pollinator unpredictability.

Community level and plant–pollinator networks

Studies of plant–pollinator interactions from the pollinator perspective in the Chilean MTE are still in their infancy. Ruz &

Herrera (2001) reported the foraging pattern of *Bombus terrestris* and *Bombus dahlbomii* in different localities of central Chile. Esterio *et al.* (2013) examined the potential impact of the exotic bumblebee *B. terrestris* on the pollination service provided by the native pollinator assemblage on the herb *M. luteus* during three consecutive years. Results revealed that *B. terrestris* was an inefficient pollinator in comparison to native bees due to the small amount of pollen delivered to stigmas and the low and intermittent visitation rate over the years studied. In spite of being a rapidly spreading species in Chile, *B. terrestris* was probably in the initial phase of the invasion process in the locality studied.

From the plant perspective, the first wide-scale patterns of plant–pollinator relationships were reported in Arroyo *et al.* (1982, 1985). By studying communities located at three altitudinal levels in the Andes, the authors described the reproductive biology and pollen vectors in 137 species. The visitation rate was substantially lower in the community at the highest elevation, where dipterans prevailed over other pollinator agents. Globally, hymenopterans were important pollinators for 50% of the biotic-pollinated species, flies for 46% of species and lepidopterans for 24% of species (some species can be pollinated by more than one insect group; Arroyo *et al.* 1982).

To see the big picture in the pollinator–elevation relationship, we compiled the number of pollinator species per plant species and their elevation from the 69 papers reviewed here to assess whether the number of pollinators decreases with elevation. We found that the number of pollinators per plant significantly decreases with elevation ($R^2 = 0.019$, $F_{1,239} = 4.541$, $P = 0.034$), although there is high variability across studies (Fig. 4). This outcome results from species turnover, where hymenopterans are more common and abundant at low elevations, whereas dipterans and lepidopterans become more abundant at higher elevations.

The analysis of plant–pollinator networks performed by Ramos-Jiliberto *et al.* (2010) revealed that network topology is substantially affected by elevation. For example, at higher elevation the distribution of the number of visitors per species is closer to random expectations, and pollination networks tend to be organised in few but strongly connected modules. Using the same database, Valdovinos *et al.* (2009) examined the way network structure and dynamics are affected by the removal of invasive plant species. Their results indicate that the presence of invasive species increases pollinator species and overall network persistence over time.

As interaction networks may suffer from incomplete sampling leading to biased estimates of network properties, Rivera-Hutinel *et al.* (2012) used species-based accumulation curves to estimate the extent to which six metrics commonly used in the network literature are affected by incomplete sampling. Using data from 186 flowering plants and 336 pollinator species, the authors concluded that most metrics are affected by sampling completeness but differed in their sensitivity to sampling effort, hence cautioning on studies that summarise information from databases with high, or unknown heterogeneity in sampling effort.

Pollination in anthropogenic ecosystems

Despite the increasing levels of anthropogenic disturbance in the Chilean MTE lowlands, there is a scarcity of information

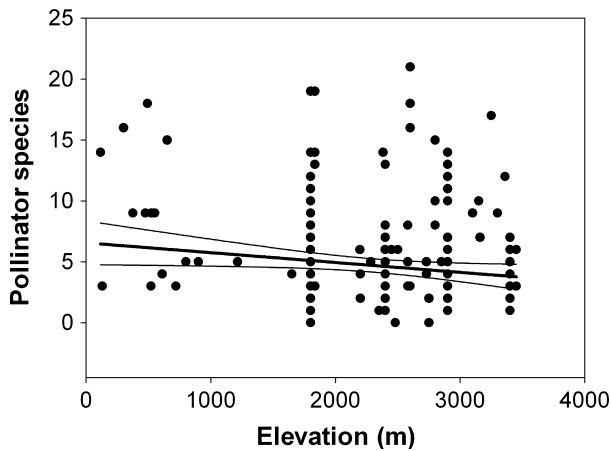


Fig. 4. Number of pollinator species per plant species as a function of elevation. Thick line represents the linear regression (slope = 0.001, $R^2 = 0.019$, $P = 0.034$) and grey lines represent its 95% confidence intervals.

for disturbed habitats or assessment of the effects of habitat disturbance on pollination. Most research on pollination is conducted above 1500 m a.s.l., where few disturbed plant populations occur, leaving lowlands less studied. Central Chile comprises a large portion of the MTE, but also contains about 79% of the country's population; this dense population concentration has led to a profound land-use change (Armesto *et al.* 2010). In this scenario, most pollination studies were conducted within the framework of habitat fragmentation (*e.g.* Valdivia *et al.* 2006, 2011), leaving degraded and transformed habitats far less studied (but see Murúa *et al.* 2010). While the effects of invasive species were studied from different perspectives, the effects of climate change were studied only in high-mountain plant populations (*e.g.* Arroyo *et al.* 2013), leaving a major knowledge gap.

Regarding habitat fragmentation, Valdivia *et al.* (2006) studied the pollination and reproductive success of *Lapageria rosea* (Philesiaceae) in continuous and fragmented populations. They concluded that both pollination rate and reproductive success were lower in fragmented forest than in the large and continuous population. Along the same lines, but this time including foliar herbivory, Valdivia *et al.* (2011) examined the distal role of forest fragmentation on foliar damage and pollination of the endemic *Bomarea salcilla* (Alstroemeriaceae). Although forest fragmentation decreased foliar herbivory, this positive effect was not sufficient to compensate for the detrimental impact of fragmentation on pollinator-mediated reproductive success.

The search for more specific interaction mechanisms among invasive and native flowering plants has been addressed in a series of studies using more restricted sets of species. For example, Molina-Montenegro *et al.* (2008) examined experimentally whether the invasive annual *Carduus pycnocephalus* (Asteraceae) gained pollinator service and increased reproduction from association with another invasive species, *Lupinus arboreus* (Fabaceae). Their results confirmed the hypothesis that the magnet species *L. arboreus* facilitated the reproduction of the associated species. In the same way, Muñoz & Cavieres (2008) tested experimentally the idea that the density of *Taraxacum*

officinale (Asteraceae), a showy alien species, had an effect on the reproductive success of the natives *Hypochaeris thrincoides* and *Perezia carthamoides* (Asteraceae). Their results indicate that while the presence of one individual of *T. officinale* around focal native individuals was neutral or promoted pollinator service and seed output, five individuals of *T. officinale* reversed the sign of the reproductive variables. These findings suggest that the reproductive impact of showy alien invasive plant species upon native species varies with the density of the alien. At the population level, Anic *et al.* (2015) studied the effect of the number of individuals on plant reproductive success (component Allee effect) using the invasive *Eschscholzia californica* (Papaveraceae) as model system. Pollination and reproductive variables were recorded in replicated patches of varying density. While pollinator visitation rate and fruit production were independent of plant density, they increased with the number of flowers in the patches, suggesting that this type of density-dependent phenomenon may help to reduce the spread rate of *E. californica*.

Taking advantage of a mosaic of coexistence patterns among the invasive *Echium vulgare* (Boraginaceae) and the native species *S. hookeri* (Solanaceae) and *Stachys albicaulis* (Lamiaceae), Carvallo *et al.* (2013) and Carvallo & Medel (2016) examined whether the presence of native species favours the pollinator visitation rate and reproduction of the invasive and *vice versa*. Results indicate that native species do not lead to an increase in visitation rate, nor reproduction of *E. vulgare*, suggesting that population persistence of the invasive species does not depend on a facilitation effect provided by native plants. The impact of the invasive *E. vulgare* on the reproduction of native species was examined by quantifying the presence of heterospecific pollen on stigmas of native species in the presence and absence of *E. vulgare*. Results revealed that in the presence of the invasive, the native species received pollen from *E. vulgare* with a reduced amount of conspecific pollen on stigmas, leading to a reduction in reproductive success.

In the context of conservation genetics, Lander *et al.* (2009, 2010, 2011) focused on the endangered endemic tree species *Gomortega keule* (Gomortegaceae) in a highly fragmented ecosystem. By using seed paternity analysis, they estimated pollen movement and dispersion kernels, concluding that insect pollinators travel outside of forest patches, beyond the scale of population fragmentation or genetic structure. Single trees play an important role as they serve as stepping-stones between fragments. They also examined pollination probabilities in places with differing land uses. The probability of a flower being pollinated was highest in pine plantations, moderate over low-intensity agriculture and native forest, and lowest over clearfells. These results suggest that pollination research in fragmented landscapes requires explicit recognition of the nature of the surrounding matrix, rather than assuming simple binary landscape models.

CONCLUSIONS

This narrative review has provided an evaluation of the current state of the art of studies on plant–pollinator relationships in the Chilean MTE. On the basis of this information it is possible to extract some conclusions, identify four major knowledge gaps and suggest potential avenues of research to develop a more complete understanding of plant–pollinator relationships

and their importance for biodiversity maintenance. The analysis of the spatial distribution of research indicates that most studies tend to concentrate in the Andes Range to the east of Santiago and the western margin of the Coastal Range, about 35.8–36.6° S. It is likely that the concentration of studies in a few conspicuous spots reflects the high intensity of land use in the Chilean MTE and an avoidance of disturbed landscapes by researchers. Here we identify a first major knowledge gap, as most of the data come from a few locations and little is known about the remaining area of the MTE. This is particularly important in Chile, as the MTE covers a large geographic extent, comprising three floristic regions with distinctive elements (Bannister *et al.* 2012), but most research is conducted in the central region. A second major gap is the low number of studies comparing disturbed and non-disturbed areas. Interestingly, 16.1% of studies focus on pollination in the context of human-induced habitat change and fragmentation, which is a relatively low figure considering that human activity is one of the most salient features of the Chilean MTE. There is a clear need to increase research from the pollinator perspective, especially in the light of recent advances suggesting a detrimental impact of the buff-tailed bumblebee, *B. terrestris*, on the native bumblebee, *B. dahlbomii* (Montalva *et al.* 2011; Morales *et al.* 2013; Schmid-Hempel *et al.* 2014). Similarly, we have a third major gap related to climate change. Only two studies (Arroyo *et al.* 1985, 2013) have explicitly addressed climate change in relation to pollination.

One of the most remarkable conclusions, and our fourth major knowledge gap, is the extremely limited or lack of knowledge of most flowering plants in the Chilean MTE. A total of 64% of the plant families that occur at the Chilean MTE remain unstudied. Even though considerable effort has been allocated to reveal the reproductive biology of many species (*e.g.* Arroyo *et al.* 1982; Arroyo & Uslar 1993; García-Franco & Arroyo 1995; Pérez *et al.* 2013), clearly more work is needed to construct basic knowledge in relation to the pollination process. This task is particularly urgent, as many species are endemic and represent the only extant species in some genera (Arroyo *et al.* 1995). In this regard, more studies are needed to determine the direct and indirect effects of invasive plants and pollinators on native flowering plants. Regarding the spatial extent of studies, most were performed on only one site, albeit some degree of spatial replication was observed in studies focused on the geographic variation of pollination features across the distribution range of plant species. Likewise, 94% of studies were conducted in only one reproductive season, some of them even encompassing just a few days, which precludes

useful generalisations on between-year plant–pollinator dynamics in the highly variable Chilean MTE.

There is a notorious absence of studies on topics related to plant demography and matrix projection analyses. For instance, to our knowledge, no study has addressed the contribution of pollination to plant population persistence in the Chilean MTE; valuable but absent information for the management of endangered populations in environments subject to high human impact. These little-studied subjects in Chile are consistent with the key questions in pollination to be addressed in the future, recently identified by Mayer *et al.* (2011) in a global review. Finally, as pollination is critical for food production and human lives worldwide (Klein *et al.* 2007; Vanbergen 2013) and directly links natural ecosystems with agricultural production systems, the ecological services provided by Chilean native pollinators need to be assessed in future studies. No information currently exists in relation to the contribution of native pollinators to crop yield in Chile, which is unfortunate as the MTE contains optimal abiotic features for the implementation of sustainable agriculture programmes. Moreover, as multiple anthropogenic pressures are primarily responsible for the general decline in insect pollinator populations, interdisciplinary research on the nature and impacts of these interactions in the Chilean MTE are needed if human food security and ecosystem function are to be preserved.

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DATA ACCESSIBILITY

Original data associated with this manuscript can be accessed at the *figshare* repository: <https://doi.org/10.6084/m9.figshare.5153968>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1. Complete references for the 69 papers included in the review. Articles are separated by the categories described in the text. Some are included in more than one category.

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