Ecosystem restoration strengthens pollination network resilience and function

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Land degradation results in declining biodiversity and the disruption of ecosystem functioning worldwide, particularly in the tropics[1]. Vegetation restoration is a common tool used to mitigate these impacts and increasingly aims to restore ecosystem functions rather than species diversity[2]. However, evidence from community experiments on the effect of restoration practices on ecosystem functions is scarce[3]. Pollination is an important ecosystem function and the global decline in pollinators attenuates the resistance of natural areas and agro-environments to disturbances[4]. Thus, the ability of pollination functions to resist or recover from disturbance (that is, the functional resilience)[5,6] may be critical for ensuring a successful restoration process[7]. Here we report the use of a community field experiment to investigate the effects of vegetation restoration, specifically the removal of exotic shrubs, on pollination. We analyse 64 plant–pollinator networks and the reproductive performance of the ten most abundant plant species across four restored and four unrestored, disturbed mountaintop communities. Ecosystem restoration resulted in a marked increase in pollinator species, visits to flowers and interaction diversity. Interactions in restored networks were more generalized than in unrestored networks, indicating a higher functional redundancy in restored communities. Shifts in interaction patterns had direct and positive effects on pollination, especially on the relative and total fruit production of native plants. Pollinator limitation was prevalent at unrestored sites only, where the proportion of flowers producing fruit increased with pollinator visitation, approaching the higher levels seen in restored plant communities. Our results show that vegetation restoration can improve pollination, suggesting that the degradation of ecosystem functions is at least partially reversible. The degree of recovery may depend on the state of degradation before restoration intervention and the proximity to pollinator source populations in the surrounding landscape[5,8]. We demonstrate that network structure is a suitable indicator for pollination quality, highlighting the usefulness of interaction networks in environmental management[6,9].

The loss of biodiversity has the potential to disrupt ecosystems and their functioning; ecological restoration is often attempted to mitigate these effects[10]. Most restoration efforts target vegetation (such as the removal of exotic plants and the deliberate planting of desirable native species) in the hope that restoring the plant community will allow other services to recover. Yet the efficacy of these interventions in restoring ecosystem functions and services has rarely been assessed quantitatively.

Pollination is an important ecosystem function, as many wild plants and crops rely heavily on pollinators for reproduction[11]. Pollinators are also particularly sensitive to anthropogenic disturbance[12,13], which poses a threat to the pollination service they provide[4]. Furthermore, restoring pollinator assemblages may be essential for ecosystem restoration. A key unsolved problem is whether the common practice of restoring plant communities also leads to the restoration of pollinator assemblages and the benefits that they deliver. Here we report data from a study of isolated, rocky mountaintops, termed inselbergs, in the Seychelles, in which we experimentally assessed the effects of vegetation restoration on pollinator assemblages and their services. In particular, we quantified pollination networks and plant reproduction in both restored and unrestored communities to assess structural and functional changes in plant–pollinator communities as a response to vegetation restoration. We investigated two main ideas: whether vegetation restoration through exotic species removal increases network interaction diversity and, if so, whether this increase in interaction diversity in turn restores pollination function and, thus, increases the reproductive output of the plant communities.

These questions are embedded in a conceptual framework: that species interaction networks are key features of ecosystems[2], thus making them useful to assess the efficacy of restoration by providing comprehensive quantitative information on the structure and function of communities[14]. Weighted network metrics allow us to tease apart the influences of species abundance, diversity, generalization and functional overlap[15] (Supplementary Methods 2).

To account for the temporal and spatial variation across a long tropical flowering season, we collected eight monthly pollination networks from eight dwarf forest plant communities on discrete, mid-altitude inselbergs (64 networks; Fig. 1 and Extended Data Table 1) on the tropical island of Mahé, Seychelles. On four of the inselbergs, all exotic plants (approximately 39,700 woody plants) were removed, referred to as 'restoration' throughout (and the sites as 'restored' sites; for site-selection criteria see Methods and Supplementary Methods 1). The four 'unrestored' sites contained a similar number of exotic species that flowered during the study (range 2–5 spp.), accounting for $25.3 \pm 15.1\%$ of all inselberg plants. Prior to restoration, restored and unrestored sites contained a similar proportion of exotic plants (0.29 ± 0.21 versus 0.25 ± 0.15 (range of data given as s.d. unless stated); $t_6 = 0.30$, $P = 0.78$; Extended Data Table 1). After restoration, pollinators of all woody flowering plant species (38 spp.) were scored for a total of 1,525 observation hours, during which we recorded 581 species–species interactions (links) and 12,235 pollinator visits to flowers. Pollinators included bees and wasps (Hymenoptera, 25 spp.); flies (Diptera, 59 spp.); beetles (Coleoptera, 38 spp.); moths and butterflies (Lepidoptera, 17 spp.); two bird species (Nectariniidae, Pycnonotidae); and three lizard species (Gekkonidae, Scincidae).

Restoration markedly changed pollinator numbers, behaviour, performance and network structure in inselberg communities. At 6–14 months after restoration, the number of pollinator species was, on average, 21.6% higher across the four restored compared to the four unrestored inselbergs (Fig. 2). Monthly pollination networks showed higher interaction richness and interaction diversity (a combined measure of interaction richness and evenness) in restored networks, whereas interaction evenness (a measure of the uniformity

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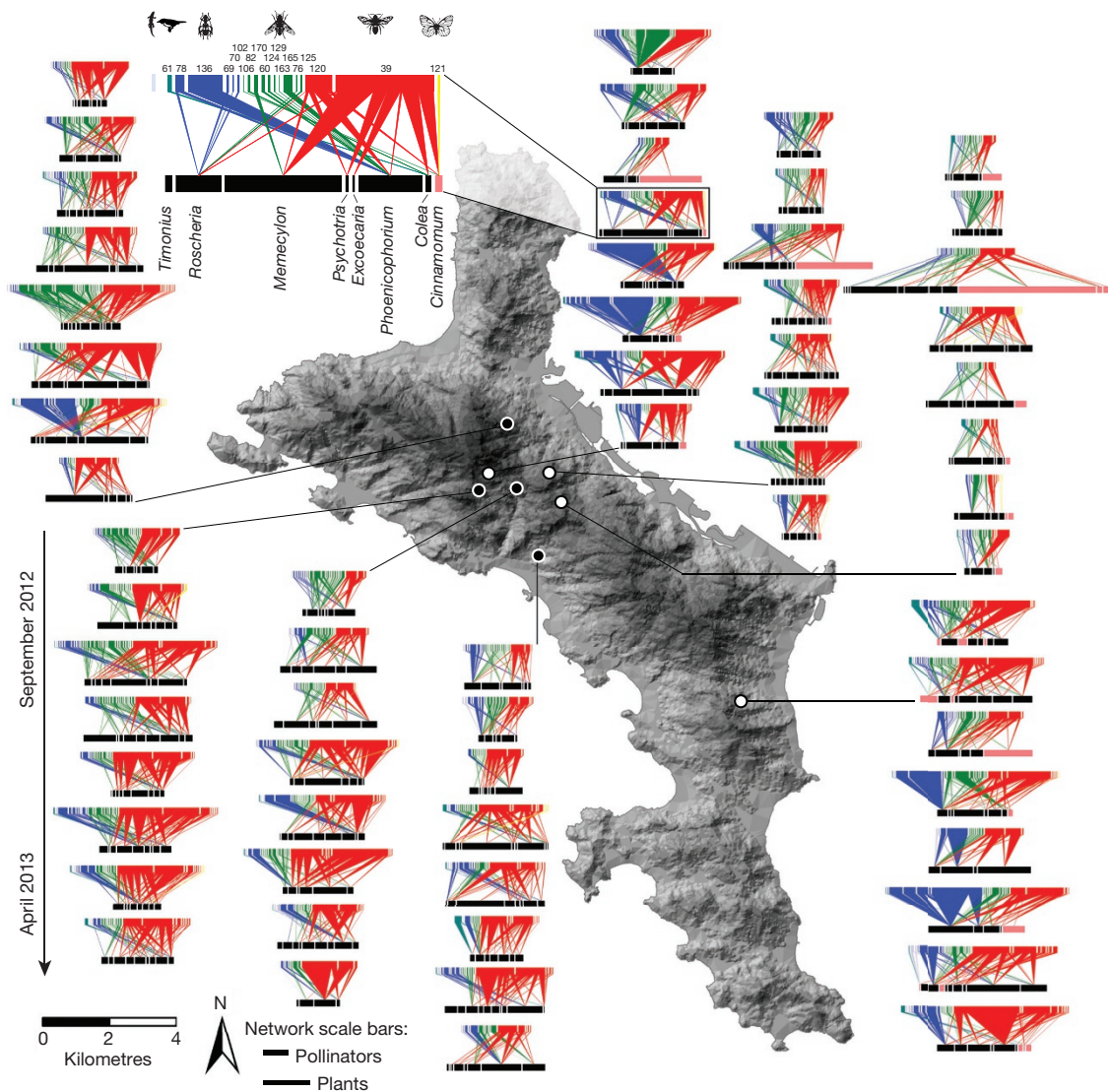
Figure 1 | The island of Mahé with study sites and pollination networks. At each of the four restored (black circles with white ring) and unrestored (white circles with black ring) sites we collected eight monthly networks between September 2012 and April 2013. The webs depict bipartite quantitative networks of interactions (links) between plants (bottom bar) and pollinators (top bar). Each block represents a species, the width of a block reflects the relative abundance of flowers and pollinators, and the width of the links shows the interaction frequency between pollinators and plants. All 64 networks are drawn to the same scale. Native and exotic plant species are shown in black and pink blocks, respectively. Pollinator groups are depicted by colours: teal, skinks and geckos; light blue, birds; dark blue, beetles; green, flies; red, wasps and bees; yellow, moths and butterflies. Scale bars: pollinators, 20 visits per flower per hour; plants, 3 flowers per cubic metre.

of the frequency of interactions) was similar between treatments (Fig. 2 and Table 1). Overall, restored networks were more generalized than unrestored networks (H_2', Fig. 2).

The observed network responses to restoration were mirrored by the plant communities. Most native plants were more generalized in restored than unrestored networks (d'_{pl}; Fig. 2; Extended Data Fig. 1), attracting more pollinator species ($\Delta S_{poll} = 9.0 \pm 5.26$ pollinator spp. on 14 of 23 plants shared between treatments). At restored sites, pollinator species were also more generalized in their partner selection (d'_{poll}; Fig. 2, Table 1). This pattern was shaped by two super-generalist and abundant pollinators, the native sweat bee *Lasioglossum mahense* (d'_{Lasio} restored versus unrestored: 0.17 ± 0.10 versus 0.28 ± 0.23) and the exotic honey bee *Apis mellifera* (d'_{Apis} restored versus unrestored: 0.22 ± 0.18 versus 0.40 ± 0.25; Extended Data Table 2), which have both been previously shown to respond most strongly to exotic plants on inselbergs[16]. Other pollinator species were also more generalized in the restored habitats (for example, d' of endemic flies, other bees and wasps, lizards and birds; $F_{1,368.3} = 5.20$, $P = 0.023$), but their effect on overall network specialization H_2' without *Apis* and *Lasioglossum*

was negligible owing to their low relative abundances (d' model without *Apis* and *Lasioglossum*: treatment effect $F_{1,61} = 0.17$, $P = 0.68$). Competition between exotic and native plants for pollinators played a minor role, as exotics accounted for only 8.3% (± 3.0 s.e.m.) of the total visitation frequency at unrestored sites.

More generalized networks (H_2') and species (d') at restored sites indicate greater functional redundancy and lower mutual dependencies in restored plant–pollinator communities. Greater generalization is also associated with larger niche complementarity of pollinators and a 'sampling effect', which refers to the increased likelihood of including highly effective pollinators in the pollinator spectrum of a plant[17,18]. These responses address the core aims of ecological restoration: elevated functional redundancy enhances ecosystem resilience[19]; lower mutual dependencies facilitate functional robustness to local species loss or decline in populations of certain pollinator species[20]; and niche complementarity and sampling effect increase the functional performance of the pollinator community[9,18].

The observed changes in pollinator interaction behaviour and network structure had implications for plant reproduction. Plants
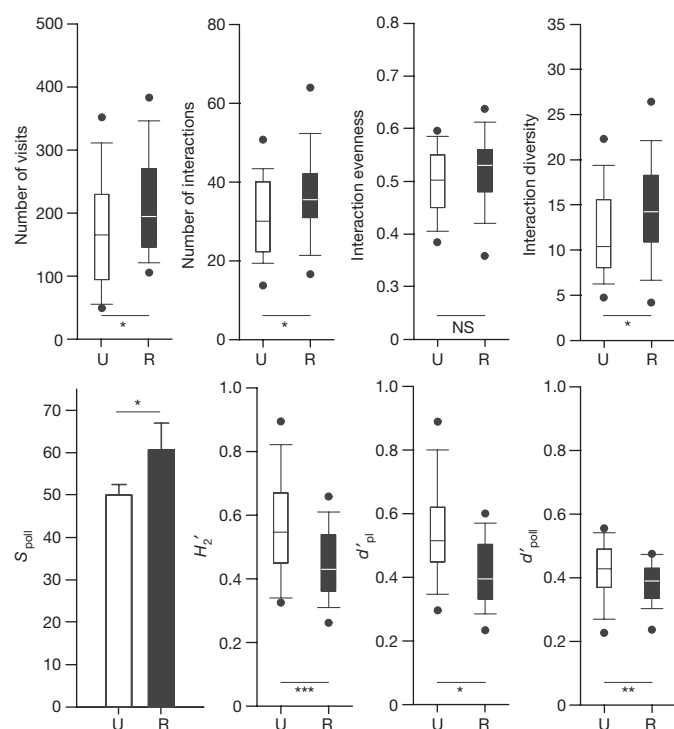
Figure 2 | Treatment effects on pollinator communities and network structure. Number of pollinator species (S_{poll}; $n = 8$ sites; Welch's $t_4 = 3.14$, $P = 0.035$; data are mean $\pm$ s.d. and shown in Extended Data Table 1) and network metrics ($n = 64$ networks; data shown in Supplementary Table 2) in unrestored (U, white bars) and restored (R, black bars) plant–pollinator communities. Metrics include number of visits, number of interactions, interaction evenness, interaction diversity, network specialization (H_2'), and plant (d'_{pl}) and pollinator (d'_{poll}) specialization. Box plots depict the median $\pm$ 5th, 10th and 25th percentiles; statistics are shown in Table 1. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, NS, not significant.

at restored sites produced 17.4% more flowers (floral abundance: 0.27 ± 0.037 versus 0.23 ± 0.037 (mean $\pm$ s.e.m.), Table 1) and attracted 22.9% more visits (6,750 versus 5,490 visits; Fig. 2), which correlated with a larger total fruit production (fruit crop) and higher proportion of flowers producing fruit (fruit set) across the most common species (Fig. 3 and Table 1). The three endemic palms *Nephrosperma vanhoutteanum*, *Phoenicophorium borsigianum*, and *Roscheria melanochaetes* were among the most abundant and generalized plant species (Extended Data Table 3) and their fruit sets benefited the most from the removal of exotics (Extended Data Fig. 2). A positive relationship between generalization and fruit production has also been observed in other island plant–pollinator communities[17], supporting the importance of super-generalist mutualists on islands[21].

The removal of exotic plants appeared to improve pollination—flowers were more frequently visited and native plants produced more fruit at restored sites. This interpretation was supported by a positive relationship between fruit set and visitation frequency (Table 1 and Extended Data Fig. 3). Plants at unrestored sites were likely to be pollinator-limited, as fruit set was lower there than at restored sites and increased as a function of visitation, approaching similar levels of fruit set only at high visitation rates (Fig. 3). Plants at restored sites had similar fruit set levels throughout the range of visitation rates, possibly owing to a saturating functional response of pollinators to increasing floral abundance[22]. This result suggests a higher pollinator efficacy compared to unrestored sites, notwithstanding the lower performance costs often associated with generalist pollinator species[23]. However, pollinator individuals, despite belonging to generalist species in the networks, may respond to the higher purity of native floral resources through changes in their foraging behaviour, which can result in higher pollination quality[24]. Thus, one plausible explanation for this increased
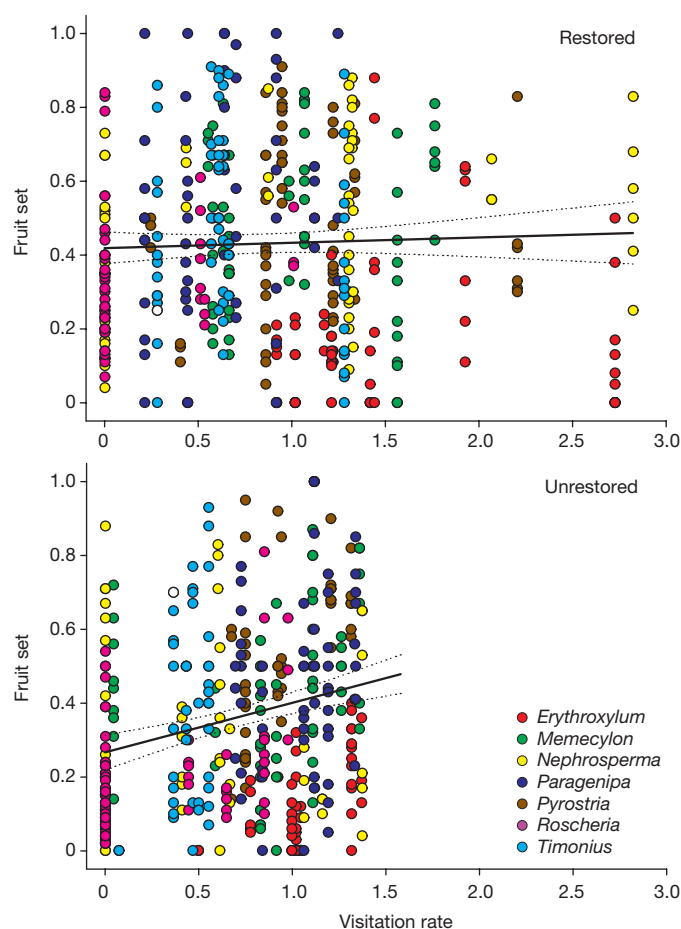

Figure 3 | Fruit set increased with visitation rate at unrestored sites. Visitation rates (square-root-transformed; $n = 810$, seven most common species across all sites) of >1.5 visits per flower per hour were only observed at restored sites. Mean fruit set was higher at restored sites than unrestored sites (see Table 1 for statistics of all ten species). Shown are lines of best fit (solid) with 95% confidence interval (dotted).

efficacy is that the removal of the dense thickets of exotic plants enabled pollinators to detect and approach native flowers, increasing visitation frequency to natives, interaction diversity, generalization of native networks and fruit set. Whether the structure and functioning of the restored networks resemble those of undisturbed areas is, however, unknown, as no such 'reference' sites exist on Mahé.

The effect of anthropogenic habitat degradation on the structure of interaction networks has been well documented[25,26]. When exotic plants invade ecosystems, a subsequent decline in pollinator visitation, reproduction of native plants, and abundance and richness of native arthropod species is frequently reported[27,28]. However, few studies have experimentally investigated the community-level effects of removing exotic plants on biotic interactions (Supplementary Table 1). Two findings stand out: that removing exotic plants may disrupt the indirect facilitation of native plants (albeit on a small spatial scale), and the restoration of biotic interactions, especially of higher trophic levels, is related to time since intervention (Supplementary Table 1). Notably, network metrics in our study also changed over the 8-month period (for example, number of visits increased, and H_2', d'_{pl} and d'_{poll} decreased), which may be a result of the season or the time since restoration, indicated by significant main and interaction effects, respectively (Table 1). Similarly, native species diversity and abundance increased across multiple trophic levels 2 years after the removal of exotic plants in the Azores[29].

Previous simulation studies on woodland restoration have indicated that plant–pollinator networks undergo a succession of increasing functional redundancy and complementarity following restoration[3].

Table 1 | Effects of vegetation restoration on plant–pollinator communities and network structure

a

Model type	Predictor	β	t	P
GLS	Number of visits (log)			
	Best model, AICcWt $=0.60$, $D^2=0.14$, ΔAICc $=1.72$			
	Month	0.068	2.94	0.005
	Treatment	−0.305	−2.42	0.019
LM	Number of interactions			
	Best model, AICcWt $=0.51$, Adj. $R^2=0.05$, $F_{1,62}=4.16$, $P=0.046$, ΔAICc $=1.95$			
	Treatment	−5.500	−2.039	0.046
LM	Interaction evenness			
	Best model, AICcWt $=0.44$, Adj. $R^2=0.11$, $F_{1,62}=8.94$, $P=0.004$, ΔAICc $=0.24$			
	Month	−0.010	−2.990	0.004
	Alternative model AICcWt $=0.39$, Adj. $R^2=0.13$, $F_{2,61}=5.53$, $P=0.006$			
	Month	−0.010	−3.013	0.004
	Treatment	−0.022	−1.406	0.165
LM	Interaction diversity			
	Best model, AICcWt $=0.42$, Adj. $R^2=0.09$, $F_{2,61}=3.96$, $P=0.024$, ΔAICc $=1.31$			
	Month	−0.553	−1.876	0.065
	Treatment	−2.835	−2.099	0.040
GLS	H_2'			
	Best model, AICcWt $=0.71$, $D^2=0.27$, ΔAICc $=1.84$			
	Month	−0.022	−3.487	0.001
	Treatment	0.131	3.882	<0.001

b

Model type	Random effect	Predictor	β	t	P
LMM	Crossed: pollinator species, site	d'_{poll} ($N_{obs}=703$; $N_{poll}=67$; $N_{sites}=8$)			
		Best model, AICcWt $=0.90$, $R^2_{LMM(m)}=0.04$, $R^2_{LMM(c)}=0.22$, ΔAICc $=5.74$			
		Month	−0.014	−2.753	0.006
		Treatment	−0.026	−0.573	0.572
		Month $\times$ treatment	0.021	2.997	0.003
LMM	Crossed: plant species, site	d'_{pl} ($N_{obs}=440$; $N_{plants}=29$; $N_{sites}=8$)			
		Best model, AICcWt $=0.77$, $R^2_{LMM(m)}=0.07$, $R^2_{LMM(c)}=0.46$, ΔAICc $=3.01$			
		Month	−0.024	−4.189	<0.001
		Treatment	0.023	0.363	0.722
		Month $\times$ treatment	0.019	2.257	0.026
LMM	Crossed: plant abundance (log), plant species, site	Floral abundance (log; $N_{obs}=108$; $N_{Plabund}=55$; $N_{plants}=23$; $N_{sites}=8$)			
		Best model, AICcWt $=0.71$, $R^2_{LMM(m)}=0.02$, $R^2_{LMM(c)}=0.56$			
		Treatment	−0.372	−2.238	0.028
GLMM (Poisson)	Nested: branch/plant individual/plant species Crossed: site	Fruit crop ($N_{obs}=1,035$; $N_{branch:indiv}=159$; $N_{indiv:plants}=53$; $N_{plants}=10$; $N_{sites}=8$)			
		Best model, AICcWt $=0.99$, $R^2_{GLMM(m)}=0.01$, $R^2_{GLMM(c)}=0.60$			
		Treatment	−0.403	−5.147	<0.001
GLMM (binomial)	Nested: branch/plant individual/plant species Crossed: site	Fruit set ($N_{obs}=1,035$; $N_{branch:indiv}=159$; $N_{indiv:plants}=53$; $N_{plants}=10$; $N_{sites}=8$)			
		Best model, AICcWt $=0.95$, $R^2_{GLMM(m)}=0.01$, $R^2_{GLMM(c)}=0.41$			
		Treatment	−0.652	−3.766	<0.001
GLMM (binomial)	Nested: branch/plant individual/plant species Crossed: site	Fruit set ($N_{obs}=975$; $N_{branch:indiv}=159$; $N_{indiv:plants}=53$; $N_{plants}=10$; $N_{sites}=8$)			
		Best model, AICcWt $=0.90$, $R^2_{GLMM(m)}=0.02$, $R^2_{GLMM(c)}=0.41$			
		Visitation rate (sqrt)	0.139	4.515	<0.001
		Treatment	−0.890	−4.833	<0.001
		Visitation rate (sqrt) $\times$ treatment	0.449	9.062	<0.001
GLMM (binomial)	Nested: branch/plant individual/plant species Crossed: site	Fruit set ($N_{obs}=975$; $N_{branch:indiv}=159$; $N_{indiv:plants}=53$; $N_{plants}=10$; $N_{sites}=8$)			
		Best model, AICcWt $=1.00$, $R^2_{GLMM(m)}=0.01$, $R^2_{GLMM(c)}=0.41$			
		Visitation frequency (sqrt)	0.077	2.111	0.035
		Treatment	−0.754	−4.414	<0.001
		Visitation frequency (sqrt) $\times$ treatment	0.358	6.229	<0.001

Presented are statistics of the best minimal adequate models. We also showed alternative models if ΔAICc < 0.5. Full models included main and interaction effects of the predictors 'month' and 'treatment' (**a**; d'_{poll} and d'_{pl}), only 'treatment' (floral abundance and fruit crop and set), or 'visitation frequency/rate' and 'treatment' (fruit set). Model selection was based on AICc, and ΔAICc indicates the difference between the best and next best model. Given are also AICc weights (AICcWt) showing model probabilities. **a**, Models are based on the number of networks ($n=64$), assuming largely spatial and temporal independence in network parameters (see Methods). **b**, Structurally complex models with replicated sampling across species or individuals at each site including 'site' as random effect. Month was not fitted for response variables that span the entire season (floral abundance, fruit crop and set). Coefficients of determination: adjusted R^2 (linear model, LM), D^2 (the amount of deviance accounted for by the model; generalized least square, GLS), and marginal and conditional $R^2_{(G)LMM}$ (R^2-equivalent for mixed models; linear mixed model (LMM) and generalized linear mixed model (GLMM)). Restored sites were used as reference level of the factor treatment. $d'_{pl}=29$ native species; $d'_{poll}=$ only bees and wasps, flies, birds and lizards with origin information. Fruit crop refers to the number of fruit produced by the plant community at each site (conservation relevance), and fruit set describes the proportion of flowers that set fruit (ecological relevance). To assess the relationship between fruit set and pollinator visitation, we modelled two measures of visitation: weighted visitation rate (see Methods) and visitation frequency. Visitation rate (visits per flower per hour) represents the number of visits of a pollinator individual to observed flowers, that is, a per-capita measure of pollination. Visitation frequency, calculated as visitation rate multiplied by the floral abundance of the visited plant species (see Methods), assesses the effect of community-wide floral abundance on the relationship between fruit set and pollinator behaviour.

Our experiments indicate that restoration trajectories towards functionally more diverse (that is, complementary) and robust (that is, redundant) plant–pollinator assemblages are established as early as the first post-restoration flowering season. The prompt response to the removal of exotics may be facilitated by high 'ecological memory' in inselberg communities[30], that is, the assemblage of functionally similar species, interactions and structures that supports reorganization of an ecosystem after disturbance[5], and the spatial proximity to pollinator source populations in the surrounding forest[8].

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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METHODS

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment.

Study sites. We collected interaction network data from eight discrete inselberg (steep-sided monolithic outcrops) plant communities on the granitic island of Mahé, Seychelles (Fig. 1; Western Indian Ocean Biodiversity Hotspot), for eight consecutive months between September 2012 and April 2013 (the full flowering season; Extended Data Table 1). The eight sites constitute the majority of mid-altitude, highly diverse inselbergs on Mahé. All study sites were surrounded by steep cliffs on at least three sides of the inselberg, separating typical inselberg vegetation on the plateau from the surrounding forest, and creating comparable inselberg climates[31]. Selection criteria for inselberg study sites included elevation between 300 and 600 m above sea level, approximately 1 ha in size, flat-topped, similar native plant communities and accessibility. Inselbergs harbour endemic dwarf forest, consisting almost entirely of perennial shrubs and small trees, forming refuges of formerly widespread woody species (Extended Data Table 3). Many inselbergs experience ecosystem degradation by encroaching exotic plant species. The most dominant exotic plants are woody perennial shrubs and trees, which are widespread invaders of island ecosystems, including *Psidium cattleianum*, *Chrysobalanus icaco*, *Cinnamomum verum* and *Alstonia macrophylla*. The establishment and subsequent spread of these plants on inselbergs have, however, been more gradual than in the surrounding forest owing to lower levels of human disturbance, harsh climate, poor soil and the steep cliffs that provide a natural barrier against plant invasion. Ecological restoration, including the removal of exotic plants, is considered a suitable tool to mitigate the threat by exotic species to the long-term viability of native ecosystems[10]. Detailed descriptions of abiotic and biotic site characteristics are given elsewhere[16,32].

To investigate the effect of vegetation restoration on plant–pollinator networks, we removed all exotic plants from four inselbergs between 15 November 2011 and 10 February 2012 by cutting stems close to the ground and applying systemic herbicide to the cut stumps[33]. Treatment sites were selected to represent low and high degrees of invasion equally, with two sites per invasion level and treatment (Extended Data Table 1). Control and treatment sites were similar in plant (adonis: $R^2 = 0.054$, $P = 0.95$, Supplementary Methods 1) and pollinator communities ($R^2 = 0.187$, $P = 0.59$, data from 2007–2008; ref 16) before the removal of the exotic plant species. There was no correlation between the spatial distance between sites and plant and pollinator community compositions (Mantel tests; pre-removal: plants $r = 0.165$, $P = 0.29$; pollinators $r = 0.197$, $P = 0.32$; post-removal: pollinators $r = 0.231$, $P = 0.16$), indicating no site-related inherent bias and spatial-autocorrelation between treatment levels (see also Supplementary Methods 2 and Extended Data Table 4). The mean number of native plant species across sites was similar between treatments (15.0 ± 1.8 versus 16.0 ± 2.5; Student's $t_6 = -0.63$, $P = 0.55$). Cut plant material was compiled and left to rot on site. Exotic plant removal is a widely used method in ecological restoration following the assisted natural regeneration approach[10]. This approach alters plant communities in two fundamental ways: (1) it markedly reduces plant density, with swathes of open habitat shortly after intervention; and (2) it increases the availability of resources owing to reduced competition for nutrients, water and space between native and exotic plants. Both alterations can affect plant–pollinator interactions directly, as flowers are more easily detectable across the landscape without changes to the effective distance between conspecifics[34], and native plants can allocate more available resources to flowers and fruit.

To ensure long-term sustainability of the restoration efforts, local authorities have committed to maintaining the management of exotic plants at the experimental sites and incorporate inselberg habitat restoration into a national conservation strategy to protect native biodiversity.

Plant–pollinator networks. To compile 64 plant–pollinator networks (8 sites × 8 months; Supplementary Table 2), we used established sampling protocols for focal point observations of plant–pollinator interactions in heterogeneous vegetation[16,35]. Binary networks consist of bars (plant and animal species) and links (interactions), in which the widths of the bars and links represent the abundance of flowers and animals and a measure of visitation strength, respectively (Fig. 1). Flower visitors (hereafter 'pollinators', a total of 144 spp.; Supplementary Table 3) were recorded if they touched the sexual parts of flowers (Supplementary Methods 2). We observed all woody flowering species (38 spp.; Extended Data Table 3), each for 3.03 ± 0.62 h per network. Flowers were recorded monthly in 1 m^3 cubes placed stratified, randomly along several transects spanning the extent of the inselbergs[16] (Extended Data Table 1). Floral abundance was expressed as the number of flowers per sample cube. Pollinator abundance was determined by the total number of visits of each pollinator taxon to flowering plants in a network. To determine the links between plants and pollinators, we calculated the visitation

frequency between an animal species i and a plant species j as mean visitation rate of animal species i multiplied by the floral abundance of plant species j visited by i[35,36]. Visitation frequency was used to calculate all network-level metrics (interaction richness, evenness and diversity, H_2', d'; Supplementary Methods 2). The observation methods used here reduce the risk of under-sampling[16,37], all metrics are fully quantitative and H_2', d' are robust to sampling bias, which is pervasive in pollination network studies[38].

We calculated two distance indices to test for qualitative and quantitative differences in plant–pollinator communities within and across sites and months. Specifically, we used the Jaccard (binary) and Bray–Curtis (quantitative) indices[39] to determine species overlap and similarities in visits among networks, respectively. Species in monthly networks within sites were unique to each network by 82% (± 4.6 s.d.; pollinators only, $67 \pm 4.3\%$; plants only, $57 \pm 10.7\%$), and these values were similar to species uniqueness in networks across sites in given months ($85 \pm 1.4\%$; Welch's $t_{8.4} = 1.88$, $P = 0.095$; pollinators only: $68 \pm 3.3\%$, Welch's $t_{12.9} = 0.42$, $P = 0.685$; plants only: $64 \pm 6.5\%$, Welch's $t_{11.5} = 1.58$, $P = 0.140$). Likewise, pollinator and flower communities were highly variable across sites and equally variable across months (mean Bray–Curtis distance $\pm$ s.d. of relative number of visits; pollinators per site: 0.43 ± 0.09, pollinators per month: 0.46 ± 0.06, Welch's $t_{12.7} = 0.64$, $P = 0.533$; flowers per site: 0.59 ± 0.06, flowers per months: 0.63 ± 0.07, Welch's $t_{13.8} = 1.17$, $P = 0.262$). The 64 networks are therefore temporally and spatially largely disconnected, which implies a high degree of ecological independence of each network. Finally, because plant communities harboured slightly different species, we conducted all relevant analyses without native plant species that occurred only in one treatment (8 spp. marked with 'np' in Extended Data Table 3). We fitted the same models as with the full dataset (see below) and found that the results were qualitatively equivalent and quantitatively slightly stronger than those of the entire plant communities (Supplementary Table 4).

Reproductive performance. We measured reproductive performance of native plants as the number of fruit produced at each site (fruit crop), and the proportion of flowers that set fruit (fruit set). We monitored fruit crop and set of ten native species, which occurred at two or more sites per treatment in sufficient numbers of individuals (>3 flowering females) for between-treatment comparison. Increasing total fruit crop is a restoration objective, and changes in fruit set indicate functional changes driven by pollinator behaviour and/or nutrient availability[40]. We determined the fruit set of 37,898 buds on 1,035 branches or inflorescences nested in 346 plants. All ten species depend mostly on pollen vectors for reproduction, as six species are dioecious or consecutively monoecious and four are self-incompatible hermaphrodites[16]. Furthermore, eight of ten species always produced fruits with one or two seeds (*Timonius flavescens* and *Nepenthes pervillei* contained multiple seeds per fruit), thus fruit set corresponded closely with seed set.

Analyses. Analyses were conducted in R 3.1.1 (R Development Core Team; http://www.R-project.org), using the following libraries: bipartite, vegan, lmer, nlme, lmerTest and MuMIn. To test the response of network metrics to restoration (Supplementary Methods 2), we fitted two types of models: (1) linear and generalized least square (GLS) models without random effects, and (2) linear mixed models (LMM) with nested random terms. Network-level response variables without replication across species or individuals within a site (that is, number of visits, number of interactions, interaction evenness, interaction diversity and H_2') were fitted with the linear model or GLS (Table 1a), depending on the variance structure. When heterogeneity was detected we used the varIdent function with GLS models to assign weight to the variance by the treatment stratum[41]. We analysed species-specific responses of plant (d'_{pl}) and pollinator specialization (d'_{poll}) and floral abundance to treatment with linear mixed models (LMM). These response variables contain data on within-site variation across species. We thus fitted species and sites as crossed random effects and month (only d') and treatment (all) as fixed effects (Table 1b). The linear and GLS models were based on the number of networks ($n = 64$), treating each network independently. The following rationale warrants the analytical approach: eight study sites may be considered statistically too low to detect ecologically meaningful results despite the extent of the ecosystem-level field experiment. To avoid an inflated 'type I error', we repeatedly sampled highly dynamic interaction networks over time. We showed that the composition of plant and pollinator communities in the networks was highly variable within and among sites and months (see above), suggesting a low degree of overlap between networks from the same site and month. Further, each observation session focused on a different plant individual, which ensured within-site spatial separation between consecutively observed interactions. Finally, support for our approach comes from the visual inspection of partial residual plots, which depict treatment effect after removing the effects of time (fixed effect) and site (random effect in the linear mixed model; Extended Data Fig. 4). We therefore considered networks independently for structurally simpler models

on network metrics (number of visits, number of interactions, interaction evenness, interaction diversity and H_2'; Table 1a) and fitted linear and GLS models with the fixed main effects month and treatment and the interaction between month and treatment. The best model was selected with the dredge function (MuMIn package) based on AICc. AICc weights are presented to indicate the level of support for selecting the most parsimonious among a set of models. ΔAICc assesses the support of the best and second best models, and alternative models were shown only when ΔAICc < 0.5 (Table 1). Also given are AICc weights (AICcWt) showing model probabilities[42]. We computed the adjusted R^2, D^2, and marginal and conditional $R^2_{(G)LMM}$ as goodness-of-fit metrics for linear, GLS, and linear mixed models, respectively. D^2 is the amount of deviance accounted for by the model[43], and marginal and conditional $R^2_{(G)LMM}$ are coefficients of determination for mixed models describing the proportion of variance explained by the fixed factors only (marginal $R^2_{(G)LMM}$) and by both the fixed and random effects (conditional $R^2_{(G)LMM}$)[44]. To test the influence of seasonality we initially ran models with each one of three time effects: linear across months, a quadratic term to reflect a hump-shaped seasonality and a factor with eight levels. All models showed a poorer (>AICc) fit of the quadratic term and the factor compared to the linear fit. We therefore fitted in all models the linear time effect.

Treatment effects on total fruit crop and fruit set were tested with generalized mixed models (GLMM) with Poisson and binomial distributions, respectively. To account for unbalanced data and spatial and within-species dependencies, we used species (in the model containing all species), plant and branch identity as nested and site as crossed random effects. In the binomial models, we also weighted sample sizes by the number of flowers recorded on each plant to calculate fruit set (cbind function). Fruit set was also tested separately for each species (Supplementary Methods 3, Extended Data Fig. 2). To assess the functional relationship between fruit set as a proxy for plant reproductive performance and pollinator behaviour, we calculated weighted visitation rate and used a reduced fruit dataset containing only those species that were visited by pollinators in a given network ($n = 975$). Visitation rate represents the number of visits of a pollinator individual to observed flowers, expressed as rate of visits per flower per hour. Weighting was achieved in two steps: first, because dioecious palms attracted a large proportion of visitors to either male or female flowers, we considered the distribution of pollinator species between sexes in a weighted visitation rate (VR) as VR (per flower per hour) = $\Sigma_i(v_i \times 2 \times \min(m_i, f_i)/(m_i + f_i))$, where v_i is the total number of visits of pollinator i; m_i and f_i are the number of visits to male and female flowers, respectively, visited by i in the network. This approach ensures that pollinators with equal visits to male and female flowers are fully weighted (a ratio of 1) whereas pollinators that only visit one sex are not considered (a ratio of 0). The second step incorporated the importance of a pollinator species for a plant species by dividing weighted visitation rate by the total sum of all visits. The same steps were repeated with visitation rate to assess the influence of community-wide floral abundance on the relationship between fruit set and pollinator behaviour (Extended Data Fig. 3).

Data availability. The plant–pollinator interaction network data (raw data) that support the findings of this study are available from the Interaction Web Database (IWDB) at https://www.nceas.ucsb.edu/interactionweb/. Data presented in the figures (except Fig. 1, which is available from the IWDB) are included with the manuscript as source data (Fig. 3 and Extended Data Figs 1, 2, 3) or in the Supplementary Information (Fig. 2). Other datasets generated/analysed during the current study are available from the corresponding author on reasonable request.

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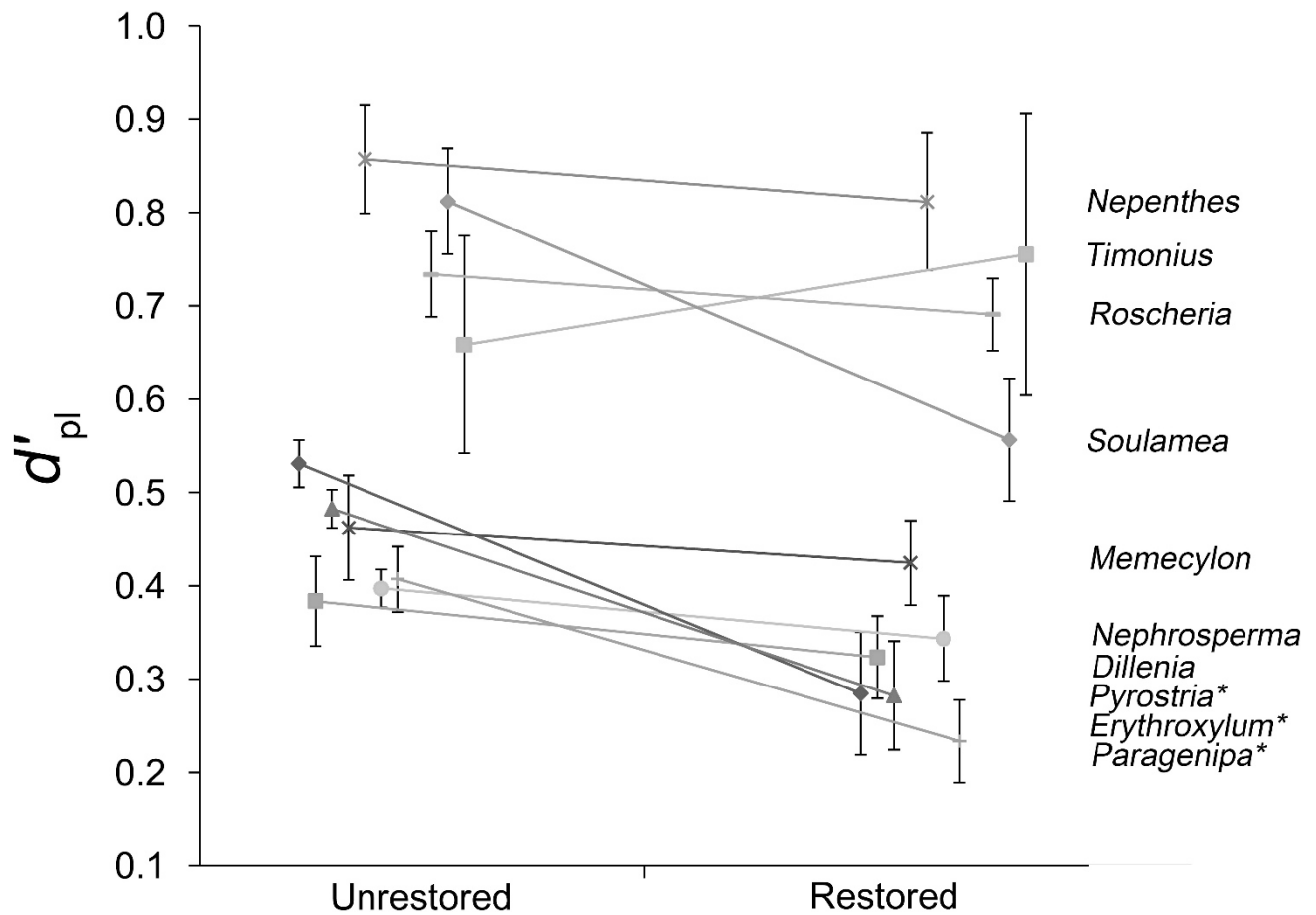
Extended Data Figure 1 | Level of specialization (d'_{pl}) of the ten most common flowering plant species across all networks. Asterisks indicate a significantly higher level of specialization (mean ± s.e.m.) in the unrestored compared to the restored networks. For full species names see Extended Data Table 3. Linear mixed model: *P. bibracteata* $t = 2.836$, $P = 0.036$; *P. lancifolia* $t = 2.644$, $P = 0.038$; *E. sechellarum* (variance structure weighted by treatment) $t = 3.141$, $P = 0.020$. Site was entered as random effect in all models. All other species $P > 0.05$.
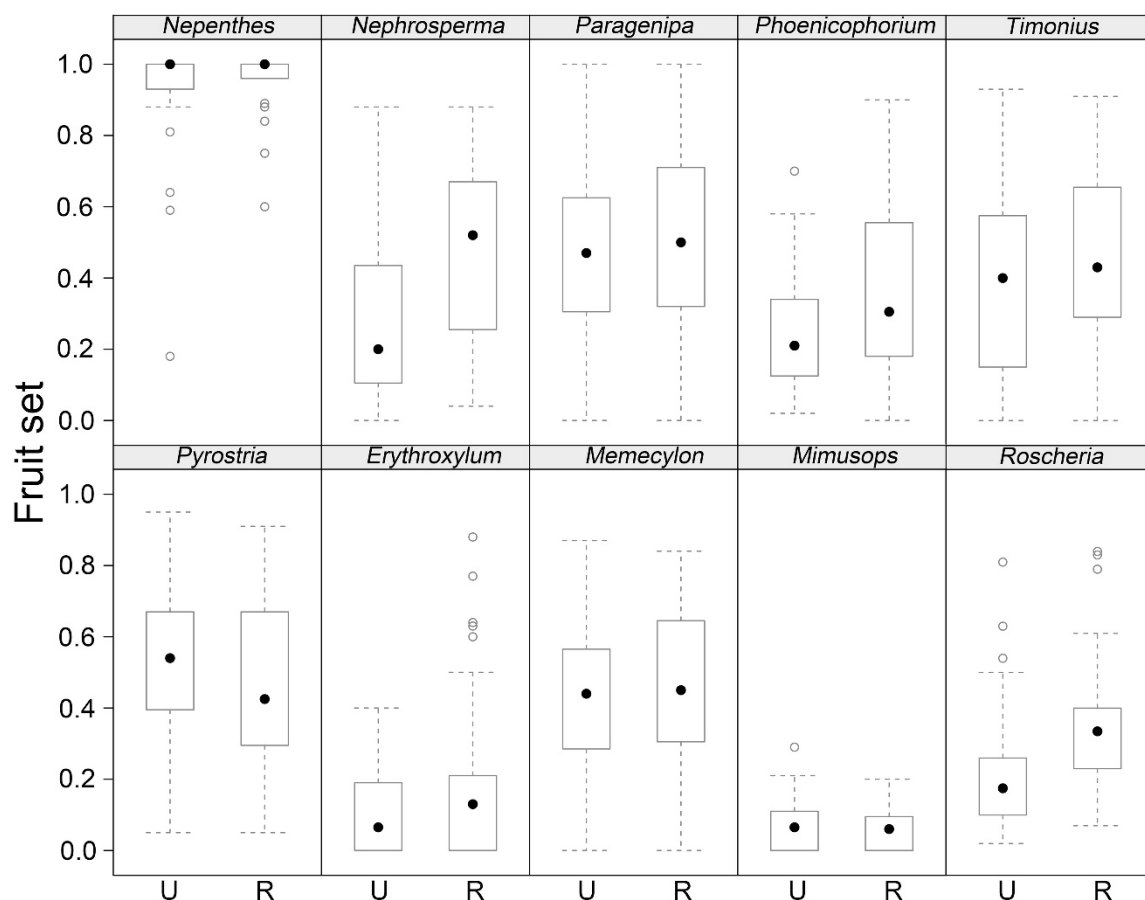
Extended Data Figure 2 | Fruit set of the ten most abundant plant species at restored and unrestored sites. The species occurred at ≥ 2 sites per treatment (*Nepenthes*, *Mimusops*), seven sites (*Roscheria*, *Timonius*), and eight sites (all others). The reproductive systems included dioecy (*Pyrostria*, *Nepenthes*, *Timonius*), monoecy with temporally separated male and female flowers (*Roscheria*, *Phoenicophorium*, *Nephrosperma*) and protandrous hermaphrodite flowers (*Erythroxylum*, *Memecylon*, *Mimusops*, *Paragenipa*). The three palm species *Roscheria*, *Phoenicophorium* and *Nephrosperma* had higher fruit set at the restored sites (GLMM: *Nephrosperma* $n = 120$, $z = 2.54$, $P = 0.011$, *Phoenicophorium* $n = 120$, $z = 2.66$, $P = 0.008$, *Roscheria* $n = 108$, $z = 2.29$, $P = 0.022$), the other species showed no clear species-specific pattern. The boxes depict the median and 25th and 75th percentiles, whiskers show $1.5 \times$ interquartile range of the data, white circles indicate outliers.
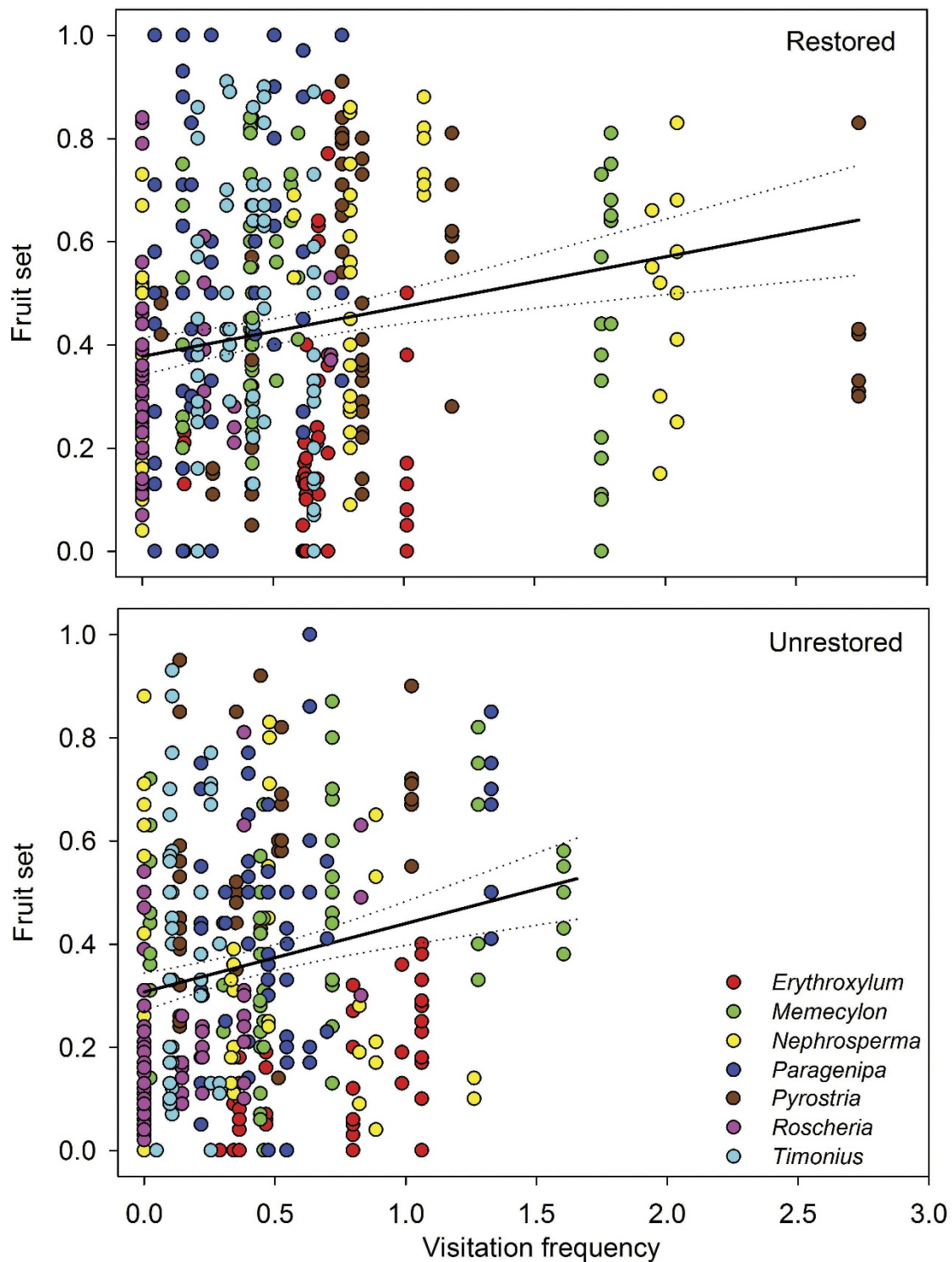
Extended Data Figure 3 | Fruit set increased with visitation frequency at unrestored sites. Square-root-transformed visitation frequency ($n = 810$, displayed seven most common species across all sites) of > 1.6 (see Methods) were only observed at restored sites. Mean fruit set was higher at restored sites than unrestored sites (see Table 1 for statistics of all ten species included in reproductive performance analysis). Shown are lines of best fit (solid) and 95% confidence interval (dotted).
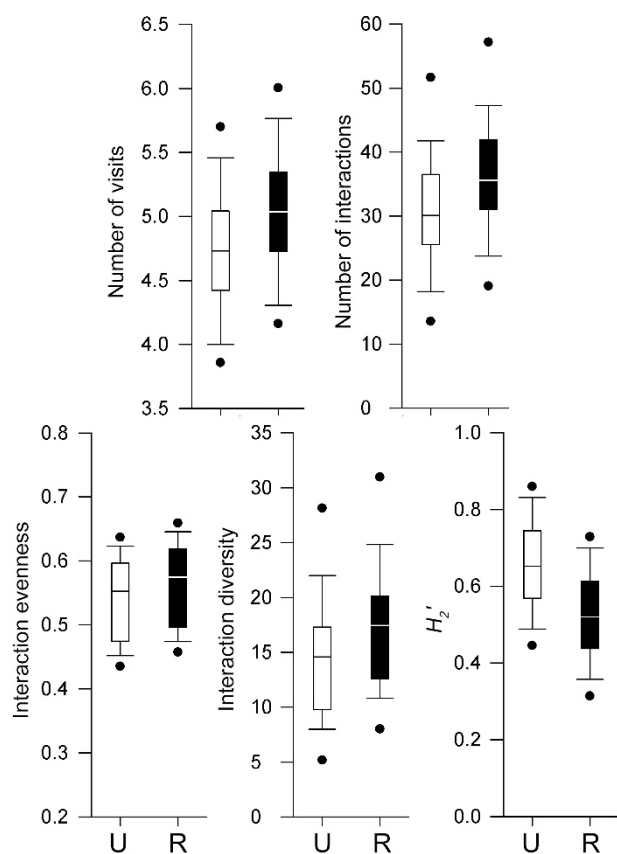
Extended Data Figure 4 | Partial residual plots of network metrics.
Box plots of partial residuals show the effect of treatment after removing
the effect of month and site. Partial residuals were calculated from linear
mixed models with month and treatment as fixed main and interaction
effects and site as random effect. Shown are partial residuals plus intercept.
Metrics include number of visits (visits, log-transformed), number of
interactions, interaction evenness, interaction diversity and network
specialization (H_2'). Boxplots depict the median $\pm$ 5th, 10th and 25th
percentiles.

Extended Data Table 1 | Study site details and summary of plant and pollinator communities

Sites	Restored				Unrestored			
	Bernica	Salazie	Tea Plantation	Trois Frères	Casse Dent	Copolia	La Reserve	Rosebelle
Location	55°26'51-53" E 4°40'8-16" S	55°26'56"-27'01" E 4°39'18-20" S	55°26'21-27" E 4°39'40-42" S	55°26'48-53" E 4°38'10-14" S	55°26'11-15" E 4°39'16-17" S	55°27'23-28" E 4°40'7-12" S	55°30'11-15" E 4°42'32-33" S	55°27'39-41" E , 4°39'38-41" S
Size (ha)	~ 1.7	~ 0.8	~ 1.4	~ 1.3	~ 0.7	~ 1.3	~ 1.3	~ 0.7
Altitude (m a.s.l.)	320	410	420	460	490	570	300	580
Number of transects	4	3	3	4	3	4	3	4
Total length transects (m)	400	350	400	425	225	400	300	300
Ratio exotic:native plants	0.03	0.44	0.47	0.22	0.15	0.10	0.39	0.38
Number of exotic plants removed	338	2855	22891	13616	n/a	n/a	n/a	n/a
Number of native plant species observed (exotics)	17	14	13	16	15 (2)	19 (2)	13 (4)	17 (4)
Number of pollinator species	53	63	59	68	51	53	49	47

Extended Data Table 2 | Results of full-factorial linear mixed model

Predictor	β	t	P
Lasioglossum mahense	0.034	0.145	0.885
Unrestored	0.860	2.661	**0.018**
L. mahense × unrestored	-0.653	-1.977	**0.050**

Comparison of species-level specialization d'_{poll} (log-transformed) between species (the exotic honey bee *Apis mellifera* versus the native sweat bee *Lasioglossum mahense*) and treatments (restored versus unrestored). Site was entered as a random effect. Numbers in bold are significant at $\alpha \leq 0.05$.

Extended Data Table 3 | List of plant species included in the study

Plant species*	Family	Origin	IUCN status†	Floral abundance‡	No. pollinator species§		Sites with flowering plants‖
					Restored	Unrestored	
Alstonia macrophylla Wall. ex G.Don	Apocynaceae	Exotic	–	0.240	na	4	R:0; U:4
Aphloia theiformis (Vahl) Benn.	Flacourtiaceae	Native	NT	0.456	7	4	R:2; U:1
Ardisia crenata Sims	Myrsinaceae	Exotic	–	0.146	na	0	R:0; U:1
Campnosperma seychellarum March	Anacardiaceae	Endemic	CR	0.144	14	10	R:1; U:2
Chrysobalanus icaco L.	Chrysobalanaceae	Exotic	–	0.231	na	6	R:0; U:1
Cinnamomum verum J.Presl.	Lauraceae	Exotic	–	2.378	na	20	R:0; U:4
Colea seychellarum Seem.	Bignoniaceae	Endemic	EN	0.008	np	4	R:0; U:1
Craterispermum microdon Baker	Rubiaceae	Endemic	EN	0.036	np	12	R:0; U:1
Deckenia nobilis H.Wendl. ex Seem.	Palmae	Endemic	NT	0.627	5	11	R:1; U:1
Dillenia ferruginea (Baill.) Gilg	Dilleniaceae	Endemic	NT	0.499	26	10	R:4; U:2
Dracaena reflexa Lam. var. *angustifolia* Baker	Dracenaceae	Native	LC	0.032	5	5	R:1; U:1
Diospyros boiviniana (Baill.) G. E. Schatz & Lowry	Ebenaceae	Endemic	VU	0.028	0	np	R:1; U:0
Erythroxylum sechellarum O.E.Schulz	Erythroxylaceae	Endemic	LC	2.655	30	18	**R:4; U:4**
Excoecaria benthamiana Hemsley	Euphorbiaceae	Endemic	VU	1.185	7	26	R:1; U:3
Glionnetia sericea (Baker) Tirv.	Rubiaceae	Endemic	EN	0.155	np	1	R:0; U:2
Gynura sechellensis (Baker) Hemsl.	Asteraceae	Endemic	VU	0.013	np	0	R:0; U:1
Ixora pudica Baker	Rubiaceae	Endemic	NT	0.174	10	4	R:2; U:1
Medusagyne oppositifolia Baker	Medusagynaceae	Endemic	CR	0.023	8	np	R:1; U:0
Memecylon elaeagni Bl.	Melastomataceae	Endemic	LC	4.795	14	12	**R:4; U:4**
Mimusops sechellarum (Oliv.) Hemsl.	Sapotaceae	Endemic	NT	0.152	6	5	**R:2; U:2**
Nepenthes pervillei Bl.	Nepenthaceae	Endemic	NT	0.911	16	10	**R:2; U:2**
Nephrosperma vanhoutteanum (H.Wendl. ex van-Houtt.) Balf.f.	Palmae	Endemic	VU	4.583	44	26	**R:4; U:4**
Northea seychellana Hook.f.	Sapotaceae	Endemic	VU	0.049	np	8	R:0; U:2
Ochna kirkii Oliv.	Ochnaceae	Exotic	–	0.075	na	3	R:0; U:1
Paragenipa lancifolia (Bojer ex Baker) Tirveng. & Robbr.	Rubiaceae	Endemic	NT	1.419	18	10	**R:4; U:4**
Peponidium carinatum (Baker) Razafimandimbison	Rubiaceae	Endemic	VU	0.010	np	1	R:0; U:1
Phoenicophorium borsigianum (K.Koch.) Stuntz	Palmae	Endemic	LC	2.166	15	38	**R:2; U:3**
Pittosporum senacia Putt. subsp. *wrightii* (Hemsl.) Cufod.	Pittosporaceae	Native	VU	0.183	3	2	R:2; U:1
Polyscias crassa (Hemsl.) Lowry & G.M.Plunkett	Araliaceae	Endemic	VU	0.255	17	6	R:2; U:1
Premna serratifolia L.	Lamiaceae	Native	LC	0.086	6	11	R:1; U:1
Psidium cattleianum Sabine	Myrtaceae	Exotic	–	0.050	na	3	R:0; U:1
Psychotria pervillei Baker	Rubiaceae	Endemic	VU	0.463	14	9	R:3; U:4
Pyrostria bibracteata (Baker) Cavaco	Rubiaceae	Endemic	LC	1.357	24	13	**R:4; U:3**
Roscheria melanochaetes (H.Wendl.) H.Wendl. ex Balf.f.	Palmae	Endemic	NT	3.412	37	36	**R:3; U:4**
Soulamea terminalioides Baker	Simaroubaceae	Endemic	VU	0.878	31	14	**R:4; U:2**
Syzygium jambos (L.) Alston	Myrtaceae	Exotic	–	0.060	na	10	R:0; U:1
Syzygium wrightii (Baker) A.J.Scott	Myrtaceae	Endemic	VU	0.078	5	9	R:1; U:1
Timonius flavescens (Jacq.) Baker	Rubiaceae	Endemic	VU	1.125	15	8	**R:4; U:4**

*The following species have recently been renamed: *Diospyros boiviniana* = *Maba seychellarum*; *Polyscias crassa* = *Gastonia crassa*; *Pyrostria bibracteata* = *Canthium bibracteatum*; *Peponidium carinatum* = *Canthium carinatum*;

†LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; –, exotic species, not listed.

‡Abundance across all networks (sum of number of flowers per cube across the eight sites).

§Number of pollinator species is equal to number of interactions. na, not applicable; np, not present.

‖R, restored sites; U, unrestored sites; bold font indicates species included in reproductive performance analysis (fruit crop and fruit set).

Extended Data Table 4 | Spatial auto-correlation coefficients of community and network parameters across the study sites

Descriptor	Moran's I	P
Plant species	-0.1805	0.550
Pollinator species	-0.1378	0.936
Number of visits	-0.0841	0.345
Number of interactions	-0.0750	0.279
Visitation frequency	-0.0598	0.156
Interaction diversity	-0.2704	**0.036**
Interaction evenness	-0.2398	0.126
H_2'	-0.1720	0.619
Floral abundance	-0.1190	0.700
d'_{pl}	-0.1627	0.726
d'_{poll}	-0.0653	0.224

Numbers in bold are significant at $\alpha \leq 0.05$.