

Ecological factors affecting gene flow between populations of *Anarthrophyllum cumingii* (Papilionaceae) growing on equatorial- and polar-facing slopes in the Andes of Central Chile

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Abstract

In the Andes of Central Chile, flowering commences 1–2 months earlier on equatorial-(north-) facing than on polar- (south-) facing slopes, and pollinator assemblages also differ between these habitats. In order to understand the potential influence of these differences on gene flow, we monitored flowering periods and insect visitation rates to flowers of 60 individuals of *Anarthrophyllum cumingii* (Papilionaceae) on two equatorial- and two polar-facing slopes in the Andes of central Chile (33°35' S;70°32' W). Flowering began about 30 days earlier on equatorial-facing slopes. Flowering periods of individuals on slopes with the same aspect had a mean overlap of 0.52, while those on opposite slopes had a mean overlap of 0.15. On equatorial-facing slopes *Yramea lathionoides* (Lepidoptera) accounted for 60% of the visits to flowers of *A. cumingii*, while on polar-facing slopes *Centris cineraria* (Hymenoptera) was responsible for more than 80% of flower visits. Average similarities of visitor assemblages among individual plants on slopes with the same aspect was 0.83, while the mean similarity between individuals on opposite slopes was only 0.23. Within slopes fluorescent dyes were dispersed up to 40 m from the donor plants, but there was no movements of dyes between individuals growing on opposite slopes, even when they were separated by less than 10 m. Synchronous blooming and a common pollen vector are necessary conditions for pollen exchange between individuals. The overall probability of pollen exchange estimated by multiplying the inter-individual overlap for both factors, was nearly 0.5 for individuals growing on slopes with the same aspect, and less than 0.04 for individuals growing on opposite slopes. Consequently, at equivalent distances, the probability of pollen exchange between individuals growing on slopes of opposite aspect is more than 10-times lower than between those growing on the same slopes. Seed dispersal cannot compensate for restricted gene flow through pollination, because seeds of *A. cumingii* were dispersed less than 2 m away from a parent plant. Presumably, restricted gene flow could enhance genetic divergence between populations on slopes of contrasting aspects. This factor could be important in contributing to the high diversity and endemism in the Chilean Andes.

Introduction

Most studies on gene flow on plant populations focus on distance between individuals as the decisive factor (Levin & Kerster 1969, 1974; Schall 1975, 1980). Other factors, such as differences in flowering periods or pollen vectors, could also affect gene flow in plant populations because pollen exchange can

only occur between simultaneously flowering individuals that share a pollinator (Handel 1983). Although variation in flowering periods (e.g., Ashton 1975; Hodgkinson and Quinn 1978; Hoefs 1979; Primack 1980, 1985a, b; Herrera 1986; Fripp et al. 1986) and pollinators (e.g. Primack 1978; Linhart & Feinsinger 1980; Price & Waser 1982) frequently occur between populations or individuals of a single species, the influ-

ence of these factors on gene flow has rarely been examined (Handel 1983).

In the Andes of Central Chile, populations of many plant species that occur on equatorial- (north-) facing slopes begin their flowering earlier than their conspecifics growing on polar- (south-) facing slopes (Arroyo et al. 1981; Reader 1984; Rozzi et al. 1989). Equatorial- and polar-facing slopes in Central Chile differ sharply in microclimatic conditions (Armesto & Martínez 1978; Armesto & Gutiérrez 1978; Armesto et al. 1979; del Pozo 1985; Rozzi et al. 1989). Because insect distribution and activity are greatly influenced by temperature (Heinrich 1974, 1975, 1979; Fogleman 1982; Kingsolver 1983, 1985a, b; Pivnick & McNeill 1986, Corbet 1990, Herrera 1995), these plant populations could also differ in their insect pollinators. Likewise, along altitudinal gradients in central Chile flowers in conspecific populations at different elevations are visited by different insect species, and this variation has been related to the decrease in temperature with increasing altitude (Arroyo et al. 1982, 1985, 1987, 1990).

We set out to quantify differences in flowering periods and pollinator species between populations of *Anarthrophyllum cumingii*, a common shrub growing on both equatorial- and polar-facing slopes in the high Andes of Central Chile. We also estimated pollen and seed dispersal distances. Finally, we discuss the significance of flowering and pollinator differences for gene flow between plant populations growing on opposite slopes.

Study area

We chose two adjacent pairs of slopes of opposite aspect, located at 2500 m elevation in the Andes of Central Chile (33°35' S; 70°32' W). One pair consisted of slopes with northeast- or equatorial- (300 °) and south- or polar- (180 °) aspects, with slope angle of 27 ° and 30 °, respectively. These slopes were separated by a gorge approximately 100 m deep. The other pair of slopes had aspects of 360 ° and 180 °, and slope angle of 22 ° and 29 °, respectively, and were separated by a smooth depression, less than 3 m wide and 2 m deep. Hence, some of the individual plants growing on opposite slopes were separated by less than 10 m.

The area has a mediterranean- type climate (*sensu* di Castri & Hajek 1976) with some degree of continental influence (Rozzi et al. 1989), and is covered with snow from June to September. Vegetation consists of a

floristically rich association of low, often spiny shrubs, perennial herbs and abundant geophytes up to 3000 m found above timberline, and known as the subandean scrub (Arroyo et al. 1983). The study was conducted on *Anarthrophyllum cumingii* (H. et A.) Phil. (Papilionaceae), a small shrub about 0.5 m² in area and less than 0.2 m in height (Rozzi 1990), endemic to the Andes of Central Chile (Soraru 1974). This is one of the dominant species occurring at similar densities on both equatorial- and polar-facing slopes between 2200 m and 2900 m. It has orange-yellow solitary flowers, is partially self-incompatible (Rozzi 1990), and is pollinated only by insects (Arroyo et al. 1982). Legumes are 2 cm long, containing 1 to 5 seeds (Soraru 1974), probably dispersed by gravity (van der Pijl 1972) over short distances.

Methods

Flowering phenology

Flowering periods for 15 individuals of *Anarthrophyllum cumingii* were recorded on each of the four slopes. Every 3 or 4 days, we counted on all the open flowers within two fixed 10 × 10 cm areas on the shrub crown.

Pollinators

Flower visitors and their visitation rates to flowers were determined by two observers simultaneously monitoring *Anarthrophyllum cumingii* individuals blooming on each slope. Observations were usually made between 9 am and 6 pm, over three alternate 10 min intervals every hour. For each time interval, we recorded the number of flowers visited on each individual of *A. cumingii* and the observed pollinator species. In all, we observed 1872 flowers on 73 shrubs for 1300 min distributed among 43 h. To determine whether insect visitors carried pollen of *A. cumingii*, we captured 25 individuals of each species that visited more than 10% of the flowers, and examined them under optical and scanning electron microscopes.

Pollen flow

To estimate pollen dispersal distances, in 1987 and 1988 we studied dispersal of fluorescent dyes (see Waser & Price 1982). Each year, fluorescent dyes were dusted on anthers of 50 flowers on two shrubs on each slope, using a different color for each shrub. Dyes were

placed on a total of 800 flowers of 16 *A. cumingii* individuals. Over the two years, we collected a total of 1300 flowers from 52 shrubs at various distances from the source plant and examined their stigmas under UV light using a magnifying glass.

Estimation of similarities

To calculate similarities in flowering periods and visitor fauna between individual plants, we used the Proportional Similarity Index:

$$P_s = 1 - 0.5 \sum |P_{ij} - P_{ik}|$$

(Colwell & Futuyma 1971),

$$P_{ij} = N_{ij}/Y_j.$$

For flowering periods, N_{ij} is the number of open flowers on individual j on date i , and Y_j is the total number of open flowers counted among all census dates on individual j . For pollinator assemblages, N_{ij} is the number of flower visits made by species i on individual j , and Y_j is the total number of flower visits by pollinator species recorded on individual j .

We used this index because we wanted to compare only temporal differences in flowering periods and species composition without taking into account differences in open flower quantities or insect abundances. We calculated P_s between individual plants on the same slope or on opposite slopes, using only plants with > 10 open flowers or > 10 pollinator visits, as the index is sensitive to small sample sizes (Kohn & Riggs 1982; Rozzi 1990). Values of P_s were subjected to arcsin transformation, then analyzed by one-way ANOVA. We evaluated differences in means with the Tukey *a posteriori* test (Sokal & Rohlf 1981).

Seed dispersal

To estimate pod dispersal distances, 400 pods belonging to 20 individuals of *Anarthrophyllum cumingii* were painted with nail-polish in December 1985. Every 3 or 4 days until February 1986, the distances of fallen pods to source individuals were recorded. Dispersal of single seeds was estimated by recording the number of seeds found around shrubs. This was done by digging 1 cm deep into the soil, in 10×10 cm quadrants, placed side by side along a 4 m transect leading away from isolated *A. cumingii* individuals (more than 10 m apart from nearest conspecifics). Four orthogonal transects were made for each of 20 individuals.

In February–March 1986 and January–February 1987, two groups of 30 *Anarthrophyllum cumingii* seeds were placed next to each of six conspecific shrubs, to assess biotic dispersal. One group was placed under a wire cage with a 7×7 mm mesh allowing ants to pass but excluding birds and rodents. The other group was placed directly on the ground. We placed 50 g of crushed oats and 50 g of ‘canary-seeds’ 25 cm away from each group of *A. cumingii* seeds, to assess the presence of potential dispersal agents.

Results

Flowering periods

Flowering periods of the four *Anarthrophyllum cumingii* populations extended from October to January (Figure 1). Flowering began in early October on both equatorial-facing slopes, and 25 days later on polar-facing slopes. Flowering overlap at the population level was more than 0.5 between populations within slopes with the same aspect, but less than 0.5 between those of opposite aspect (Table 1). Temporal distributions of flowering periods differed significantly between populations on slopes of opposite aspects, but did not differ between the two polar-facing ones (Table 1). Temporal distributions also differed significantly between populations on equatorial-facing slopes, but the magnitude of the difference was lower than that found between opposite slopes.

Flowers of individuals growing on the equatorial-facing slope of the smaller depression experienced severe predation by moth larvae. This may explain the lack of flowering peak in the phenology curve of this population which contrasts with the characteristic leptokurtic curves of the other three *A. cumingii* populations (see Figure 1). The intense predation made the census of open flowers very difficult and decreased drastically the actual numbers of flowers counted. Therefore we omit this population from the analysis at the individual level, for phenology and pollinators.

Considering the phenology of each individual, flowering periods varied significantly between populations in respect to the average day that individuals: (1) started to flower ($F = 12.6$; $P \leq 0.01$), (2) presented the maximum number of opened flowers ($F = 10.8$; $P \leq 0.01$), (3) exhibited the last opened flower ($F = 7.4$; $P \leq 0.01$), and (4) the duration of their flowering periods ($F = 4.4$; $P \leq 0.01$). All these differences were significant only between pairs grow-

Table 1. Mean overlap of the flowering periods of *Anarthrophyllum cumingii* populations growing on equatorial- (Eq.) and polar- (Po.) facing the slopes of gorge (1) and the depression (2). Below each similarity value the maximal difference between accumulated frequency and the statistical significance of the difference according to Kolmogorov-Smirnov's test (Steel & Torrie 1980).

Compared pair of populations					
Eq.1-Eq.2	Po.1-Po.2	Eq.1-Po.1	Eq.1-Po.2	Eq.2-Po.1	Eq.2-Po.2
0.564	0.647	0.163	0.146	0.327	0.346
0.430	0.254	0.837	0.854	0.423	0.440
$P < 0.001$	n.s.	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$

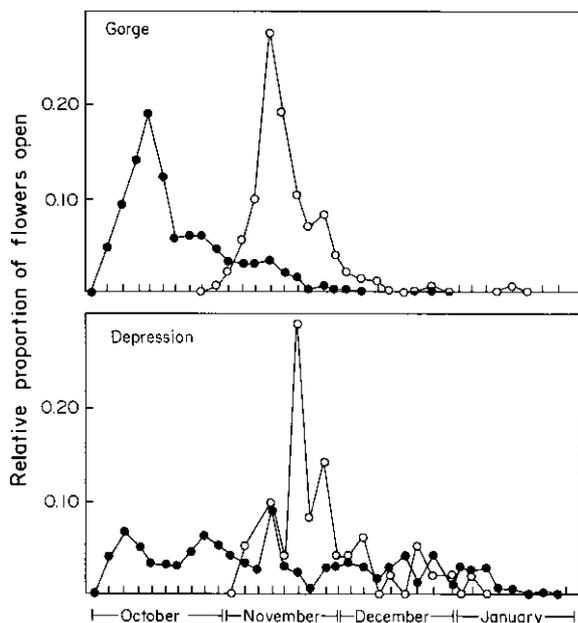


Figure 1. Proportion of total flowers produced that were open on each census date in the *Anarthrophyllum cumingii* populations on equatorial- (solid circles) and polar- (open circles) facing slopes, in each of two sites (Gorge and Depression).

ing on slopes with opposite aspect (Table 2). Shrubs growing on equatorial-facing slopes began and had their peak flowering, on the average, about 30 days earlier than shrubs on polar-facing slopes. Individuals on equatorial-facing slopes finished flowering only 10 days earlier than those on polar-facing slopes, and so the duration of their flowering periods was longer (Table 2). Mean overlaps of flowering periods between individuals growing on slopes with the same aspect were about 0.5, that is significantly higher than those, of about 0.15, between individuals growing on slopes with opposite aspect ($F = 18.9$; $P \leq 0.001$) (Table 3).

Pollinators

Flowers of *A. cumingii* were visited by one hummingbird and five insect species, one lepidopteran and four hymenopterans. Three of these species accounted for less than 1% of the visits to flowers. The lepidopteran *Yramea lathonioides* (Nymphalidae) and the hymenopterans *Centris cineraria* (Anthophoridae) and *Hypodinerus caupolicanus* (Vespidae) each represented more than 10% of the total visits. Pollen grains of *A. cumingii* were found on the bodies of individuals of these three species, although the densities of pollen grains carried were much lower on butterflies than on hymenopterans (Rozzi 1990).

Visitation rates to *A. cumingii* flowers by each pollinator species varied between opposite slopes. During November, the month when flowers bloomed simultaneously on both slopes, the greatest proportion of visits to flowers were made by *Y. lathonioides* on equatorial-facing slopes, but from *C. cineraria* on polar-facing ones (Figure 2). During November, similarities between insect visitor faunas were around three times higher between visitor populations with the same aspect than between populations on opposite slopes. Similarity was greater between plant populations on the polar-facing slopes, and the lowest similarities occurred between these populations and the equatorial-facing population of the deep gorge. Similarities of visitor assemblages to individual plants were also significantly greater between individuals growing on slopes with the same aspect ($F = 18.3$; $P \leq 0.001$) (Table 3).

Dispersal of fluorescent dyes transported by pollinators from source plants varied between 0 and 40 m (Figure 3). But, it is important to note that dyes were dispersed only between flowers on plants within each slope, and not between flowers of *A. cumingii*

Table 2. Average day (\pm standard deviation) in which individuals of *Anarthrophyllum cumingii* started to flower (Beginning), presented the maximum number of opened flowers (Peak), exhibited the last opened flower (End), and duration of their flowering periods (Duration = End-Beginning), in the populations of the equatorial- (Eq.) and polar- (Po.) facing slopes of the gorge (1) and the depression (2). Correlative values were assigned to each day starting with the same day 1 for all individuals, defining as day 1 the in which the first opened flower was observed in any of the *A. cumingii* individuals of the studied populations.

Slope	Flowering			
	Beginning	Peak	End	Duration
Eq.1 (n = 15)	8.4 \pm 11.0a	22.0 \pm 15.1a	58.5 \pm 14.4a	50.1 \pm 16.0a
Po.1 (n = 13)	36.0 \pm 14.2b	47.3 \pm 12.5b	69.5 \pm 15.2b	33.5 \pm 19.8ab
Po.2 (n = 15)	39.1 \pm 7.8b	45.9 \pm 10.3b	67.6 \pm 15.4b	28.5 \pm 18.6b

Table 3. Mean similarities (based on Proportional Similarity Index, see Methods) of flowering periods (Pf) and pollinator assemblages (Pp) between *Anarthrophyllum cumingii* individuals growing on the equatorial- (Eq.) and polar- (Po.) facing slopes of the gorge (1) and the depression (2). In each column rows followed by the same letter do not differ significantly. A global estimation for the mean probability of pollen exchange between individuals was estimated multiplying Pf by Pp.

Aspect of slopes	Compared slopes	Similarity		
		Flowering Pf	Pollinators Pp	Global Pf \times Pp
Equal:	Eq.1-Eq.1	0.462a	0.761a	0.352
	Po.1-Po.1	0.530a	0.886a	0.470
	Po.1-Po.2	0.565a	0.857a	0.484
Opposite:	Eq.1-Po.1	0.151b	0.248b	0.037
	Eq.1-Po.2	0.141b	0.219b	0.031

shrubs growing on opposite slopes. Dyes were most often found on the stigmas of other flowers in the source shrubs or in shrubs <3 m away from the source. However, a significant proportion of dyes were transported to distances longer than 10 m, mainly on equatorial-facing slopes. Remarkably, although some source individuals growing on slopes with opposite aspect were separated by <10 m, no fluorescent dye was ever found to be dispersed from equatorial- to polar-facing shrubs, or *vice-versa* (see Figure 3).

Seed dispersal

Of the painted pods 88% remained on the shrubs even after deshiscence. The others dispersed to <1 m, but none of these contained seeds. Over 90% of *Anarth-*

rophyllum cumingii seeds were found within 0.5 m of the parent shrub, and the longest dispersal distance recorded was 2 m.

In all the treatments and for the two years of study, seeds of *A. cumingii* seeds remained untouched, but crushed oats and ‘canary seeds’ were completely removed during the first 10 days. We observed ants, birds and rodents collecting or eating oats and ‘canary seeds’. Therefore, *A. cumingii* seeds appear not to be dispersed biotically.

Discussion

Flowers on individuals of *Anarthrophyllum cumingii* on equatorial- and polar-facing slopes lacked any obvi-

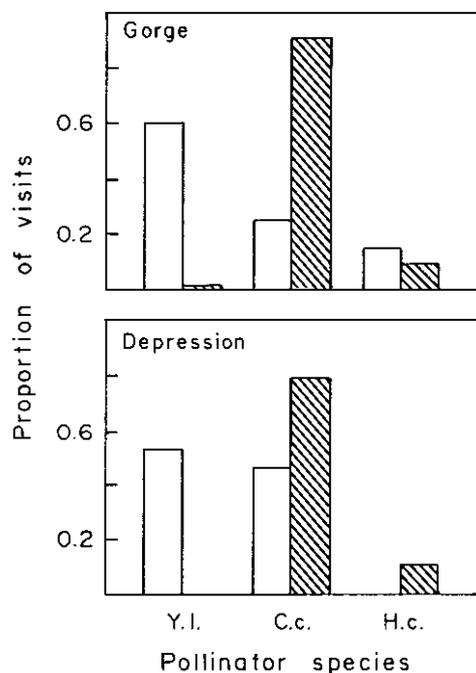


Figure 2. Proportion of visits to *Anarthrophyllum cumingii* flowers effected by *Yramea lathonioides* (Y.l.), *Centris cineraria* (C.c.) and *Hypodinerus caupolicanus* (H.c.), on equatorial - (□) and polar- (▨) facing slopes, in each of two sites (Gorge and Depression), in November 1985.

ous phenotypical differences. Although in some cases they were separated by only a few meters, they differed in their pollinating agents. Equatorial-facing slope plants received mostly lepidopteran visits, while polar-facing individuals were visited mainly by hymenopterans. This questions the 'pollination syndrome' concept (sensu Faegeri & van der Pijl 1979), and suggests that it should be used with caution, because insect visitors are often determined not only by floral features, but also by a variety of local conditions, such as microclimate (see Herrera 1995).

Differences in pollinator assemblages could effect differences in the genetic structure of populations. Neighborhood sizes might be larger on equatorial- than on polar-facing slopes due to the longer distances flown by butterflies as compared to bumblebees (Rozzi 1990). More than 90% of flights of hymenoptera pollinators were among flowers of the same *A. cumingii* individual, and less than 1% of the flights between flower visits included distances longer than 10 m. In contrast, individuals of the butterfly *Y. lathonioides* did most of their flights between flowers of different individuals of *A. cumingii*, and more than 10% of the flights between

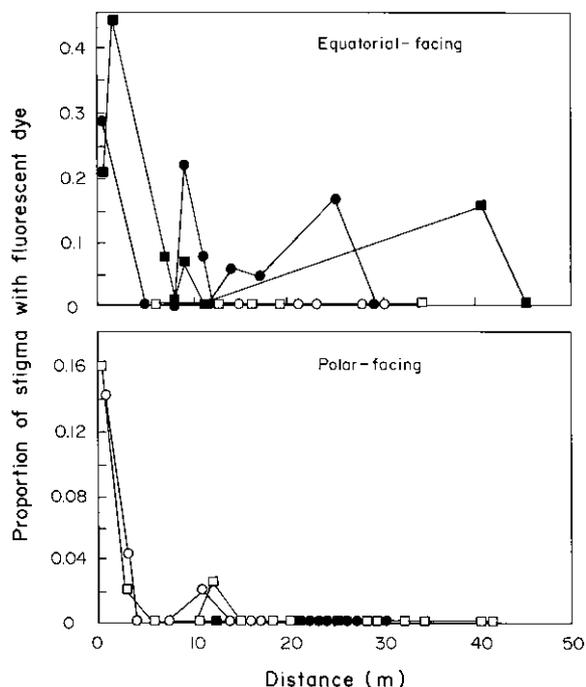


Figure 3. Dispersal distances of fluorescent dyes from 4 source (donor) individuals of *Anarthrophyllum cumingii*, 2 growing on equatorial- (solid circles and squares) and 2 growing on polar- (open circles and squares) facing slopes. The X axis indicates distances of receiving flowers from the source individuals. The Y axis values correspond to the proportion of examined flowers that received dyes coming from each of the 4 source individuals. Results for receiving flowers located on the equatorial facing slope are showed in the upper graph, and for receiving flowers on polar facing slopes are represented in the bottom one.

visits to flowers were over distances longer than 10 m (Rozzi 1990). The longer distances flown by butterflies may account for the longer dispersal distances of fluorescent dyes recorded in populations growing in equatorial-facing slopes (see Figure 3). These differences in flight behavior among pollinators (see also Schmitt 1980; Waser 1982), together with smaller pollen loads carried by butterflies (Courtney et al. 1982; Wiklund et al. 1981; Jennersten 1984; Murphy et al. 1984; Rozzi 1990), could determine variation in the quantity and quality of pollination and seed production (Waser 1983; Oshawa & Namai 1987), which could be significant for the reproductive success in Andean zones of 'high environmental stress' (Arroyo et al. 1988).

Although panmixis constitutes an ideal model for natural populations (Schaal 1975), it has been shown that genetic cohesion of populations could be maintained under extremely low gene flow levels (Slatkin

& Maruyama 1975; Slatkin 1985; Varvio et al. 1986). How low gene flow levels must be to permit genetic differentiation and speciation will depend on the intensity of selective pressures leading to divergence (Ehrlich & Raven 1969, Mascie-Taylor et al. 1986), ecological factors, and the biology of the organisms (Loveless & Hamrick 1984). Although in this work we did not measure effective gene flow levels, we evaluated ecological factors that affect gene flow. Overlap in flowering periods and pollen vectors are both necessary conditions for pollen exchange between individuals. Both overlap indices can be multiplied to obtain a global estimate of the probability of pollen exchange (Table 3). The product of both indices of overlap was higher than 0.4 for individuals growing on slopes with the same aspect, but was less than 0.04 for those growing on slopes with opposite aspect. Consequently, pollen exchange between individuals growing on slopes of opposite aspect would be more than 10 times lower compared to that between individuals on slopes of the same aspect. Pollen flow is likely to be the principal component of gene flow in populations of *A. cumingii*, because estimated pollen dispersal distances were much greater than seed dispersal distances. Thus, a reduction of pollen flow could severely limit gene flow.

Three characteristics in the *A. cumingii* system could favor a reduction in gene flow, potentially leading to genetic differentiation and speciation. First, differences in flowering periods and pollinator species would be maintained from year to year, because they are related to microclimatic differences between opposing slopes (Rozzi et al. 1989, Rozzi 1990). These habitat differences may be a general phenomenon over broad areas with mountainous topography as in central Chile. Supporting this generalization, the magnitude of the displacements of flowering periods between *A. cumingii* populations on opposite slopes reported here are similar to those recorded by Arroyo *et al.* (1981) for the same species between equatorial- and polar-facing slopes in the same area in 1978–1979. Differences in pollinator assemblages between opposite slopes were also consistent through 1986–1988 (Rozzi 1990). Second, the long-term maintenance of these phenological and pollinator differences would determine a high level of endogamy that would generate low intra-population and high inter-population genetic variability (Brown 1979 in Soltis & Bloom 1986). The contrast between intra- and inter-population genetic variability should be more pronounced in self compatible species (Hughes & Richards 1988; Abbot &

Gomes 1989; Clay & Levin 1989), and *Anarthrophyllum cumingii* is a partly self compatible species (Rozzi 1990). The degree of self compatibility associated with reduced gene flow may produce a subdivision of the population to subpopulations, decreasing effective population sizes and increasing homozygosity (Kerster & Levin 1968; Schaal 1975; Varvio et al. 1986; Bos & Haring 1988). Third, microclimatic differences between slopes may determine changes in ‘selective pressures’ and favour speciation through disruptive selection (Nevo et al. 1982), which in turn would be promoted by a reduction in gene flow (see Barton & Charlesworth 1984; Mascie-Taylor et al. 1986). If the speciation mechanisms are operating, and flowering and pollinators differences increase the probability of genetic differentiation, this could contribute to the high levels of plant diversity and endemism in the Chilean Andes (Arroyo et al. 1984, 1988), and possibly other mountain regions of intermediate latitudes.

It is interesting to note, however, that populations on contrasting slopes show little, if any phenotypic variation. If this pattern reflects a lack of genetic differentiation, how do *A. cumingii* populations remain undifferentiated despite a major reduction in gene flow? Ehrlich and Raven (1969) suggested that gene flow is subordinated to other factors in maintaining genetic cohesion within species. Adaptive genetic combinations could be maintained in populations independent of gene flow levels. Long-lived plant species with complex development are genetically very conservative (Loveless & Hamrick 1984), probably due to ontogenetic constraints. *A. cumingii* is a long lived species, and the situation described in this work would provide an ideal test of this hypothesis as an alternative to speciation mechanisms that emphasize genetic differentiation.

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