

# Specialization and rarity predict non-random loss of interactions from mutualist networks

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**One sentence summary:** Low interaction frequency and high specialization between interacting partners additively increase the vulnerability of mutualistic interactions to disruption in a fragmented habitat.

**Abstract**

The loss of interactions from mutualistic networks could predict both plant and animal species extinctions. Yet, the characteristics of interactions that predispose them to disruption are largely unknown. We analyzed 12 pollination webs from isolated hills (“sierras”), in Argentina, ranging from tens to thousands of hectares. We found evidence of a non-random loss of interactions with decreasing sierra size. Low interaction frequency and high specialization between interacting partners contributed additively to increase the vulnerability of interactions to disruption. Interactions between generalists in the largest sierras were ubiquitous across sierras, but many of them lost their central structural role in the smallest sierras. Thus, particular configurations of interaction networks, along with unique ecological relationships and evolutionary pathways, could be lost forever following habitat reduction.

**Text**

Interspecific interactions link species within complex trophic and non-trophic webs (1-3). Disruption of individual interaction links can compromise both the survival of formerly interacting species pairs and of other species with whom they are directly or indirectly linked (4-5). For mutually-beneficial interactions, such as those between plants and pollinators, the loss of interactions from a pollination web can jeopardize plant sexual reproduction directly through pollen limitation (6-7), and reduce pollinator fitness by decreasing the availability of floral resources (8-9). Mutualists can persist to different extents after link disruption, depending on individual longevity, initial population abundance, generalization in the use of mutualistic partners, and importance of the pollination mutualism itself for species survivorship (10-11). Consequently, loss of mutualistic interactions from a pollination web usually precedes species loss (12), as has been observed following habitat fragmentation (9, 13) and species invasion (14-15). This extinction lag suggests that interactions, rather than species statistics, should be the main focus of studies of web dynamics and stability under different environmental change scenarios, and justifies the management of interspecific interactions as target activities of conservation and restoration programs (16).

Despite much progress in understanding the structure and dynamics of mutualistic webs, we still have a limited ability to predict species extinctions. This ability would improve if we could identify those interactions most susceptible to disruption. However, increasing predictive ability rests on two untested assumptions: first, that interactions are lost non-randomly from webs following disturbance; second, and analogous to the “response traits” of species (17), particular traits that characterize mutualistic interactions increase their chance of disruption. Here we explore these two hypotheses using 12 pollination webs from untilled hills or "sierras" that rise from the

Pampas of Argentina (18). Ranging from tens to thousands of hectares, these sierras were once connected by a matrix of natural grassland, but are nowadays completely isolated by an intensively-managed surrounding agricultural matrix. Therefore, they can be viewed as representing a gradient of habitat reduction. In addition to containing several endemic species of Gondwanan origin, these sierras still preserve many floristic elements that were formerly common in the surrounding plains and elsewhere in southern South America (19). Previous work revealed that the number of plant and pollinator species and interaction links between them increase with area of the sierras, and that the rate of increase was half as great for species as it was for the number of links (13). However, why specific links are lost in smaller sierras whereas others persist remains unexplained.

Among all 12 pollination webs we recorded 1170 distinct interactions (links) among 96 and 172 species of plants and flower visitors, respectively (Fig. 1). When sierras were ordered by decreasing size, we found that interactions present in the each sierra tended to be proper (i.e., nested) subsets of those recorded in the next-larger sierra ( $Z = 6.80$ ,  $P < 10^{-11}$  and  $Z = 5.43$ ,  $P < 10^{-7}$  based on the completely-randomized and marginal-conditioned null models, respectively). This result is consistent with the hypothesis that mutualistic interactions are lost non-randomly as habitat size decreases. Furthermore, interactions were more nested than plant and pollinator species themselves (fig. S2), probably indicating their greater susceptibility to habitat reduction (13). Thus, some mutualistic species could persist despite the disruption of some of their interactions, potentially because of mutualism redundancy and other buffering life-history traits (10), or simply as part of an extinction debt (20).

This pattern of non-random losses prompted the question of which traits of plant-pollinator interactions make them most susceptible to disruption. We analyzed

two traits, interaction frequency and degree of generalization (estimated here as the average number species with which the plant and pollinator interact), which required no detailed information about the species involved, beyond knowing with how many species they interacted and how frequently (21). We chose these traits because, first, locally rare plant-pollinator interactions should be particularly susceptible to habitat reduction because any further decrease in interaction frequency, perhaps related to declining species abundance, could trigger complete disruption (22-23). Second, interactions between plant and pollinator species with limited numbers of alternative partners (i.e., interactions of low degree) should also be particularly susceptible beyond any confounding effect of interaction frequency, because they cannot be "subsidized" or "rescued" by third parties when, for instance, interacting species become spatially or phenologically isolated from each other (4, 24). Thus, low-frequency interactions and/or interactions between specialists should be restricted to continuous habitat or large habitat fragments, whereas frequent interactions and/or interactions between generalists should be more resistant to habitat reduction, and therefore be more ubiquitous (i.e., occurring in habitat fragments of all sizes).

For each sierra, we characterized the ubiquity of each plant-pollinator interaction as the proportion of other sampled sierras in which it also occurred. Specifically, we predicted that interactions from a large sierra with a high frequency and/or degree (i.e., involving generalist species) should be more ubiquitous than interactions with a low frequency and/or degree, which are expected to be disrupted by habitat reduction and thus absent from the small sierras. Therefore, the positive relationship between interaction ubiquity and the two interaction traits, frequency or degree, which we predicted for large sierras should weaken in the small sierras that have already been mostly depleted of fragmentation-susceptible pollination interactions. In addition to the

ubiquitous interactions, a small sierra could also have some less-ubiquitous, perhaps facultative interactions that might occur at any frequency and have any degree of generalization, which could further weaken the relationship between ubiquity and the interaction traits.

Following our prediction, the relationship between interaction ubiquity and its two predictors, local interaction frequency and degree of generalization, became increasingly positive with increasing sierra size (Fig. 2). Particularly, these relationships were strongest among interactions recorded in sierras > 100 ha (fig. S1, A to H) and became weaker or disappeared for interactions in sierras <100 ha (fig. S1, I to L). For example, on Volcán, one of the largest sierras (>2000 ha), expected ubiquity increased from 0.15 to 0.82 and from 0.09 to 0.76 over the range of interaction frequencies and degree of generalization, respectively (fig. S1B). In contrast, on Difuntito, one of the smallest sierras (13 ha), expected ubiquity increased only from 0.12 to 0.38 over the range of interaction frequencies, and remained fairly constant (~0.15) over the range of interaction generalization (fig.S1J). The results from this small sierra also illustrate that the non-random loss of vulnerable interactions is, to some extent, unrelated to changes in interaction diversity, because the pollination web of Difuntito (the only fenced sierra protected from grazing and fire) was unexpectedly rich in species and interactions (13). However, its position within the general pattern depicted in Fig. 2 was in no way anomalous, suggesting that this sierra lacked most of the vulnerable interactions recorded in the largest sierras. This result further stresses the importance of an area-per-se effect on the selective loss of interactions.

Interaction frequency and degree of generalization had largely independent effects on interaction loss. First, these two traits of interactions were correlated positively, but generally weakly within sierras ( $r < 0.55$  in all cases), with the strength

of this correlation increasing marginally with sierra size (fig. S2). Second and more importantly, the increasingly positive relationship between interaction ubiquity and interaction frequency or degree of generalization with increasing sierra size (Fig. 2) persisted after accounting for any collinearity between the predictors by using partial model coefficients (fig. S3). Thus, particular traits of plant-pollinator interactions, specifically low frequency and high specialization, contribute systematically and additively to their vulnerability to habitat reduction. Consequently, disruption of rare mutualistic interactions and those between reciprocal specialists may signal future biodiversity loss, and so should be the primary focus of biodiversity monitoring and restoration programs.

Frequent interactions between generalist plants and pollinators establish the architectural core of pollination networks (25), which provides stability and resilience to the entire web (1-2, 25-26) and governs coevolutionary dynamics of generalists engaged in strong interactions with other generalists and asymmetrically with most specialists (27-28). Differential loss of infrequent and relatively-specialized interactions accentuated this intrinsic asymmetry of networks (29-30) with decreasing habitat area, which was evidenced here by a weak but increasingly negative association between the specialization of plants and that of their interacting animal partners (fig. S4). This result suggests that many specialists persist in fragmented landscapes by interacting with locally and regionally resilient generalists, around which interactions become increasingly concentrated. Such “super-generalists”, also described for pollination webs on islands and in communities with many invaders (14, 31), should represent strong novel demographic and selection pressures for persisting specialists.

Our results also hint at subtle, but important, qualitative changes in the structure of the web core. Increasingly positive relationships between interaction ubiquity and

interaction traits, frequency and degree of generalization (Fig. 2), indicate that the core in the largest sierras included a set of regionally-widespread, robust interactions that was present in both large and small sierras (fig. S1). However, a trend towards decreasing interaction frequency and degree of generalization indicates a displacement of several of these ubiquitous interactions from the inner core to relatively more marginal positions within the web as sierra size decreases (fig. S5). Even though some interactions (e.g., between species coded 32 and 108; table S4) remain part of this core irrespective of the size of the sierra (fig. S1), the central structural role played previously by some of these ubiquitous interactions could remain vacant or be replaced by more facultative interactions present in one or a few small sierras (e.g., interaction between species coded 56 and 259 in Amarante and Difuntito; fig. S1, H and J, and table S4). Thus, because of this core shift, species surviving in small habitat fragments could be subject to more variable ecological and evolutionary dynamics in space and perhaps time.

Functional redundancy in mutualistic interaction networks provides relative stability to minor or moderate random losses of species and interactions (4, 32), but non-random disruption can affect species survival and adaptation more immediately and profoundly. Particularly, infrequently-occurring and geographically-restricted interactions that involve efficient pollination for the plant and/or some critical floral resource for the pollinator can be highly relevant at both ecological and evolutionary time scales (33-34), and their disruption could lead to time-lagged species decline (35). Using a comparative interaction-network approach, we provided evidence that these particular interactions, occurring at low frequency and involving specialists that lack alternative mutualists, are the most likely to be lost, which could accelerate the rate of species extinctions. In combination, our results suggest that non-random interaction



loss following habitat fragmentation and other anthropogenic disturbances will disrupt the most co-dependent mutualisms and alter configurations of interaction networks, along with unique ecological relationships and evolutionary pathways.

## References and Notes

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## Figure legends

**Fig. 1.** Combined plant–animal pollinator interaction matrix depicting the 1170 distinct interactions among 96 and 172 species of plants and flower visitors, respectively, recorded across the 12 sierras. Species are ranked according to decreasing number of interactions per species. A colored cell specifies an observed interaction. Different colors and color hues indicate the number of sierras in which each interaction was found (from 1 to 12). Interactions occurring in most sierras, both large and small, are mostly restricted to the upper-left corner of the matrix. The interaction matrix of each sierra is provided as supporting online material (fig. S1, A to L).

**Fig. 2.** The dependence on sierra size of the relationship between interaction ubiquity and interaction (A.) frequency and (B.) degree of generalization. Dependence is represented by regression coefficients ( $\beta \pm 95\%$  CI's) from binomial generalized linear models conducted for each of the 12 sierras. Individual coefficients whose confidence intervals do not overlap the dotted line differ significantly from zero. Solid lines and summary statistics indicate that the linear relationship between ubiquity and each interaction trait increases significantly with sierra area. Specific results for Difuntito (D), a small sierra, and Volcan (V), a large sierra, discussed in the text are shown in fig. S1, B and J, respectively.

## References and Notes

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