



Specialization and Rarity Predict Nonrandom Loss of Interactions from Mutualist Networks

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increase of charcoal lagged *Sporormiella* decline by ~100 years, grass followed *Sporormiella* decline by ~300 years, the rise in sclerophyll vegetation lagged *Sporormiella* decline by ~400 years, and total pollen influx from forest trees increased after 1600 years.

The fire increase that followed megafaunal decline could have been anthropogenic, but the extended trajectory of the rise in charcoal and its close matching with falling *Sporormiella* suggest instead that relaxation of herbivory directly caused increased fire, presumably by allowing the accumulation of fine fuel. The subsequent vegetation transformation could be explained in two ways: (i) by direct effects of relaxed herbivore pressure on vegetation density and composition or (ii) by release of fire as an ecological force, causing destruction of fire-sensitive rain-forest vegetation with replacement by fire-tolerant sclerophyll taxa and grasses. We compared the importance of these two mechanisms by measuring the effects of *Sporormiella* and charcoal in linear models predicting changes in percent sclerophyll (lagged by four depth intervals, or ~400 years) over the interval shown in Fig. 2. We controlled temporal autocorrelation by fitting generalized least-squares models with an exponential correlation structure (26). The standardized regression coefficients (SRCs = coefficients/SE) were -2.81 for *Sporormiella* and 2.53 for charcoal when fitted as single-term models; in a two-term model, the respective SRCs were -1.42 and 1.95. The changes in SRC values suggest that (i) there were independent contributions of both falling *Sporormiella* and rising charcoal to the subsequent rise in sclerophyll vegetation and (ii) the effect of charcoal was ~35% stronger.

After its initial rise charcoal remained high, and around 29 to 31 ka there was a large increase in macrocharcoal indicating that, for the first time in its history, the swamp itself was extensively

burnt (20); short-lived spikes in *Sporormiella* associated with this burning probably represent grazing over the swamp bed by extant herbivores (probably kangaroos). Charcoal rose further in the Holocene, in complete contrast to the absence of fire in the previous interglacial.

Finally, we compared the magnitude of the ecological changes that followed megafaunal decline around 41 ka with earlier climate-driven shifts from 74 and 120 ka, by calculating standardized estimates of the sizes of effects of each event on *Sporormiella*, charcoal, and percent sclerophyll (Fig. 3). There was no significant effect on *Sporormiella* from the two episodes of climate drying, suggesting that the megafaunal extinction was not the culmination of a long-term decline driven by an increasingly arid climate. Had that been true, the Lynch's Crater record should have shown evidence of declines of megafaunal biomass at times when the climate of the region became substantially more arid. Instead, megafaunal biomass was insensitive to episodes of climate drying, before declining abruptly during a period of stable climate. The increase in charcoal counts and the compositional shift to sclerophyll vegetation that followed megafaunal extinction were as large or larger than changes in the same directions associated with the two major climate changes in the earlier part of the last glacial cycle.

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Supporting Online Material

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Materials and Methods
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Specialization and Rarity Predict Nonrandom Loss of Interactions from Mutualist Networks

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The loss of interactions from mutualistic networks could foreshadow 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 nonrandom 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 relations and evolutionary pathways, could be lost forever after habitat reduction.

Interspecific interactions link species within complex trophic and nontrophic 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 connected

(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 can 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). Consequent-

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ly, loss of mutualistic interactions from a pollination web usually precedes species loss (12), as has been observed after 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: (i) interactions are lost nonrandomly from webs following disturbance; and (ii), 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.

Across all 12 pollination webs, we recorded 1170 distinct interactions (links) among 96 and 172 species of plants and flower visitors, respectively (Fig. 1 and fig. S1). When sierras were ordered by decreasing size, we found that interactions present in each sierra tended to be proper (i.e., nested) subsets (20) of those recorded in the next-larger sierra ($Z = 6.80$ and $Z = 5.43$ based on the completely randomized and marginal-conditioned null models, respectively; $P < 10^{-6}$ in both cases). This result is consistent with the hypothesis that mutualistic interactions are lost nonrandomly as habitat size decreases. Furthermore, interactions were more nested than plant and pollinator species themselves (fig. S2), which probably indicates their greater and more proximate 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 (21).

This pattern of nonrandom 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 of 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 (22). 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). The second reason was that 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., occur 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

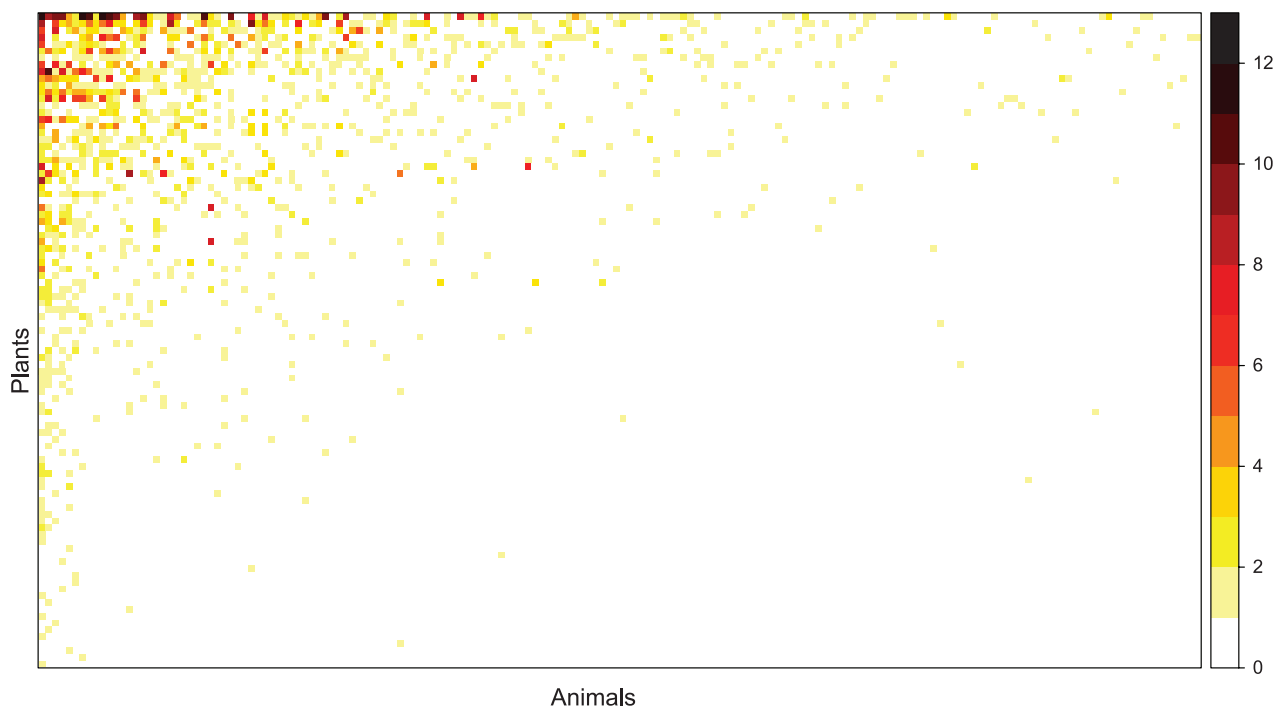


Fig. 1. Combined plant-animal pollinator interaction matrix depicting the 1170 distinct interactions among 96 and 172 species of plants and flower visitors, respectively, recorded across the 12 sierras. Species are ranked according to decreasing number of interactions per species. A colored cell specifies 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).

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 relation 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.

Following our expectation, the relation 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 relations 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 Volcan, 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 nonrandom 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). Nevertheless, its position within the general pattern depicted in Fig. 2 was in no way anomalous, which suggested 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 only marginally with sierra size (fig. S3). Second, and more important, the increasingly positive relation 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. S4). 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 they should be the focus of biodiversity monitoring and restoration programs. In

particular, specialized interactions should be of primary concern, as their disruption could lead to the rapid loss of species that lack alternative efficient mutualists. Based on our results, a low interaction frequency would further increase the vulnerability of such interaction links.

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). This core also governs coevolutionary dynamics of generalists engaged in strong interactions with other generalists and asymmetrically with most specialists (27, 28). The differential loss of relatively specialized interactions in particular would accentuate this intrinsic asymmetry of networks (29, 30) after habitat reduction, which was evidenced here by a weak but increasingly negative association between the specialization of plants and that of their interacting animal partners with decreasing sierra size (fig. S5). 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 “supergeneralists,” 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 relations between interaction ubiquity and the two predictive 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 were present in both large and small sierras (fig. S1). However, a trend toward decreasing frequency and degree of generalization of many of the most ubiquitous interactions

(fig. S6) indicates their displacement from the inner core to relatively more marginal positions within the web as sierra size decreases. 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 Difuntito (fig. S1J 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 nonrandom disruption can affect species survival and adaptation more immediately and profoundly. Particularly, infrequently occurring and geographically restricted specialized 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 provide evidence that these particular interactions, occurring at low frequency and between species 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 nonrandom interaction disruption after habitat fragmentation and other anthropogenic disturbances will affect the most codependent and rare mutualisms and alter configurations of interaction networks, along with unique ecological relations and evolutionary pathways.

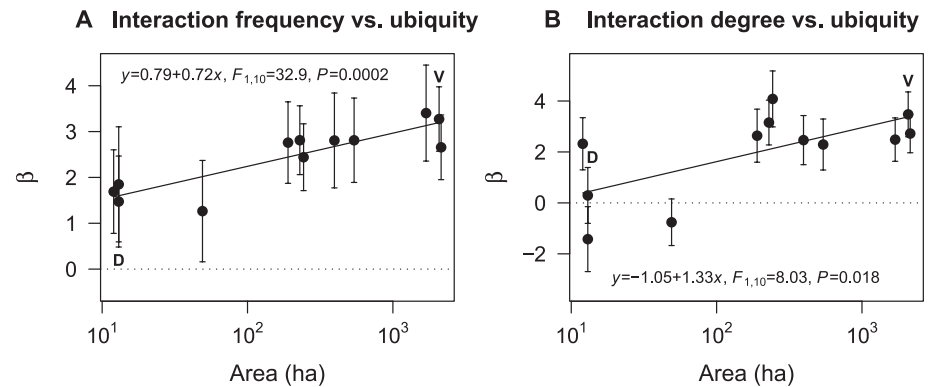


Fig. 2. The dependence on sierra size of the relation between interaction ubiquity and interaction frequency (A) and degree of generalization (B). Dependence is represented by regression coefficients ($\beta \pm 95\%$ confidence intervals) from binomial generalized linear models conducted for each of 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 relation 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.

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Supporting Online Material

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Materials and Methods

SOM Text

Figs. S1 to S6

Tables S1 to S4

References (36–50)

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Evolutionary Conservation of Species' Roles in Food Webs

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Studies of ecological networks (the web of interactions between species in a community) demonstrate an intricate link between a community's structure and its long-term viability. It remains unclear, however, how much a community's persistence depends on the identities of the species present, or how much the role played by each species varies as a function of the community in which it is found. We measured species' roles by studying how species are embedded within the overall network and the subsequent dynamic implications. Using data from 32 empirical food webs, we find that species' roles and dynamic importance are inherent species attributes and can be extrapolated across communities on the basis of taxonomic classification alone. Our results illustrate the variability of roles across species and communities and the relative importance of distinct species groups when attempting to conserve ecological communities.

Present-day ecosystems face threats, such as climate change and invasive species, that permeate entire communities (1). Partly for this reason, ecology has moved toward more holistic approaches that consider all species in an ecosystem and the network of interactions between them (2). This network approach has led to a greater understanding of the structural properties of ecological systems (3) and the community-wide consequences of empirically observed network structure (4, 5). A drawback of this community focus is that the interplay between individual species and community-level dynamics has largely been ignored (6, 7). Because conservation ef-

forts are generally focused on species, this problem has precluded a deeper assessment of the conservation implications of network theory (1).

Here we focus on the species level, to understand the generality of species' roles and their dynamic importance when embedded in their community's network. The prevailing notion is that the ecological role of a species in a network is a direct result of its interactions with other species (8–10), in particular the prey it consumes and the predators that consume it. However, given structural definitions of species' roles, it is often unclear how to extrapolate from a species' structural role to its dynamic relevance. With this in mind, we introduce here a definition of species' roles based around the concept of "network motifs" (11).

Any network can be decomposed into a set of smaller subnetworks which, when reassembled, form the original network. Depending on the type of network studied, particular subnetworks ap-

pear more frequently than would be expected at random and represent fundamental building blocks: These are referred to as network motifs (11). Crucially, the number and type of motifs that make up a food web are known to directly affect the web's stability and persistence (12–16). In ecological networks, motifs provide a meso-scale characterization of community structure by quantifying how collections of three species come together to form a larger community (17, 18). Here, we take network motifs one step further to better highlight the behavior of their most basic component: the individual species.

By definition, any motif of size n is composed of n species; for reasons of symmetry, however, each species does not necessarily appear in a unique position (Fig. 1). As an illustrative example, consider the two unique motifs made up of two species: $A \rightarrow B$ and $A \leftrightarrow B$ (19). In the first motif, the positions of A and B are not equivalent, because they allow us to distinguish between the two species. On the other hand, the positions of A and B are indistinguishable in the second motif. This implies that, formally, a motif of n species can have anywhere from 1 to n unique positions. If we consider three-species combinations, we find that there are 13 unique motifs composed of 30 unique positions (20, 21) (fig. S1).

We examined the motif pattern of all species from 32 empirical food webs that describe which predator-prey interactions are observed in the community (21) (table S1). These food webs come from a variety of different environments, encompassing marine, terrestrial, freshwater, and estuarine habitats. To quantify the roles of all species in a food web, we directly enumerate, across all motifs, the frequency c_{ij} that species i appears in each position j . Therefore, in each network, the motif profile of any species i is provided by its vector $\vec{c}_i = \{c_{i1}, c_{i2}, \dots, c_{i29}, c_{i30}\}$.

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