Topological change of Andean plant–pollinator networks along an altitudinal gradient

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ABSTRACT

Pollination interaction networks exhibit structural regularities across a wide range of natural environments. Long-tailed degree distribution, nestedness, and modularity are the most prevalent topological patterns found in most bipartite networks analyzed up to day. In this work we evaluate the variation of these topological properties along an altitudinal gradient. To this end, we examined four plant–pollinator networks from the Chilean Andes at 33°S, in range from 1800 to 3600 m elevation. Our results indicate that network topology is strongly and systematically affected by elevation. At increasing altitude, the number of potential visitors per plant decreased, and species' degree distributions are closer to random expectations. On the other hand, the nested structure of mutualistic interactions systematically decreased with elevation, and network modularity was significantly higher than random expectations over the entire altitudinal range. In addition, at increasing elevations the pollination networks were organized in fewer and more strongly connected modules. Our results suggest that the severe abiotic conditions found at increased elevations translate into less organized pollination networks.

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1. Introduction

The study of plant–pollinator interaction systems has experienced a revitalized development in recent years due to the incorporation of tools coming from complex systems theory (Bascompte and Jordano, 2007). The current knowledge about mutualistic networks, and plant–pollinator systems in particular, indicates that certain structural patterns of interactions can be persistently found across many ecosystems.

Three structural regularities for plant–pollinator networks are (a) their cumulative degree distribution follows a long-tailed function, often described by a truncated power law model (Jordano et al., 2003), (b) their interaction arrays exhibit a nested structure (Bascompte et al., 2003), and (c) the species and their mutualistic interactions are organized into interconnected sub-units or modules (Olesen et al., 2007; Dupont and Olesen, 2009). These findings have shown that mutualistic interactions are not randomly assembled within communities, suggesting the presence of general underlying mechanisms for community assembly and evolution. These common structural properties appear to be linked to the robustness of ecological networks to environmental perturbations (Fortuna and Bascompte, 2006). In this regard, it has been hypothesized that a long-tailed frequency distribution of species degree (number of interaction per species) makes the network more robust to random deletion of species (Albert et al., 2000; Memmott et al., 2004). Likewise, a nested organization of plant–pollinator links, where interactions among specialist species are minimized, has been suggested to confer robustness against the random loss of species. On the other hand, a modular or compartmentalized network structure may prevent the spread of local deleterious effects throughout the community (Melián and Bascompte, 2002) and reduce system reactivity (Ruiz-Moreno et al., 2006). In consequence, integrity and persistence of ecological communities are expected to depend on the type and intensity of habitat perturbation, as much as on the structure of the ecological interaction networks.

Mountain ecosystems have been considered as model systems to test diverse physiological, ecological, and evolutionary questions (e.g., Körner and Spehn, 2002). Increased altitudes in mountain ecosystems often associate with harsh conditions for life. Reductions in available land area, atmospheric pressure, and air temperature, together with increasing levels of solar radiation

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are the main abiotic conditions that change with elevation in most mountain ranges of the world (Körner, 2007). Furthermore, strong winds and short growing seasons are typical of higher elevations in the Andean region. These environmental gradients impose severe constraints for growth, survival and reproduction of organisms. Pollinator activity in the Chilean Andes tends to decrease with increasing elevation, in part due to reductions in species richness, population abundance, and visitation rate (Arroyo et al., 1985). These findings have permitted tests of hypotheses regarding the evolution of self-compatibility at higher elevations (Billings, 1974; Arroyo et al., 1983, 1985; Arroyo and Squeo, 1990), which provided evidence for a low dependence of plant reproduction from biotic pollination at higher elevations. In the Andean zone of central Chile, it has been reported that species richness and diversity, biotic pollination, and seed dispersal decrease with elevation (Cavieres et al., 1999).

Although the effects of environmental gradients on the structural properties of pollination systems have been addressed by previous authors (Arroyo et al., 1982; Warren et al., 1988; Eiberling and Olesen, 1999; Malo and Baonza, 2002; Olesen and Jordano, 2002; Devoto et al., 2005), most work has focused on patterns of variation in either the numerical dominance of different taxa, species richness, number of interactions, or network connectance. Studies relating topological network properties of entire pollination systems to environmental gradients, and particularly altitudinal gradients, are still scarce in the literature. Dupont et al. (2003) detected nestedness in pollination networks from high elevation zones, although they assessed statistical significance by means of a null model that is too liberal and prone to detect nestedness even in randomly assembled systems (Ulrich and Gotelli, 2007). Overall, little is known about the relationships between altitude and relevant structural properties of large pollinator networks.

In this work we examine whether the architecture of plant–pollinator networks varies over a gradient of environmental and biotic conditions imposed by elevation. For our purposes, we analyze cumulative degree distribution, nestedness, and modularity of four plant–pollinator networks located at the same latitude but at differing elevations.

2. Methods

2.1. Study site and data collection

Our analyses are based upon four interaction networks belonging to four non-overlapping altitudinal ranges, from 1800 to 3600 m elevation. All four studied communities belong to the Andean zone of central Chile, at 33°S latitude. At the lowest altitude habitat (Lagunillas, 33°36′S, 70°17′W), we recorded insect visitation on flowers in anthesis during the flowering season, from December 2006 until February 2007. We considered a visit when insects made contact with the reproductive structures of flowers. Two sampling procedures were adopted. First, we recorded the number of visits per insect species on each plant species, through repeated 15-min observation periods. Second, we recorded the visits made by insects by walking along random transects. Plant species were sampled in proportion to their availability in the field. The surface area of the study site was near 44 ha, and the sampling effort was 196 h distributed on 14 days. Plants and insects were identified to the lowest level of taxonomic resolution. For the other three communities (Cordón del Cepo, 33°17′S, 70°16′W) we took the data published by Arroyo et al. (1982). The published information was available in tabular form, and the sampling procedure was quite similar to ours (Arroyo et al., 1982). We constructed adjacency matrices for each community, with insect species in columns and plant species (all herbs) in rows. The matrix elements m_{ij} are ones or zeros, representing observed and unobserved effective visits of insect j on plant i, respectively.

2.2. Analyses

The mutualistic networks were represented as bipartite graphs (Strogatz, 2001; Newman, 2003) in PAJEK (Batagelj and Mrvar, 1996). For each system we calculated the network connectance (Yodzis, 1980) as $C = L/(A \times P)$, where L is the observed number of plant–animal links, and A and P are the number of animal and plant species, respectively. Nestedness was measured through the matrix temperature T, with values ranging from 0 for perfectly nested networks to 100 for perfectly non-nested networks (Atmar and Patterson, 1993). A perfectly nested network implies that the more specialist species interact with species that are proper subsets of those species interacting with the more generalist ones (Bascompte et al., 2003). In order to evaluate statistical significance of observed nestedness, we compared the value T of each adjacency matrix against the distribution of T obtained from 1000 random matrices from the null model II of Bascompte et al. (2003). The null model assumes that each plant–animal pair interacts with a probability proportional to the observed number of interactions of both species (Bascompte et al., 2003). The null model lacks nestedness but maintains the size, shape, connectance, and heterogeneity of the adjacency matrix. These calculations were performed with the programs BINMATNEST (Rodríguez-Gironés and Santamaría, 2006) and ANINHADO (Guimarães and Guimarães, 2006). Finally, we standardized the nestedness index T by means of standard normal deviates (z-scores) in order to compare the degree of nested structure among the studied networks. A z-score below -1.65 indicates that the measured T falls below 95% of the empirical distribution of T obtained from the null model (i.e. $P < 0.05$).

The number of species a focal species interact with is represented by its degree. We calculated the cumulative degree distribution $P(k)$ (Newman, 2003) of animals and plants for each network. This distribution shows the fraction of plant (or animal) species in the network that interacts with k or more animals (or plants). For each observed distribution we fitted three alternative models: exponential, $P(k) \sim e^{-\alpha k}$; power law, $P(k) \sim k^{-\gamma}$; and truncated power law, $P(k) \sim k^{-\gamma} e^{-k/k_c}$, which reduces to the exponential and power law as $\gamma \to 0$ and $k_c \to \infty$, respectively. The Akaike's Information Criterion was used to assess the relative performance of each model. One hundred random matrices were generated for each network using the null model II of Bascompte et al. (2003), which preserves the size, shape and connectivity of the corresponding observed network. For each of the null matrices we fitted each model to calculate standard normal deviates (z-scores) of the fitted parameters. Values of z-scores outside ± 1.96 indicate that the observed parameter value is different from those of the null model, at a significance level of 5% (i.e. $P < 0.05$).

The degree of organization of the plant–animal interactions into interconnected modules was measured through the modularity index M (Guimerà and Amaral, 2005a,b).

$$M = \sum_{S=1}^{N_M} \left(\frac{L_S}{L} - \left(\frac{k_S}{2L} \right)^2 \right)$$

where N_M is the number of modules in the network, L_S is number of species interactions within-module S, L is total number of interactions in the network, and k_S is the sum of interactions of all species in S. The simulated annealing algorithm of Guimerà and Amaral (2005a,b) was used to find the network partition that maximizes M. From that partition, we obtained the number and size of modules, and calculated the fraction of network interactions (links) that occurred within-modules as well as among-modules.

Table 1
Basic features of the studied plant–pollinator systems. Network A was built from original data; networks B–D built from data in Arroyo et al. (1982).

	A	B	C	D
Altitude range (m.a.s.l. $\times 10^3$)	1.8–2.2	2.2–2.6	2.7–3.1	3.2–3.6
Plant species	77	88	45	46
Insect species	110	103	64	31
Network connectance	0.043	0.042	0.070	0.075

The statistical significance of modularity M was assessed through estimating M on 100 random networks with the same size and degree distribution than the real network (Guimerà et al., 2004).

3. Results

A basic characterization of the four pollination networks here studied is shown in Table 1. At increasing elevations, the network size tends to decrease while connectance tends to increase. Note that the number of plants surpasses the number of animals at the top. The bipartite graphs of the studied pollination networks are shown in Fig. 1.

All four networks exhibited a significant nested structure, regardless of the algorithm that was used. In order to standardize the degree of nestedness by matrix size and heterogeneity, the standard normal deviates (z-scores) of matrix temperature were calculated with respect to the empirical distribution of temperature values obtained from the null model (Fig. 2). These analyses revealed that the degree of nestedness tends to decrease monotonically with elevation. This result was robust to the algorithm used for packing the adjacency matrices and assessing their temperature.

Model selection by Akaike's Information Criterion (AIC) favored the power law function in all cases, except for the degree distribution of plants at the lowest elevation where the exponential model was the best candidate. The truncated power law model in all cases gave the highest explained variance, although it has one more parameter than its competitors and hence its AIC value was higher. Since a quantitative comparison among different distribution shapes is problematic, we focused on the exponent γ of the fitted truncated power law distribution $P(k) \sim k^{-\gamma} e^{-k/k_c}$. This parameter always had higher values for animals than plants. Nevertheless, the difference between values of γ for animals and plants decreased linearly with elevation (Fig. 3). In addition, our results reveal that the differences between the observed γ-values and those obtained from the null matrices vanished at increasing altitudes. Animals exhibited significantly ($P < 0.05$) larger γ-values, as compared to the null model, at altitudes A and B. At the two highest altitudes, on the contrary, animals exhibited γ-
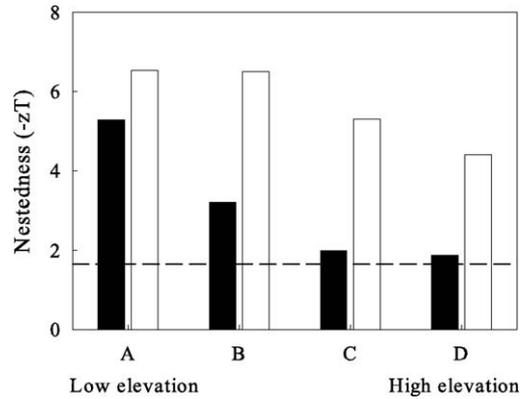

Fig. 2. Standardized matrix nestedness (negative z-scores of temperature) of pollinator networks at different altitudes, using the algorithms of ANINHADO (black bars) and BINMATNEST (white bars). Values above dashed line are significantly higher ($P < 0.05$, one-tailed test) than those of the null model.
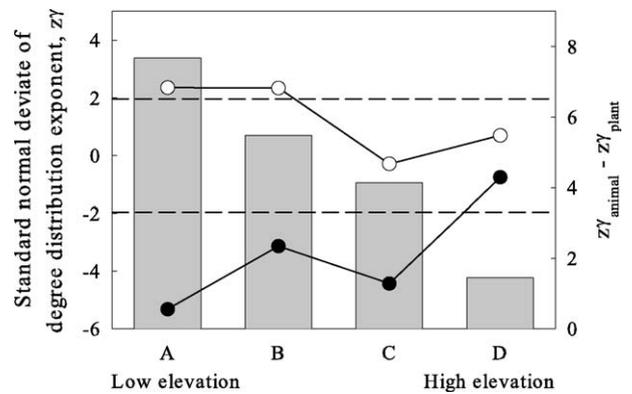

Fig. 3. Standard normal deviates (z-scores) of the fitted parameter γ from the truncated power law degree distributions of the networks at different altitudes. Closed circles are γ estimates for plants; open circles are γ estimates for animals. Values outside dashed lines are significantly different ($P < 0.05$) from null models. Bars represent the difference between standardized γ-values for animals and plants (right axis).

values indistinguishable from the null model. On the other hand, plants exhibited smaller γ-values than the obtained from the null model at altitudes A, B, and C, but they did not differ from the null model at the highest altitude (Fig. 3). Thus, after controlling by network size and shape, plants tend to decrease their relative number of super generalists at higher elevations while animals tend to increase it. Therefore, the differences of γ-values with
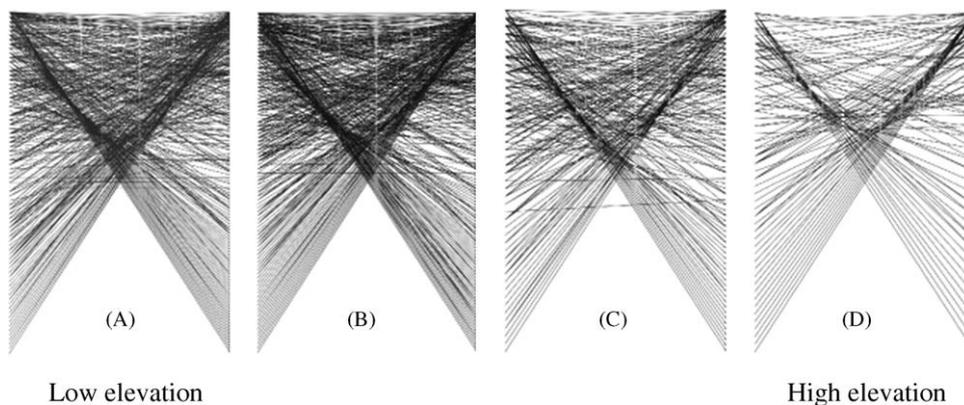

Fig. 1. Bipartite graphs of Andean plant–pollinator networks, sorted by ascending altitude (see Table 1 for details). Left vertices are plant species; right vertices are insect visitors.
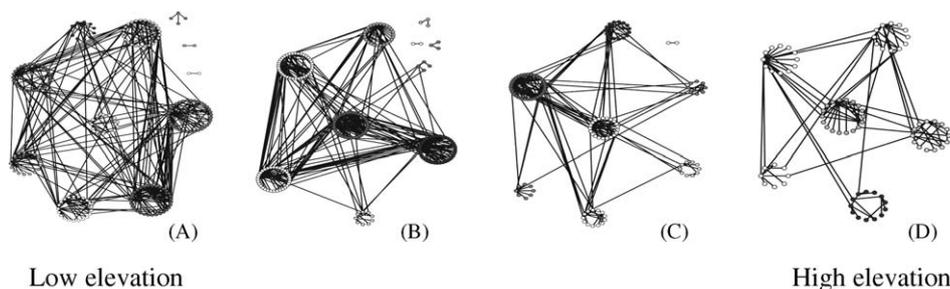
Fig. 4. Modularity graphs for pollination networks. Species belonging to the same module are arranged together. Some interactions occur between species in the same module, while other interactions connect different modules.

random expectation vanished and the asymmetry between degree distributions (i.e. γ-values) of animals and plants decreased with altitude.

Modularity was significant ($P < 0.05$) regardless altitude. In order to control for network size and connectance, the z-scores of the modularity index (zM) were calculated (Fig. 5). The standardized modularity did not exhibit a systematic trend over altitude. Nevertheless, the number of modules in each network decreased with elevation, from 11 at the lower altitude to 10, 8, and 6 for increasing elevations (Fig. 4). In addition, the mean relative size of modules within each network increased with elevation, as also did the fraction of within-module interactions (Fig. 5). In other words, at increasing elevation modularity remained significant and modules were increasingly connected within them.

4. Discussion

Environmental stress associated with elevation has been shown to affect physiological traits of organisms, as well as population abundances and species richness of both plant and animal assemblages. Nevertheless, the effects of altitude on the architecture of interspecific relationships are largely unknown. In this work we have shown that the topology of plant–pollinator networks exhibits a strong variation over an altitudinal gradient. In agreement with previous work, our results showed that the number of species for both plants and their flower visitors decreased with elevation, although this effect was more pronounced in animals. Therefore, the number of potential visitors per average plant decreased with elevation and hence there were fewer generalist plants at higher altitudes. The reverse trend held for animals. This was verified by the observed patterns of

networks' degree distribution, where the steepness of the cumulative curves increased for plants and decreased for animals. Moreover, at increasing elevations species' degree distributions became closer to the random expectations, up to be undistinguishable from the null models at the top. On the other hand, the nested structure of mutualistic interactions was systematically reduced with altitude. Current theory indicates that the combined effect of a long-tailed degree distribution and nestedness of interactions in mutualistic networks confer robustness against species loss (Memmott et al., 2004; Fortuna and Bascompte, 2006). The recent work of Bastolla et al. (2009) provides evidence that a nested architecture of mutualistic interaction relaxes competition within plants and within pollinators, thus promoting species richness and enhancing biodiversity. Therefore, loss of departure from random expectations of both degree distribution and nestedness at increasing altitudes may lead to poorer and more fragile communities from a dynamic perspective.

The last structural feature we investigated here was modularity, or the degree of species organization into densely connected modules or compartments. Our analyses showed that network modularity was significantly higher than random expectations over the entire altitudinal range. In addition, at increasing elevation the pollination networks were structured into fewer and more strongly connected modules. Olesen et al. (2007) found, using the same algorithm as ours, that smaller pollination networks tend on the average to loose their modular structure. In the present study, the decrease in species richness with altitude did not associate with a decrease in modularity. This suggests that modularity, and therefore the resistance to spreading of harmful perturbations over the entire community, is conserved over the altitudinal gradient. Nevertheless, we cannot rule out that the observed altitudinal trends in module size and within-module connectivity represent a side product of differences in network size (Olesen et al., 2007).

Overall, our results suggest that the more severe abiotic conditions associated to higher elevations lead to more randomly organized interaction networks in terms of degree distribution and nestedness, but they do no affect modular structure, in spite of certain shifts in size and shape of constituent modules. The present work is among the first attempts to reveal the structural responses of ecological networks to environmental stress. Doubtless, our results lack generality because they are based on a single altitudinal transect (Körner, 2007). In order to search for a robust pattern of topological variation of pollination networks with elevation, more cases are in need to be studied across latitudes. Unfortunately, the inherent difficulty of sampling entire pollination networks imposes obvious limitations to this task, and the available data do not suffice. Future work is needed that focused on how the different structural features of ecological networks interact in shaping the dynamics and persistence of natural communities in heterogeneous environments. A reciprocal provocation between good theory and high quality data will ensure
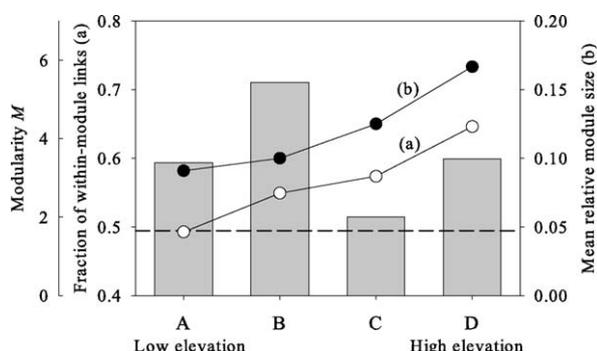

Fig. 5. Modularity features of the studied pollination networks. Bars represent the z-scores of the modularity index M and the dashed line indicates the lower limit for a modularity index significantly higher ($P < 0.05$, one-tailed test) than those of the null model. Superimposed curves represent the following: (a) fraction of within-module interactions in the network; (b) mean relative size of modules $(1/N_M) \sum_{S=1}^{N_M} m_S/m_T$, where m_S is the number of species belonging to module S, m_T is the total number of species in the network, and N_M is the number of modules in the network.

definite advances in our understanding of the functioning of complex living systems.

Acknowledgements

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