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Effect of Hurricane Karl on a plant–ant network occurring in coastal Veracruz, Mexico

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Abstract: We analysed the effect of a hurricane on a plant–ant network and on vegetation cover. Plant cover was sampled using linear sampling in several vegetation types: deciduous forest, a dry forest, sand dune pioneers, sand dune scrub, ecotone of freshwater marsh, deciduous forest and dune scrub, and mangrove forest. We sampled ant–plant interactions and vegetation cover before and after Hurricane Karl hitting (September 2010) the central coast of the state of Veracruz, Mexico. The pre-hurricane network consisted of 16 plant and 25 ant species in 52 associations. The post-hurricane network consisted of 17 plant and 20 ant species in 56 associations. We found a significant decrease in the total linear cover of EFN-bearing plants between October 2009 (646 m, no hurricane effect) and October 2010 (393 m, after hurricane Karl) (total sample length 2025 m). Both networks were significantly nested (0.999 and 0.973, $P < 0.001$), suggesting that network topology remained similar. Our results show changes in several network characteristics and species proportions. The number of plant species that contributed to nestedness vs. idiosyncratic species did not differ significantly in the pre-hurricane network, while the number of plant species that contributed to nestedness vs. idiosyncratic species did differ significantly in the post-hurricane network. The number of ant species that contributed to nestedness vs. idiosyncratic species differed significantly in the pre-hurricane network, and also in the post-hurricane network. Differences in nestedness contributions of species before and after the hurricane reflect an alteration from a generalized, highly nested, more stable pre-disturbance network, to a more low-degree or specialized network (i.e. fewer interactions among generalist species, those species with the most associations). The maintenance of important core components of the network after a huge disturbance, suggests a short-term resilience typical of mutualistic networks.

Key Words: communities, extrafloral nectaries, mutualism, networks, resilience, stability

INTRODUCTION

A fundamental objective of ecological network research is to understand how natural complexity can persist and affect ecosystem function (Ings *et al.* 2009). This is essential to predict and mitigate the consequences of increasing environmental perturbation (Ings *et al.* 2009, Tylianakis *et al.* 2010). A number of natural perturbations alter ecosystems in different ways. Hurricanes, for instance, exhibit a wide range of devastating effects on biological communities (Coder 2006, Flynn *et al.* 2010, Kupfer *et al.* 2008, Ross *et al.* 2001). For instance, in Florida damage varied among species whether they were trees (no vital effect) or shrubs (most frequently damaged but highly resilient), or if species were rare (minimally affected) or common, or the type of vegetation (Menges *et al.* 2011).

Since species interactions are involved in continuous and dynamic multiple forms and outcomes, whose ultimate expression is a complex network (Bascompte & Jordano 2007), hurricanes could greatly affect network structure. To our knowledge the effect of hurricanes on a complex network of interactions has not been reported. Mutualistic networks are characterized and defined by a nested pattern (Bascompte *et al.* 2003, Rico-Gray *et al.* 2012), indicating that generalist species (those with the most associations) interact with each other and form a central core of species, specialist species (those with fewer associations) interact with generalists; interactions among specialists are usually absent. The asymmetric

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shape of this network implies that the community of species is forming a robust and sustainable response to the loss of species (Bascompte & Jordano 2007).

On 17 September 2010 Hurricane Karl impacted the central coast of the state of Veracruz, Mexico, as a category-3 hurricane degrading fast to category 1 (Saffir–Simpson scale). The eye of the storm entered land *c.* 30 km south of our study site, near the city of Cardel. Previous research suggested (1) changes in the abundance of associations between ants and plants bearing extrafloral nectaries (EFNs) (Díaz-Castelazo *et al.* 2004, Rico-Gray 1993), (2) that the number of ant–plant associations may be influenced by climatic factors (Rico-Gray *et al.* 2012), and (3) the existence of temporal variation in the ant–plant interaction network in the study site (Díaz-Castelazo *et al.* 2010). The impact of the hurricane was amidst our monthly ant–plant sampling (1989–2011). As we already had data on vegetation cover and on the ant–plant network of interactions, we continued our sampling in order to compare the data obtained before and after the impact of the hurricane. We considered that the hurricane would have an impact on the interaction network of EFN-bearing plants and associated ant foragers. We hypothesized that after the hurricane the community would experience a decrease in overall connectivity (nestedness, connectance), but mainly, a turnover of specific roles in each network and a change in pairwise interactions (i.e. change in the identity of species of network cores and species with idiosyncratic interactions), all these as a consequence of a decrease in the cover of EFN-bearing plants and the differential susceptibility of species to abiotic disturbance. To that effect, we carried out a pre- vs. post-hurricane comparison of vegetation cover and network parameters, such as nestedness (*N*), number of interactions or links, and position of species along the core-periphery gradient of the networks and along the gradient of nestedness contributors/idiosyncratic species of the networks. Also, in order to assess whether changes in nestedness between September and October 2010 were due to the hurricane, using the same field and statistical methods we also analysed nestedness for a previous sampling date (September vs. October 1999).

STUDY SITE AND METHODS

Field work was carried out at Centro de Investigaciones Costeras La Mancha CICOLMA), located on the coast of the state of Veracruz, Mexico (19°36′N, 96°22′W; <100 m asl). The climate is warm and sub-humid; a rainy season occurs between June and September, total annual precipitation is *c.* 1500 mm, and annual temperature is 22–26 °C. The major vegetation types present are tropical deciduous forest, tropical dry forest, sand dune scrub, mangrove forest, freshwater marsh and flooded deciduous forest (Moreno-Casasola 2006). Field work consisted of obtaining the linear cover of extrafloral nectary-bearing plants (EFN-bearing plants) and recording ant–plant associations. Both were done along six transects representing different vegetation types in the area: sand dune pioneers, sand dune scrub, deciduous forest, dry forest, freshwater lagoon, flooded forest and mangrove forest (Díaz-Castelazo *et al.* 2010, Rico-Gray 1993). Pre-hurricane sampling was done in September 2010 (except for plant cover which was done in September 2009), and post-hurricane sampling was done on October 2010 (Díaz-Castelazo *et al.* 2004, 2010; Rico-Gray 1993). In order to better understand the effect of the hurricane in network structure and differentiate it from a seasonal effect (between months), we compared our 2010 September–October networks with previous data where no hurricane happened (September–October of 1999).

Total cover of EFN-bearing plants was obtained using linear cover of plants per transect (Díaz-Castelazo *et al.* 2004) sampled pre- and post-hurricane, total sample length was 2025.28 m. Linear cover was defined as the portion of the transect length occupied by EFN-bearing plants, and obtained with the line-intercept technique (Pemberton 1990) along the six transects. Due to the fact that transects were composed of different vegetation types, to compare the cover of EFN-bearing plants obtained both before and after the hurricane, the analysis was done with a repeated measures-ANOVA using Statistica for Windows v 7.0.

We recorded all occurrences of ants collecting nectar from plants. On each visit we recorded ant species, plant species and food source. Once an individual plant was marked as visited by ants, it was subsequently re-checked throughout the study. We selected nectar as ant food resource, which is produced either by the surface of reproductive structures (spike, pedicel, bud, calyx or fruit) or secreted by vegetative structures in plants (shoots, petioles, bracts or stems). Ants were considered to be feeding on nectar when immobile, with mouthparts in contact with nectar-secreting tissues. Nectar-feeding ants often showed obviously distended gasters (Rico-Gray 1993).

Structural features analysed for each network included degree, network connectance, nestedness and species-specific contributions to nestedness (Atmar & Patterson 1993). Degree is defined as the number of links or interactions among ant and plant species (Díaz-Castelazo *et al.* 2010). Network connectance is defined as the proportion of realized links of the total possible in each network: $C = I/(P \times A)$, where I is the total number of interactions recorded for the network, P is plant species richness and A is ant species richness. Nestedness, estimated as N ($N = (100-T)/100$), is a network pattern consisting of a core of reciprocal generalists accompanied by specialist species that interact almost exclusively with generalists (Atmar & Patterson 1993, Bascompte *et al.* 2003, Guimarães & Guimarães 2006), where N = 0 is no nestedness and N = 1 is total nestedness.

The latter features allowed us to identify the proportion of idiosyncratic species, which are the species that show patterns of interactions in a way that departs from a perfectly nested pattern, as well as nestedness contribution of species among networks (Bascompte & Jordano 2007). Nestedness, species contribution to nestedness, and determination of idiosyncratic species were obtained using Aninhado (Almeida-Neto *et al.* 2008, Guimarães & Guimarães 2006). Comparisons of the proportions between species in the networks contributing to the nestedness of idiosyncratic species were made using χ^2 goodness-of-fit tests (Zar 1999).

We also characterized a given species being as part of the central core of species or, alternatively, as one of the peripheral species of the networks. We used categorical core-periphery analysis for bipartite networks (Borgatti & Everett 1999), where core and periphery are identified by sorting ant and plant species in such a way that the connectance among core species is maximized while minimizing connectance among peripheral species. The placement of species as components of the core or the periphery of the networks was analysed using UCINET for Windows 6.0. Core component significance always refers to 95% or more of the UCINET runs ($P < 0.0001$).

RESULTS

We found a significant decrease in the total linear cover of EFN-bearing plants between October 2009 (646.5 m, no hurricane effect) and October 2010 (393.5 m, after hurricane Karl) (RM-ANOVA $F = 41.15$, df = 1, $P < 0.01$) (Figure 1). Pre- (N = 0.999) and post-hurricane (N = 0.973) networks were significantly nested ($P < 0.001$) (Table 1). The comparison using previous data (year 1999) yielded a similar significant result (September N = 0.84, and October N = 0.81, $P < 0.05$; Table 1). The number of plant species that contributed to nestedness vs. idiosyncratic species did not differ in the pre-hurricane network ($\chi^2 = 4$, df = 1, $P > 0.054$), while the number of plant species that contributed to nestedness vs. idiosyncratic species did differ significantly in the post-hurricane network ($\chi^2 = 6.73$, df = 1, $P = 0.01$). Furthermore, the number of ant species that contributed to nestedness vs. idiosyncratic species differed in the pre-hurricane network ($\chi^2 = 8.5$, df = 1, $P < 0.01$), and also in the post-hurricane network ($\chi^2 = 9.05$, df = 1, $P = 0.01$) (Table 1, Figure 2).

Camponotus planatus and *Dorymyrmex bicolor* were the most extreme generalist ant species (i.e. those with the most associations) in both networks. In the pre-hurricane network the former interacted with six and the latter interacted with five plant species, while in the post-hurricane network, *C. planatus* and *D. bicolor* interacted with eight and seven plant species, respectively. Three ant species (*C. planatus*, *D. bicolor*, *Camponotus linnaei*) were part of the core in the pre-hurricane network, whereas 21 ant species (84% of ant species in the network) were strictly on the periphery of the network, while one ant species (*Monomorium pharaonis*) maintained its position as it occurred in the same proportion (50%) between the core and the periphery. For the post-hurricane network, *C. planatus*, *D. bicolor* and *Paratrechina longicornis* were core species, 16 ant species (76.2% of ant species in the network) were strictly peripheral (χ^2 test, $P < 0.01$), and two species (*Forelius pruinosus* and *Wasmannia auropunctata*) maintained their position as they occurred in the same proportion (50%, χ^2 test, $P < 0.01$) between the core and the periphery. *Camponotus linnaei* was a core member in the pre-hurricane network, and became a part of the periphery in the post-hurricane network. *Paratrechina longicornis* was part of the periphery of the pre-hurricane network, and became a part of the core in the post-hurricane network.

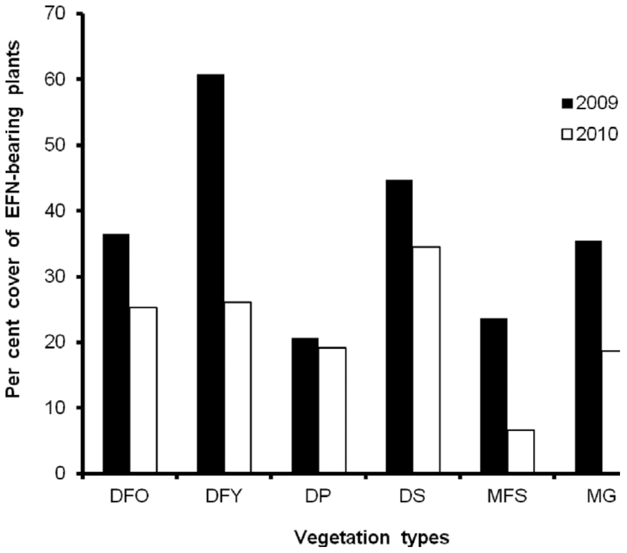

Figure 1. Comparison of per cent linear covers of EFN-bearing plant species, between October 2009 (no hurricane effect) and October 2010 (hurricane effect) at La Mancha on the coast of Veracruz, Mexico. Types of vegetation and transect lengths are: DFO = deciduous forest (370 m); DFY = dry forest (226 m); DP = sand dune pioneers (638 m); DS = sand dune scrub (162 m), MFS = ecotone of freshwater marsh, deciduous forest and dune scrub (458 m), MG = mangrove forest (171 m). Columns depict total linear cover (m) of EFN-bearing plants and percentages are cover relative to each transect total length. Total sample length was 2025 m.

In contrast to ant species, half of the plant species in the pre-hurricane network were part of the core, five species (31.2%) were strictly peripheral ($P < 0.01$), and two species (*Passiflora* sp., *Amphilophium paniculatum*)

Table 1. Values from the analyses of the parameters considered for the plant–ant networks sampled at La Mancha on the coast of Veracruz, Mexico, in all cases pre- and post-hurricane (September 2010 and October 2010, respectively). For comparison purposes also presented is nestedness for a previous sample (*N*, 1999), no hurricane effect neither pre or after the sample was taken. Comparisons of the proportions between the networks were performed using χ^2 goodness-of-fit tests.

Parameter	Pre-hurricane September	Post-hurricane October	P
Plant species	16	17	
Ant species	25	20	
Associations	52	56	
Nestedness (*N*, 2010)	0.999	0.973	< 0.001
Nestednes (*N*, 1999, no hurricane)	0.836	0.814	< 0.05
Mean idiosyncratic temperature	18.1	26.8	
Connectance for community network	0.13	0.16	
Number and % plant species contributing to nestedness	8 (50%)	2 (11.8%)	< 0.01
Number and % idiosyncratic plant species	8 (50%)	17 (88.2%)	< 0.01
Number and % ants contributing to nestedness	5 (20%)	1 (5%)	< 0.01
Number and % idiosyncratic ant species	20 (80%)	19 (95)	< 0.001

maintained their position occurring in the same proportion of randomizations (50%, P < 0.01) between the core and the periphery. Whereas only six plant species were part of the core of the post-hurricane network (P < 0.01), nine plant species (50% of plant species in the network) were strictly peripheral (P < 0.01), while *Turnera ulmifolia* and *Ipomoea pes-caprae* maintained their position as they were present in the same proportion

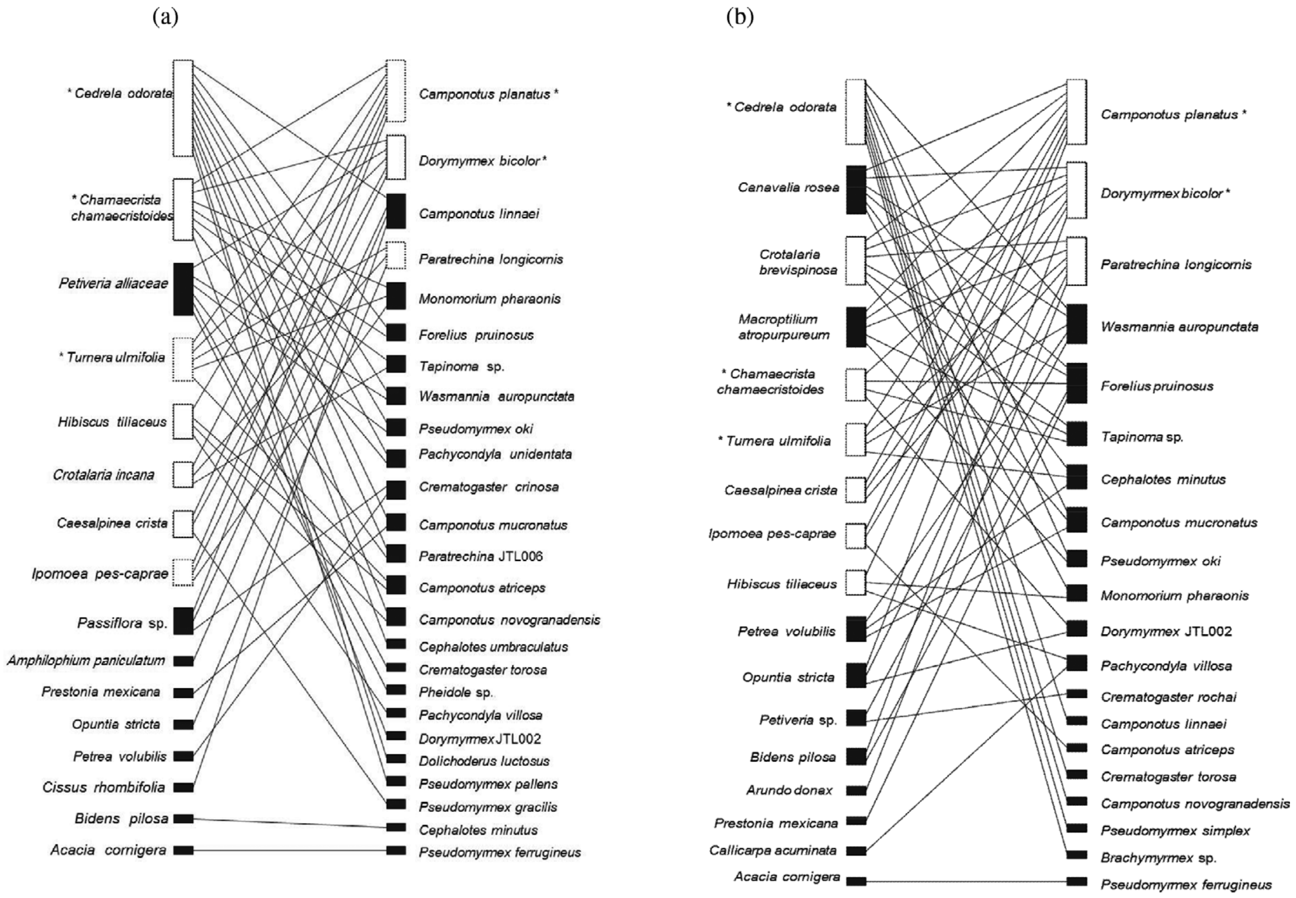

Figure 2. The pre- (September 2010) (a) and post- (October 2010) (b) hurricane plant–ant interaction networks, sampled at La Mancha on the coast of Veracruz, Mexico. The lines between bars indicate associations between ant and plant species. *Indicates those species that were present in the core of the network in at least 65% of the UCINET runs. The size of bars indicates frequency. For both networks, bars in the left column indicate plant species, and bars in the right column indicate ant species. Ant nomenclature follows Bolton & Alpert (2006) and Longino (2010). Plant nomenclature follows Moreno-Casasola (2006).

(50%, P < 0.01) between the core and the periphery. Several plant species changed roles before and after the hurricane. For instance, *Petiveria alliacea* and *Terminalia catappa* which were rare at the networks (but common at the study site) after being part of the core of the pre-hurricane network, became part of the periphery of the post-hurricane network, as opposed to *Opuntia stricta*. The main plant species contributing to nestedness in the pre-hurricane network, *Prestonia mexicana*, was an idiosyncratic plant species in the post-hurricane network, and *Passiflora* sp. practically disappeared after the hurricane. *Cedrela odorata*, an idiosyncratic species before the hurricane (i.e. with an association pattern different to the other plants before the hurricane), was the main plant species contributing to nestedness after the hurricane.

DISCUSSION

Although nestedness values did not differ before and after the hurricane, suggesting that the topology of the network remained similar (Díaz-Castelazo *et al.* 2010, Rico-Gray *et al.* 2012), a similar comparison using previous data yielded the same result, suggesting that the slight decrease in nestedness (*N*) percentages between September and October even in a hurricane (2010) or a non-hurricane year (1999), reflect only seasonal differences (since September corresponds to the end of the rainy season). On the other hand, our results do show significant changes in several other network characteristics, species proportions and in the cover of EFN-bearing plants. In summary, the pre-hurricane network exhibited a more stable structure.

We found significant differences between the total linear cover of EFN-bearing plants estimated before and after the hurricane. The resulting effect is a decrease of plant parts bearing extrafloral nectaries, which in turn is a decrease of potential sources of nectar for foraging ants, thus affecting network structure. In general, damage to trees has been associated with debris deposition (Menges *et al.* 2011), which is partly the case in our example. Several network parameters for plants before and after the hurricane provide evidence of immediate community alterations: (1) mean idiosyncratic temperature was lower in the pre-hurricane network, suggesting a more stable assemblage of species before the disturbance; (2) the per cent of plant species that contributed to nestedness was higher before the hurricane, suggesting that high abundance of EFN-bearing plants contribute to the interconnectedness and stable structure of the community before the phenomenon; (3) the per cent of idiosyncratic plant species was lower before the hurricane and increased after the phenomenon indicating an emerging pattern of differential non-generalized interactions, probably due to opportunistic encounters of foraging ants and nearby plant resources still available; and (4) the number of EFN-bearing plant species consistently forming the core of the network clearly dropped after the hurricane, reflecting not only the loss in cover, but the susceptibility of certain plant species to provide nectar for ants. For instance, climbers clearly changed roles after the disturbance since they were practically wiped out from their supporting plant species.

In contrast to plants, ants have been considered as resilient components after experiencing a strong hurricane (Morrison 2002); however, although both our networks were highly nested, the structural positions of individual ant species within the networks clearly differed in only 1 mo. The per cent of ant species that contributed to nestedness decreased after the hurricane suggesting that fewer ants remained as super-generalist species. This is reinforced by the increase of idiosyncratic ant species after the hurricane. In contrast to plants, where the number of core species dropped, ants maintained three species as core components of the network: *Camponotus planatus* and *Dorymyrmex bicolor*, whose constant relevance as a visitor of EFN-bearing plants is explained by their habits and biology. *Camponotus planatus* is a widespread species and the most common second-growth ant species in the neotropics (may occur in both mature forest and in highly disturbed areas). This ant is particularly fond of carbohydrates and is one of the most frequent visitors of extrafloral nectaries (Longino 2010). Similarly, *D. bicolor* is a neotropical species tolerant to and common in highly seasonal habitats and typical of sparse vegetation. This ant forages mainly on sugary secretions such as those from EFNs and honeydew-producing Hemiptera (Longino 2010). Furthermore, *Paratrechina longicornis*, a well-known invasive ant species, was incorporated to the core of the network after the disturbance, possibly due to its tramp behaviour and tolerance to disturbance (Schultz & McGlynn 2000). Species changes after disturbance have also been reported for other communities (butterflies; Kunte 2008).

The connectance value for the whole community network was slightly lower before the hurricane, suggesting that ant species switched links among plant species while searching for alternative food sources. The comparison between species in the core and periphery of the networks shows changes before and after the hurricane for ants and for plants. This is particularly important, since core species connect to hyper-interactive species in the other trophic level, even though they may not have a higher number of associations within the network (de Nooy *et al.* 2005). The ants *D. bicolor* and *C. planatus*, and the plants *C. odorata*, *Chamaecrista chamaecristoides* and *Crotalaria incana* maintained their place in the core of the network, suggesting that even after the hurricane these nodes could be responsible for network topology, possibly being key species within the mutualistic community. The differences in nestedness contributions of species before and after the hurricane reflect a clear alteration from a generalized, highly nested pre-disturbance network, to a more low-degree or specialized network (fewer interactions among generalist species). However, the maintenance of important core components of the network after a huge disturbance, such as a hurricane in coastal communities, suggests a short-term resilience typical of mutualistic networks.

The effect of the hurricane on network patterns could be confounded with the 'natural' changes taking place in this seasonal environment. Previous work has shown different patterns for this site: (1) short-term changes (within a year) (Rico-Gray *et al*. 2012), and (2) long-term changes (10-y comparison) (Díaz-Castelazo *et al*. 2010). Although in all cases changes in nestedness were not enough to be significant and modify network topology, they do suggest, however, a strong resilience in topology, changes being reflected on species composition and their associations (Morrison 2002). Finally, both networks were nested, suggesting that network topology remained similar (see also Table 1 for 1999 result). Differences in nestedness contributions of species before and after the hurricane reflect an alteration from a generalized, highly nested, more stable pre-disturbance network, to a more low-degree or specialized network. The maintenance of important core components of the network after a huge disturbance, suggests a short-term resilience typical of mutualistic networks.

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