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Flowering phenologies of hummingbird plants from the temperate forest of southern South America: is there evidence of competitive displacement?

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Plant species sharing pollinators may compete through pollination. This type of competition may lead to overdispersed flowering phenologies. However, phenological segregation is difficult to detect in seasonal climates. We compared patterns of phenological overlap in assemblages of ornithophilous plants from three localities of the temperate forest of southern South America with those generated by four different null models. These species were all visited and presumably pollinated by a single species, the hummingbird *Sephanoides sephaniodes*, which makes this situation ideal to evaluate the role of pollination-mediated competition. For one site, we compiled data on flowering phenologies for three different years. Three models considered the flowering period of the whole assemblage of ornithophilous plants as the phenological window within which flowering phenologies were randomized, but made no further assumptions on how species should be distributed within that temporal frame. The fourth model assigned differential probabilities to different time intervals based on the flowering onset of non-ornithophilous plant species. Observed mean pairwise overlaps for all localities and years were well within the interval defined by the 2.5 and 97.5% percentiles of the randomized distribution of expected mean pairwise overlaps according to models 1–3. However, model 4 showed a consistent trend towards overdispersion of ornihophilous phenologies, which show a shift towards mid- to late-summer flowering. Thus, to the extent that the distribution of flowering of non-ornithophilous species reflects the constraints imposed by a highly seasonal climate, our results provide support to the proposal that pollinator sharing may cause evolutionary displacement or ecological sorting of flowering phenologies. Other factors, such as phylogenetic inertia, could also contribute to explain extant phenological patterns in the highly endemic ornithophilous flora of the temperate forest of southern South America.

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Plant species sharing one or more pollinators may compete through pollination. The mechanisms involved include the dilution of pollinator visits – when pollinator availability becomes a limiting resource – and improper pollen transfer. This last mechanism may affect pollination through 1) the deposition of hetero-

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specific pollen on a flower's stigma that may interfere with a species' own pollen germination and pollen tube growth (Waser and Fugate 1986, Feinsinger and Tiebout 1991, Murphy and Aarsen 1995, McLernon et al. 1996), and 2) the loss of pollen to heterospecific stigmas and other flower parts (Murray et al. 1987, Armbruster et al. 1994, Murcia and Feinsinger 1996).

It has been suggested that competition through pollination may lead to the staggering of flowering phenologies in a given plant assemblage through either the evolutionary displacement of blooming times or through an ecological sorting process that eliminates inferior competitors from communities leading to the coexistence of plant species that minimize flowering overlap. However, the influence of this type of competition on community patterns of flowering phenology and the appropriate methods to detect these patterns remain controversial (Stiles 1977, Poole and Rathcke 1979, Gleeson 1981, Thomson and Rusterholz 1982, Fleming and Partridge 1984, Pleasants 1990, Stone et al. 1998).

Although competition for pollination as a factor influencing phenological patterns of flowering has arguably received the most attention in the ecological literature, it is not the only force likely to influence these patterns. Positive interactions, particularly indirect facilitation mediated by pollinators, can also potentially affect phenological patterns, although with an effect opposite to that produced by competition (i.e. aggregation and high overlap of flowering times; Moeller 2004). Flowering phenology may also be molded by abiotic environmental factors such as climate, probably the most important factor affecting flowering times (Rathcke and Lacey 1985, Fenner 1998). Even in the aseasonal tropics climatic conditions change, albeit subtly, over the year, greatly influencing flowering phenology (Bawa 1983, Ashton et al. 1988). However, this is more apparent in temperate environments where temperature becomes both an important proximate cue and an ultimate selective factor influencing plant blooming (Lechowicz 1995, Diekmann 1996) and reproductive success (Totland 1994).

The analytical tools to explore assemblage patterns in flowering of plants sharing pollinators have evolved from observational (Stiles 1977, Schemske et al. 1978) to the use of null models (Armbruster 1986, Armbruster et al. 1994, Gotelli and Graves 1996, Gotelli 2001). Typically, these models contrast an index characterizing the degree of overlap observed between the flowering phenologies of a set of co-occurring plant species with a statistical distribution of the index generated by randomization of flowering periods over the blooming season. An extremely small percent of values of the index that are lower than, or equal to the observed value would reflect an unexpected pattern of staggered flowering phenologies, consistent with the pollinator-mediated competition hypothesis. Except for a few examples that show extreme overdispersion (Ashton et al. 1988, Stone et al. 1998), null models of flowering phenologies have been extremely difficult to falsify (Poole and Rathcke 1979, Rathcke 1984, Pleasants 1990).

The dearth of falsification by null model analyses may be due either to the fact that competition through pollination is irrelevant in molding flowering phenologies or that existing null models are not sensitive enough to detect the signal of competition against a multitude of selective factors and constraints. First, the role of competition in structuring communities may be underestimated because extant plant assemblages are in part the result of the resampling of species from a pool that could have already being structured by competition (the "Narcissus effect"; Colwell and Winkler 1984). Second, assemblage patterns are usually influenced by strong phylogenetic inertia that conditions and limits the evolutionary response of species to any selection force (Kochmer and Handel 1986). Third, climate seasonality may impose a strong constraint on flowering (Rathcke and Lacey 1985, Fenner 1998). Thus, even though competition through pollinator sharing can also affect flowering times in highly seasonal environments, null models that fail to incorporate this seasonality will also fail to detect the consequences of this indirect pollinator-mediated, plant-plant interaction. So far, null models have included seasonality in a raw fashion at best by restricting randomized phenologies to the flowering period observed for the whole plant assemblage (Rathcke 1988, Pleasants 1990). However, this approach might be insufficient to capture the strong climatic changes that usually occur within any flowering season in temperate regions.

Here we analyze patterns of flowering phenologies of plants sharing a hummingbird pollinator from different localities of the temperate forest of southern South America (hereafter TFSSA). This temperate biome, which extends between 37 and 55°S along the Pacific rim of South America, is characterized by one of the highest incidences of bird pollination (ornithophily) known for any flora worldwide (Armesto et al. 1996, Aizen et al. 2002). Paradoxically, this rich guild of ornithophilous plants shares only one major pollinator, *Sephanoides sephaniodes*, the southernmost hummingbird in the world and the only hummingbird native to the TFSSA. Typically, the number of ornithophilous plant species increases from the eastern-most xeric boundary of this biome at the eastern foothills of the Andes, to the western-most mesic boundary of this biome at the Pacific coast (Aizen et al. 2002). Along this strong E-W precipitation gradient there is also a turnover of forest types and plant species (Aizen and Ezcurra 1998) allowing us to assess phenological patterns in ornithophilous assemblages, which not only vary in their total number of plant species and composition but also in other environmental and biological aspects.

In addition, the search for strict repetitive time sequenes in the order of flowering among a set of ornithophilous species shared by geographically-distant and somewhat different assemblages, let us make inferences on the role of phylogenetic inertia in community structure (Kochmer and Handel 1986).

We applied four different null models to assess flowering patterns in these ornithophilous pollinator assemblages. Seasonality is built in these models either by simply restricting flowering times of individual species to the observed blooming period for the whole assemblage or by assigning changing probabilities of blooming over the year based on the flowering onset of non-ornithophilous species. Here we addressed the following questions: 1) are patterns in flowering phenology in the ornithophilous flora of the TFSSA consistent with the pollinator-mediated competition hypothesis? 2) Does consistency of the observed patterns with the pollinator-mediated hypothesis depend on how seasonality is built in a null model? 3) Are the flowering sequences of species consistent between years and across different communities?

Methods

Data

We used phenological data on ornithophilous plants growing in the northern region of the TFSSA. These data came from four studies conducted at three different sites along a longitudinal band: a study by Aizen and Rovere (unpubl.) in Puerto Blest, Nahuel Huapi National Park, Argentina (41°01′S, 71°50′W) and a study by Ruffini (1992) in the same area (hereafter Blest); a study by Riveros (1991) in Termas de Puyehue, Puyehue National Park, Chile (40°42′S, 72°19′W, hereafter Puyehue); and the studies by Smith-Ramírez (1993) and Smith-Ramírez and Armesto (1994) in the Cordillera de Piuchué, Chiloé Island, Chile (42°50′S, 74°10′W, hereafter Chiloé). Blest and Puyehue are ca 50 km apart, and Chiloé is ca 300 km from both sites.

The ornithophilous species included in these studies as well as their flowering months in the different localities are listed in Table 1. These species include vines, epiphytes, shrubs and treelets and share all or most of the traits that characterize the flowers pollinated by hummingbirds (Proctor et al. 1996): tubular red or orange corollas, copious amounts of diluted nectar, and lack of odor. Most of these species are self-incompatible and although some of them are also visited by insects, the hummingbird *S. sephaniodes* is the main flower visitor and presumably their most effective pollinator (Riveros 1991, Smith-Ramírez 1993). This hummingbird has also been observed to transport the pollen of all the species listed in Table 1 (Ruffini 1992, Smith-Ramírez 1993, Aizen and Rovere unpubl.).

Because these studies were conducted by different authors, in different localities and different years, they also differ in how phenologies were recorded. At Blest, Aizen and Rovere (unpubl.) counted flowers on tagged branches or whole plants from 10 individuals per species at about weekly intervals over two flowering seasons 1998/1999 (mid August–late May; 42 sampling intervals) and 1999/2000 (late August–late May; 36 sampling intervals). A similar procedure was used by Ruffini (1992) to estimate flowering phenology at the same area, with the exception that she sampled at biweekly intervals during the 1988/1989 flowering season (mid September–mid May; 16 sampling intervals). In Puyehue, Riveros (1991) monitored the presence or absence of open flowers in tagged branches or whole plants of 3–10 individuals per species once every two weeks during the 1987/1988 season (mid September–early March; 12 sampling intervals). However, her data were reported qualitatively as the period when a given species was found in flower (Riveros 1991, Riveros and Smith-Ramírez 1996). Finally, Smith-Ramírez (1993) monitored the presence of flowers in 7–8 individuals per species at monthly intervals from December 1986 to November 1988. Here, we included only her complete phenologies corresponding to the 1987/1988 flowering season (September–April; 8 sampling periods). We

Table 1. Ornithophilous plant species present in each of the three localities of the temperate forest of southern South America. Information on the flowering period observed at each site is included.

	Blest	Puyehue	Chiloé
Asteranthera ovata (Gesneriaceae)	Jan–Feb	Nov–Jan	Oct–Mar
Campsidium valdivianum (Bignoniaceae)	Aug–Dec	–	Sep–Mar
Crinodendron hookerianum (Elaeocarpaceae)	–	–	Nov–Dec
Desfontainia spinosa (Desfontainiaceae)	Jan–May	–	Jan–Mar
Embothrium coccineum (Proteaceae)	Nov–Dec	Nov–Jan	Nov–Jan
Escallonia rubra (Escaloniaceae)	Dec–Feb	–	–
Fascicularia bicolor (Bromeliaceae)	–	–	Feb–Apr
Fuchsia magellanica (Onagraceae)	Nov–May	Nov–Feb	Jan–Mar
Mitraria coccinea (Gesneriaceae)	Dec–Feb	Jan–Feb	Dec–Mar
Notanthera heterophylla (Loranthaceae)	–	–	Oct–Feb
Philesia magellanica (Philesiaceae)	–	–	Dec–Feb
Raphitamnus spinosus (Verbenaceae)	–	Sep–Nov	Oct–Dec
Sarmienta repens (Gesneriaceae)	–	Nov–Feb	Oct–Mar

excluded the phenology of the ornithophilous mistletoe *Tristerix corymbosus* from the Chiloé and Puyehue data sets because this parasitic plant flowers all year around (Chiloé) or during most of the year (Puyehue). Being the only plant species that is in full bloom during the main course of the winter in the TFSSA (Aizen 2003), its inclusion in the analysis could result in a segregated flowering pattern that might reflect seasonal climatic constraints rather than any consequence of pollinator-mediated, plant-plant interaction. It is within these constraints that we aimed at assessing any signature of this indirect form of interaction. Information on the onset and months of flowering from the non-ornithophilous species was obtained from Brion et al. (1988), Riveros (1991) and Smith-Ramírez and Armesto (1994) for Blest, Puyehue, and Chiloé, respectively (Fig. 1).

We standardized ornithophilous phenologies, so that the sum of either the number of flowers or individuals in flower counted over the flowering period of each species equaled one. For Puyehue, where data were binary (i.e. plants were recorded only as flowering or not flowering in a particular flowering period), we assumed either a uniform or a symmetric binomial distribution of flowers over the blooming period of each species. For instance, if a species flowered over five time intervals to fit a binomial distribution we assigned to the first interval the probability of 0 events occurring out of four events, the second the probability of one event, and so on, assuming that each event has a $p = 0.5$.

Following Pleasants (1990), we estimated the overlap (O) between any species pair (sp. i and sp. j) according to

$$O_{ij} = \sum_{t} \min(p_{it}, p_{jt}),$$

where p_{it} and p_{jt} are the proportions of either flowers or flowering individuals of species i and j occurring at time interval t. This index ranges from 0 when there is no phenological overlap, to 1 when there is complete overlap between any given pair of species. For each community and year, we estimated mean pairwise overlap averaging the overlaps between all possible pairwise

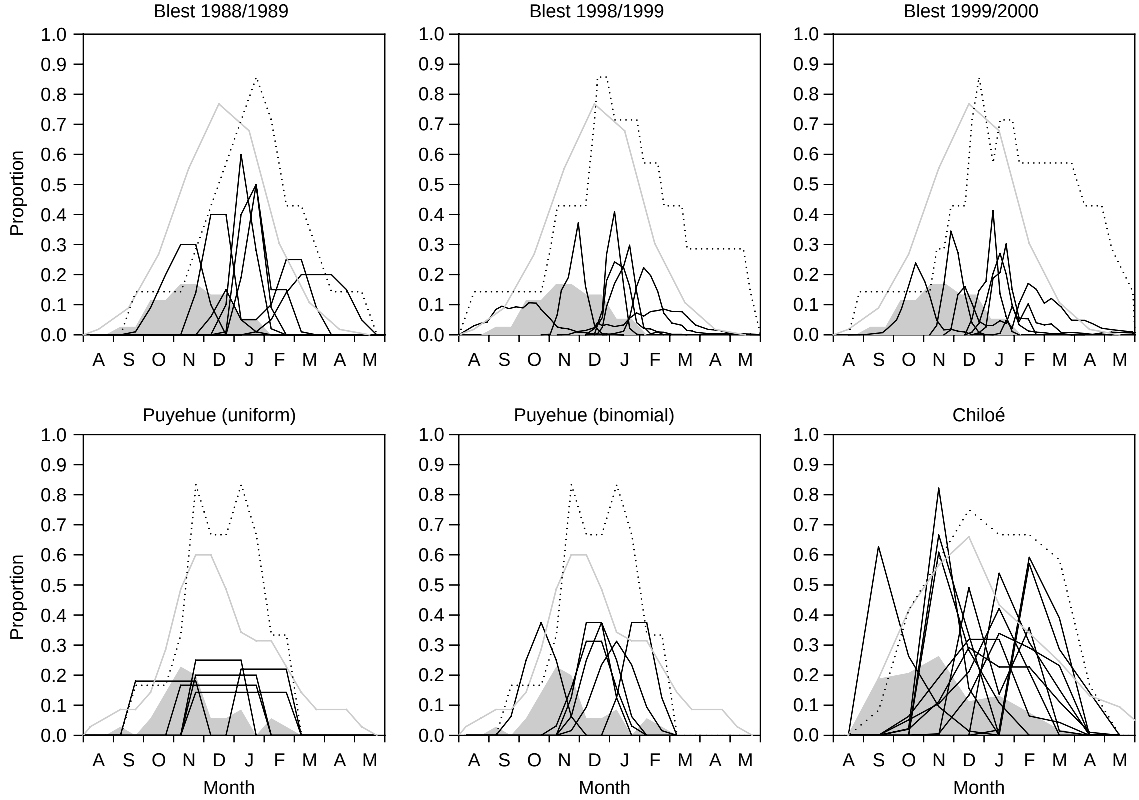

Fig. 1. Flowering phenologies (black lines) of the ornithophilous plant species from three localities (over three years for Blest) of the temperate forest of southern South America (species lists in Table 1). The dotted lines indicate the proportion of all the ornithophilous species studied at each of the three localities ($n = 7$ species for Blest; 6 for Puyehue; and 12 for Chiloé) found in flower over the extent of the flowering season. The gray solid lines indicate the proportion all sampled non-ornithophilous species found in flower at each sampling interval from August to May at each locality ($n = 56$ species for Blest, 35 for Puyehue, and 53 for Chiloé). The gray-filled curves represent the proportion of all sampled non-ornithophilous species that begin flowering in a given time interval. These latter curves were used as probability functions for assigning random starting flowering intervals to ornithophilous species according to null model 4 (see Methods).

combinations of species (Pleasants 1990). This observed mean pairwise overlap was compared with a frequency distribution of 1000 mean pairwise overlaps obtained from randomized flowering phenologies, as described below.

Null model analyses

We generated randomized phenological patterns according to four null models. Algorithms were written in the Matlab/Octave language and along with the phenological data sets used as inputs are available from the authors upon request. All models were based on the randomization of the start of flowering periods and conservation of the duration and shape of each species' phenology curve. The first three models assumed that the probability of flowering was uniform among periods and species, and differed in the rules of whether and how species' phenologies overlapped the limits of the phenological period. In all four models the flowering season was defined for each community and year as the period between the start of the flowering period of the first ornithophilous species to bloom in the flowering season and the end of the flowering period of the last species to bloom.

In null model 1 (the "wrap-around" model), a species' phenology could spill over the extremes of the flowering season, so that if it started flowering in a period too close to the end of the flowering season to fit the entire length of the species' phenology, flowering could continue at the start of the flowering season. The fact that species could spill over the limits of the flowering season increases the expected dispersion of randomized phenologies. However, if no species spilled over the end of the flowering season and the first or last few flowering periods were not occupied by any species, the length of the randomized flowering season could be shorter than the observed flowering season. Although this model may produce disjoint randomized flowering phenologies, it is the only one based on a complete uniform distribution, because even the extreme intervals of the entire flowering season have the same probability to be occupied by as many species as any other middle interval. Thus, it constitutes a benchmark for comparison with the other three models.

In null model 2 (the "bounded" model), species were not allowed to exceed the limits of the flowering season. This was achieved by shortening the period in which a species could start flowering by the length of its flowering phenology. As in the previous model, the length of the randomized flowering season could be equal to, or shorter than the observed flowering season if no species occupied the first or last flowering periods, but never longer. Thus, bounding in this model increases expected overlap among randomized phenologies.

In null model 3 (the "fixed-length" model), species were not allowed to exceed the limits of the flowering season, as in model 2. In addition, it was required that at least one species flowered in the first and the last flowering interval, so that the randomized flowering season had exactly the same length as the observed flowering season. This was achieved by picking and reassigning at random a species' phenology if either the first or last time interval remained vacant. The latter process was repeated as many times as necessary until the extreme intervals were occupied by at least one species. Under this model, the expected overlap among randomized phenologies should be lower than in null model 2, but higher than in null model 1.

The fourth model (the "unequal-probability" model) assumed that the probability of any species to start flowering at a particular flowering period was proportional to the number of non-ornithophilous species that started flowering in that period. No other restrictions were imposed to the model except that, like model 2, species' phenologies could not exceed the extremes of the flowering season observed for the whole ornithophilous assemblage. Because non-ornithophilous species in principle cannot compete with ornithophilous species for pollinators, and because environmental conditions could affect species not sharing pollinators in similar ways, this model allowed us to generate expected overlap values for a situation in which species phenologies are presumably determined principally by environmental factors. In particular, the number of species in flower in the TFSSA is strongly influenced by temperature (Smith-Ramírez and Armesto 1994). Thus, the expected overlap in this model, and how it compares with the previous three models, will depend on the distribution of flowering phenologies of non-ornithophilous species along the flowering season. If, for example, flowering of non-ornithophilous species were uniformly distributed along the flowering season, the amount of overlap expected under this model would be similar to that expected under model 2. If, in contrast, flowering of non-ornithophilous species were highly aggregated with a well-defined peak, randomized flowering phenologies would exhibit a high degree of overlap.

Cross-correlations

We used correlation analysis to study the consistency in the flowering sequence of the ornithophilous species of the TFSSA between years (Blest) and sites (Blest vs Chiloé). For these comparisons, we excluded the data from Puyehue because this community shared only four species with either Blest or Chiloé. We analyzed the time of flowering initiation and peak flowering using Spearman rank correlations considering August as month 0.

We also evaluated the constancy of patterns of species pairwise overlap using Mantel correlations because overlaps between all possible species pairs are not independent estimates. The specific question posed here was whether pairwise phenological overlap among species was correlated among years or sites.

Results

Although the flowering of the study ornithophilous plant assemblages extends over a prolonged period (from late winter to late autumn), it is most apparent during summer months, from December to February. Particularly, the flowering of the ornithophilous species seems to be relatively more frequent and well-distributed during those months than the flowering of the non-ornithophilous species as a group, which shows a very clear and distinctive peak in late spring in all three communities (Fig. 1).

Mean observed pairwise overlaps of the ornithophilous species ranged between 0.3089 (Blest 1998/1999) and 0.5406 (Puyehue, uniform). These observed values were within the expectations generated by null models 1–3 (Fig. 2). Particularly, we could not reject any of the null hypotheses associated with these three models. Thus, there was no evidence from our datasets that flowering phenologies of ornithophilous assemblages of the TFSSA were overdispersed based on these results, as predicted from pollinator-mediated competition theory.

In contrast to results for models 1–3, a clear trend towards a staggered pattern of flowering phenologies emerged when randomizations were run according to the distribution of the flowering onset of the non-ornithophilous species (model 4). In Blest, we found that only a low percent of the expected values of the overlap index resulting from model 4 were lower than, or equal to, the observed values (5.8% for 1988/1989, 8.4% for 1998/1999, and 3.7% for 1999/2000). For Puyehue, none of the 1000 randomly-generated values were lower than the observed value in the case of the uniform-shaped flowering phenologies, and only two values were smaller than the observed value in the case of the binomial-shaped flowering phenologies. Thus, the highly significant result produced by model 4 for this particular assemblage was not influenced by the exact shape of the flowering phenologies. Lastly, in Chiloé observed mean pairwise overlap was lower than any of the expected values generated by this null model (Fig. 2).

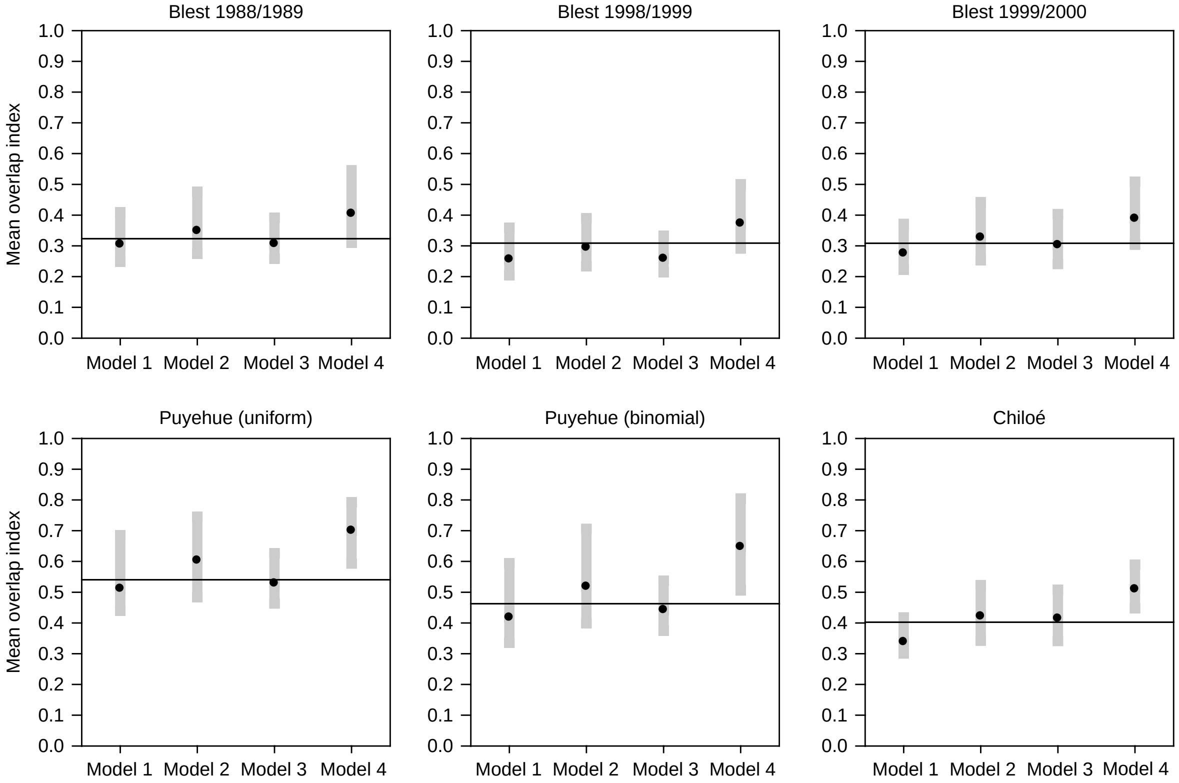

Fig. 2. Results of null model analyses (see Methods) for each of the three ornithophilous plant assemblage analyzed (over three years for Blest). Dots represent the mean value and gray bars the range between the 2.5 and 97.5% percentiles of the randomized distribution of expected mean pairwise overlap. Solid lines indicate observed mean pairwise overlaps.

More generally, our results exhibited some consistent trends according to the null model used. Whereas the means of the expected distributions of the mean pairwise overlap produced by model 1 were smaller than the observed means, the expected mean values of the index for model 2 were larger except in one case (i.e. Blest 1998/1999; Fig. 2). Null model 3 produced narrower distributions and mean values that were intermediate between those generated by models 1 and 2. Means from model 4 were always greater than the observed values (as described above) and the expected means of the distributions from models 1–3 (Fig. 2).

Correlation analyses showed an extremely high degree of consistency between years in the sequence of flowering, time of peak flowering, and pairwise overlap in Puerto Blest (Table 2). Cross-correlations between Blest and Chiloé also proved that the sequence of flowering peaks for the species shared in common between these two localities was similar. Results also showed that species pairs exhibiting a low (or a high) overlap in Blest also tended to exhibit a low (or a high) overlap in Chiloé.

Discussion

Patterns of flowering phenology in assemblages of ornithophilous plants from the TFSSA do not minimize mean pairwise species overlap and, therefore, are not unexpectedly overdispersed according to models that take into account the length of the flowering season but do not make any further assumption on how flowering phenologies are distributed within the observed flowering season. In particular, we were unable to reject any of the null hypotheses associated with models 1–3 for any of the three plant assemblages studied. Furthermore, in one of the assemblages analyzed (Blest) results were the same over three different flowering seasons. However, a consistent pattern of staggered ornithophilous flowering phenologies emerged over sites and years when randomizations were performed based on probabilities generated by the flowering onset of the non-ornithophilous species. This pattern involves the presence of a relatively high proportion of ornithophilous species with mid- and late-summer flowering phenologies (Fig. 1). Thus, to the extent that the non-ornithophilous species flower mostly independently of each other and their phenologies reflect the overriding influence of climate, we found an overdispersed flowering pattern among plants pollinated by the hummingbird *Sephanoides sephaniodes*, as predicted by the pollinator-mediated competition hypothesis. Interestingly, this pattern emerged independent of the different methods used to measure and characterize phenology in each of the three assemblages studied.

In contrast to previous null model analyses of flowering phenologies, which have incorporated seasonality by simply restricting randomizations to the observed flowering period for the whole assemblage (as our models 1–3; Rathcke 1988, Pleasants 1990), our fourth model considers varying probabilities of blooming over the season as explained above. As an alternative, we might have modeled this probability function based on the expected ecophysiological response of the species to environmental variables, such as photoperiod, temperature, or water availability in the absence of any other factor. At least in the TFSSA, no single abiotic environmental factor appears to determine flowering patterns, however. Flowering in this biome clearly reflects the rapid spring increase in temperature, with most species blooming in November–December, during the transitional period between the relatively wet early spring and dry summer, and few insect-pollinated species flowering from mid to late summer (Smith-Ramírez and Armesto 1994, Riveros and Smith-Ramírez 1996) despite high availability of insect pollinators (Aizen 2001). What determines the lack of many non-ornithophilous species flowering during the summer is unknown. Whatever these factors are, the use of a single environmental variable to generate flowering probabilities for the null model would have been an oversimplification and the use of two or more would have probably involved too many assumptions. On the other hand, the composite flowering curve of non-ornithophilous species, which are mostly pollination generalists (Aizen et al. 2002, Smith-Ramírez et al. 2005), provides a simple, empirical and direct measure of seasonal variation in flowering conditions as perceived by the plants themselves.

Table 2. Spearman rank correlation coefficients (r_s) of the onset and peak of flowering, and Mantel correlation coefficients (r_m) of pairwise species overlap between years (Blest only) and sites (Blest vs Chiloé) of ornithophilous plant species.

Comparison	Onset		Peak		Pairwise overlap	
	n	r_s	n	r_s	n	r_m
Between years						
Blest 1988/1989 vs Blest 1998/1999	7	0.972***	7	0.972***	21	0.899***
Blest 1988/1989 vs Blest 1999/2000	7	0.972***	7	0.963***	21	0.893***
Blest 1998/1999 vs Blest 1999/2000	7	1.000***	7	0.972***	21	0.948***
Between sites						
Blest 1988/1989 vs Chiloé	6	0.559	6	0.986***	15	0.599*
Blest 1998/1999 vs Chiloé	6	0.522	6	0.956***	15	0.732***
Blest 1999/2000 vs Chiloé	6	0.522	6	0.956***	15	0.711***

Although we found a consistent pattern of overdispersed flowering phenologies according to one of our models, we should ask whether there is any evidence for the process and mechanisms that might generate the observed flowering pattern (Waser 1978, Waser and Fugate 1986, Feinsinger and Tiebout 1991, Caruso 1999). In Blest, flowering sequences of species were highly correlated among years, so temporally predictable pollinator-mediated plant-plant interactions between particular species pairs are possible in this assemblage (Table 2). In addition, pollen of each ornithophilous species is transferred to the stigmas of at least one other ornithophilous species, showing that improper pollen transfer is taking place. Most importantly, reproductive levels of the majority of these species in this particular assemblage are depressed during periods of high phenological overlap (Aizen and Rovere unpubl.). Even though the latter results are of a correlative nature, they suggest that the process and some of the mechanisms involved in the pollinator-mediated competition hypothesis are indeed occurring in these plant assemblages.

In addition to divergent flowering periods, one potential "axis" of differentiation among plants sharing a major pollinator is flower architecture. Particularly, similarity in the placement of sexual parts (i.e. anthers and stigmas) among flowers of different co-occurring species is expected to affect the magnitude of heterospecific pollen transfer by determining the site where pollen is placed on, and then picked up from a pollinator's body (Murray et al. 1987, Armbruster et al. 1994, Murcia and Feinsinger 1996). Ruffini (1992) found, however, that most species visited by *S. sephaniodes* at Blest deposited pollen indistinctively on the distal part of the beak, crown and throat of this hummingbird. She also collected samples with pollen from two or three species intermixed on the bird's body. In addition, segregated pollen placement on a pollinator does not necessarily translate into differential pollen transfer to stigmas. As shown by the elegant experiments of Murcia and Feinsinger (1996) with captive hummingbirds and flowers from a tropical plant assemblage, most pollen from a focal flower is lost during the first heterospecific visits irrespective of similarity in sexual architecture or placement of pollen on the bird among plant species. Therefore, there is nil or at most little evidence that differentiation in flower morphology could weaken selection for divergent flowering phenologies in hummingbird plant assemblages in general, and in ours in particular.

The flowering of many ornithophilous species during the summer and early autumn in the TFFSA (Table 1) could have been facilitated by the fact that the hummingbird *Sephanoides sephaniodes* is active year-round (Ruffini 1992, Smith-Ramírez 1993). However, hummingbird populations, at least in the Nahuel Huapi area, peak in the autumn (Aizen 2003), when the number of species and flower abundance of hummingbird-pollinated plants decline (Ruffini 1992). An exception is the hummingbird-pollinated mistletoe *Tristerix corymbosus*, the only plant species that is in full bloom during the main course of the winter. Yet, in this species the differentiation and development of flower buds occur during the warm temperatures of the summer, and the cold winter temperatures still exert a strong influence on this mistletoe by lowering the rate of flower opening and increasing flower longevity (Aizen 2003, 2005). Thus, the overall flowering pattern of the study ornithophilous plant assemblages still reflects the prevailing seasonality characteristic of a temperate region despite the trend towards overdispersed phenologies exhibited during the main course of the blooming season.

One question that needs to be addressed is why different ornithophilous assemblages exhibited similar overdispersed phenologies. Because the vegetation of the TFSSA has developed under the influence of strong environmental gradients, continuous large-scale disturbances, and several glaciation events (Markgraf et al. 1995, Kitzberger et al. 1997, Aizen and Ezcurra 1998, Premoli et al. 2000), we might predict that the composition and abundance of individual species of ornithophilous plant assemblages have been highly dynamic over space and time, a scenario that does not favor in situ evolution of character displacement. Therefore, the finding of a congruent pattern of overdispersed phenologies across three different assemblages suggests that community structure is perhaps the result of a non-random sampling process from a common species pool, favoring the coexistence of certain combinations of spring- and summer-flowering ornithophilous species (cf. Colwell and Winkler 1984).

Phylogeny and historical-related factors may also limit or delineate the evolutionary response of flowering times to different selection pressures and contribute to mold flowering patterns. A common structural feature of many different plant communities is that taxonomically-related species tend to have similar flowering phenologies (Kochmer and Handel 1986, Johnson 1992, Wright and Calderón 1995). Competitive displacement is then expected to be more easily detected within the constraints imposed by common ancestry (see also Vamosi et al. 2006). Thus, it is not surprising that the few studies revealing segregated flowering phenologies so far, dealt with closely related co-occurring congeneric (e.g. *Acacia*, Stone et al. 1998) or confamilial (e.g. Dipterocarpaceae, Ashton et al. 1988, Bombacaceae, Lobo et al. 2003) species. Because the ornithophilous flora of the TFSSA is composed mostly of taxonomically isolated taxa (Table 1; see also Cocucci 1991, Smith-Ramírez 1993, Aizen and Ezcurra 1998), we could not test for similarity in flowering times among phylogenetically closely-related species (but see Smith-Ramírez and Armesto 1994 for examples from the non-ornithophilous flora) or incorporate phylogeny as a factor in our model. That said, our results do show that the species shared by two different localities ca 300 km apart (i.e. Blest and Chiloé) exhibit similar flowering phenological patterns (Table 2). These two localities are characterized by somewhat different ornithophilous plant assemblages (Table 1) and environmental conditions (temperatures are milder at Chiloé than Blest; Aizen and Ezcurra 1998). This spatial consistency in the sequence of flowering and amount of pairwise phenological overlap, supports the hypothesis that flowering phenology is a character that is well-preserved within the evolution of a plant lineage (Kochmer and Handel 1986).

Plant phenology, like many other plant reproductive features, results from the interaction among different historical and ecological factors, including climate, biotic relationships, and selection on correlated traits (Primack 1987, Fox and Kelly 1993, Aizen 2003). As in other fields of community ecology, the use of null models has proved to be a useful tool to detect phenological patterns in assemblages of flowering plants and even to infer subtle operating processes (Ashton et al. 1988). The use of null models here allowed us the detection of overdispersed flowering phenologies in three temperate assemblages of ornithophilous plants, but only after seasonality was accounted for in a realistic way, a result that has a clear and direct methodological implication. A repetitive flowering sequence among the ornithophilous species shared by two of the study assemblages also indicates that any competitive displacement mediated by their hummingbird pollinator should have been occurred within the limits imposed by factors related to phylogeny.

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References

Aizen, M. A. 2001. Flower sex ratio, pollinator abundance, and the seasonal pollination dynamics of a protandrous plant. – Ecology 82: 127–144.

Aizen, M. A. 2003. Influences of animal pollination and seed dispersal on winter flowering in a temperate mistletoe. – Ecology 84: 2613–2627.

Aizen, M. A. 2005. Breeding system of *Tristerix corymbosus* (Loranthaceae), a winter-flowering mistletoe from the southern Andes. – Aust. J. Bot. 53: 357–361.

Aizen, M. A. and Ezcurra, C. 1998. High incidence of plant-animal mutualisms in the woody flora of the temperate forest of southern South America: biogeographical origin and present ecological significance. – Ecología Austral 8: 217–236.

Aizen, M. A. et al. 2002. Historia natural de los mutualismos planta-animal del Bosque Templado de Sudamérica Austral. – Rev. Chilena Hist. Nat. 75: 79–97.

Armbruster, W. S. 1986. Reproductive interactions between sympatric *Dalechampia* species: are natural assemblages "random" or organized? – Ecology 67: 522–533.

Armbruster, W. S. et al. 1994. Floral character displacement generates assemblage structure of western Australian triggerplants (*Stylidium*). – Ecology 75: 315–329.

Armesto, J. J. et al. 1996. The importance of plant-bird mutualisms in the temperate rainforest of southern South America. – In: Lawford, R. G. et al. (eds), High latitude rainforests and associated ecosystems of the west coast of the Americas. Springer, pp. 248–265.

Ashton, P. S. et al. 1988. Staggering flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. – Am. Nat. 117: 993–997.

Bawa, K. S. 1983. Patterns of flowering in tropical plants. – In: Jones, C. E. and Little, R. J. (eds), Handbook of experimental pollination biology. Van Nostrand, pp. 394–410.

Brion, C. et al. 1988. Flora de Puerto Blest y sus alrededores. – Editorial de la Univ. Nacional del Comahue.

Caruso, C. M. 1999. Pollination of *Ipomopsis aggregata* (Polemoniaceae): effects of intra- vs. interspecific competition. – Am. J. Bot. 86: 663–668.

Cocucci, A. A. 1991. Kolibriblüten der Subantarktis. – Der Palmengarten 1/91: 1–8.

Colwell, R. K. and Winkler, D. W. 1984. A null model for null models in biogeography. – In: Strong, D. R. et al. (eds), Ecological communities: conceptual issues and the evidence. Princeton Univ. Press, pp. 344–359.

Diekmann, M. 1996. Relationship between flowering phenology of perennial herbs and meteorological data in deciduous forests of Sweden. – Can. J. Bot. 74: 528–537.

Feinsinger, P. and Tiebout, H. M. 1991. Competition among plants sharing hummingbird pollinators: laboratory experiments on a mechanism. – Ecology 72: 1946–1952.

Fenner, M. 1998. The phenology of growth and reproduction in plants. – Perspect. Plant Ecol. Evol. Syst. 1: 76–91.

Fleming, T. H. and Partridge, B. L. 1984. On the analysis of phenological overlap. – Oecologia 62: 344–350.

Fox, G. A. and Kelly, C. K. 1993. Plant phenology: selection and neutrality. – Trends Ecol. Evol. 8: 34–35.

Gleeson, S. K. 1981. Character displacement in flowering phenologies. – Oecologia 51: 294–295.

Gotelli, N. J. 2001. Research frontiers in null model analysis. – Global Ecol. Biogeogr. 10: 337–343.

Gotelli, N. J. and Graves, G. R. 1996. Null models in ecology. – Smithsonian Inst. Press.

Johnson, S. D. 1992. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. – J. Ecol. 81: 567–572.

Kitzberger, T. et al. 1997. Climatic influences on fire regimes along a rain forest-to-xeric woodland gradient in northern Patagonia, Argentina. – J. Biogeogr. 24: 35–47.

Kochmer, J. P. and Handel, S. N. 1986. Constraints and competition in the evolution of flowering phenology. – Ecol. Monogr. 56: 303–325.

Lechowicz, M. J. 1995. Seasonality of flowering and fruiting in temperate forest trees. – Can. J. Bot. 73: 175–182.

Lobo, J. A. et al. 2003. Factors affecting phenological patterns of bombacaceaous trees in seasonal forests in Costa Rica and México. – Am. J. Bot. 90: 1054–1063.

Markgraf, V. et al. 1995. Neogene paleoenvironmental and paleoclimatic change in southern temperate ecosystems: a southern perspective. – Trends Ecol. Evol. 10: 143–147.

McLernon, S. M. et al. 1996. Heterospecific pollen transfer between sympatric species in a midsuccessional old-field community. – Am. J. Bot. 83: 1168–1174.

Moeller, D. A. 2004. Facilitative interactions among plants via shared pollinators. – Ecology 85: 3289–3301.

Murcia, C. and Feinsinger, P. 1996. Interspecific pollen loss by hummingbirds visiting flower mixtures: effects of floral architecture. – Ecology 77: 550–560.

Murphy, S. D. and Aarsen, L. W. 1995. Reduced seed set in *Elytrigia repens* caused by allelopathic pollen from *Phleum pratense*. – Can. J. Bot. 73: 1417–1422.

Murray, K. G. et al. 1987. Evaluation of character displacement among plants in two tropical pollination guilds. – Ecology 68: 1283–1293.

Pleasants, J. M. 1990. Null model tests for competitive displacement: the fallacy of not focusing on the whole community. – Ecology 71: 1078–1084.

Poole, R. W. and Rathcke, B. J. 1979. Regularity, randomness, and aggregation in flowering phenologies. – Science 203: 470–471.

Premoli, A. C. et al. 2000. Isozyme variation and recent biogeographical history of the long-lived conifer *Fitzroya cupressoides*. – J. Biogeogr. 27: 251–260.

Primack, R. B. 1987. Relationships among flowers, fruits and seeds. – Annu. Rev. Ecol. Syst. 18: 409–430.

Proctor, M. et al. 1996. The natural history of pollination. – Harper Collins.

Rathcke, B. 1984. Patterns of flowering phenologies: testability and causal inference using a random model. – In: Strong, D. R. et al. (eds), Ecological communities: conceptual issues and the evidence. Princeton Univ. Press, pp. 383–393.

Rathcke, B. 1988. Flowering phenologies in a shrub community: competition and constraints. – J. Ecol. 76: 975–994.

Rathcke, B. and Lacey, E. P. 1985. Phenological patterns of terrestrial plants. – Annu. Rev. Ecol. Syst. 16: 179–214.

Riveros, M. 1991. Aspectos sobre la biología reproductiva en dos comunidades del sur de Chile, 40°S. – Ph.D. thesis, Univ. de Chile.

Riveros, M. and Smith-Ramírez, C. 1996. Patrones de floración y fructificación en bosques del sur de Chile. – In: Arroyo, J. J. et al. (eds), Ecología de los bosques nativos de Chile. Editorial Universitaria, pp. 235–250.

Ruffini, A. E. 1992. Interacciones entre *Sephanoides sephaniodes* (Molina) y las plantas que poliniza en el bosque de *Nothofagus*. – Licenciatura thesis, Univ. Nacional del Comahue.

Schemske, D. W. et al. 1978. Flowering ecology of some spring woodland herbs. – Ecology 59: 351–366.

Smith-Ramírez, C. 1993. Los picaflores y su recurso floral en el bosque templado de la isla de Chiloé, Chile. – Rev. Chilena Hist. Nat. 66: 65–73.

Smith-Ramírez, C. and Armesto, J. J. 1994. Flowering and fruiting in the temperate rainforest of Chiloé, Chile – ecologies and climatic constraints. – J. Ecol. 82: 353–365.

Smith-Ramírez, C. et al. 2005. Diversity, flower visitation frequency and generalism of pollinators in temperate rain forests of Chiloé Island, Chile. – Bot. J. Linn. Soc. 147: 399–416.

Stiles, F. G. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. – Science 198: 1177–1178.

Stone, G. N. et al. 1998. Partitioning of pollinators during flowering in an African *Acacia* community. – Ecology 79: 2808–2827.

Thomson, J. D. and Rusterholz, K. A. 1982. Overlap summary indices and the detection of community structure. – Ecology 63: 274–277.

Totland, Ø. 1994. Intraseasonal variation in pollination intensity and seed set in an alpine population of *Ranunculus acris* in southwestern Norway. – Ecography 17: 159–165.

Vamosi, J. C. et al. 2006. Pollination decays in biodiversity hotspots. – Proc. Nat. Acad. Sci. USA 103: 956–961.

Waser, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. – Ecology 59: 934–944.

Waser, N. M. and Fugate, M. L. 1986. Pollen precedence and stigma closure: a mechanism of competition for pollination between *Delphinium nelsonii* and *Ipomopsis aggregata*. – Oecologia 70: 573–577.

Wright, S. J. and Calderón, O. 1995. Phylogenetic patterns among tropical flowering phenologies. – J. Ecol. 83: 937–948.

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