2

3   **Ecosystem restoration strengthens pollination network resilience**

4   **and function**

5

6   Christopher N. Kaiser-Bunbury[1], James Mougal[2], Andrew E. Whittington[3], Terence

7   Valentin[2], Ronny Gabriel[2], Jens M. Olesen[4], and Nico Blüthgen[1]

8

9   [1] Ecological Networks, Department of Biology, TU Darmstadt, 64287 Darmstadt,

10   Germany

11   [2] Seychelles National Parks Authority, PO Box 1240, Mahé, Seychelles

12   [3] Department of Archaeology, Anthropology & Forensic Science, Bournemouth

13   University, Poole, BH12 5BB, UK

14   [4] Ecology and Genetics, Department of Bioscience, Aarhus University, 8000 Aarhus

15   C, Denmark

16

17   Abstract

18   Land degradation results in declining biodiversity and disruption of ecosystem

19   functioning worldwide, particularly in the tropics[1]. Vegetation restoration is a common

20   tool to mitigate these impacts, increasingly aiming to restore ecosystem functions

21   rather than species diversity *per se*[2]. However, evidence from community

22   experiments on the impact of restoration practices on ecosystem functions is

23   scarce[3]. Pollination is an important ecosystem function, and global pollinator

24   declines attenuate the resistance of natural areas and agro-environments to

25   disturbances[4]. Thus, the ability of pollination functions to resist or recover from

26   disturbance (i.e. the functional resilience)[5,6] may be critical for ensuring a successful

27   restoration process[7]. We use a community field experiment to investigate the effects

28   of vegetation restoration – here the removal of exotic shrubs – on pollination. We

29   analyse 64 plant-pollinator networks and reproductive performance of the ten most

30   abundant plant species across four restored and four unrestored, disturbed

31   mountaintop communities. Restoration resulted in a marked increase in pollinator

32   species, visits to flowers, and interaction diversity. Interactions in restored networks

33   were more generalised than in unrestored networks, indicating higher functional

34   redundancy in restored communities. Shifts in interaction patterns had direct and

35   positive effects on pollination, especially increasing relative and total fruit production

36   of native plants. Pollinator limitation was prevalent at unrestored sites only, where

37   fruit set increased with pollinator visitation, approaching the higher fruit set levels of

38   restored plant communities. Our results show that vegetation restoration can

39   improve pollination, suggesting that degradation of ecosystem functions is at least

40   partially reversible. The degree of recovery may depend on the state of degradation

41   prior to restoration intervention and the proximity to pollinator source populations in

42   the surrounding landscape[5,8]. We demonstrated that network structure is a suitable

43   indicator for pollination quality, underpinning the usefulness of interaction networks in

44   environmental management[6,9].

45

46   Main text

47   The loss of biodiversity has the potential to disrupt ecosystems and their functioning.

48   Ecological restoration is often attempted to mitigate these effects[10]. Most restoration

49   efforts target vegetation – such as the removal of exotic plants and the deliberate

50   planting of desirable native species – in the hope that restoring the plant community

2

51   will allow other services to recover. Yet the efficacy of these interventions for

52   restoring ecosystem functions and services has rarely been assessed quantitatively.

53

54   Pollination is an important ecosystem function, as many wild plants and crops rely

55   heavily on pollinators for reproduction[11]. Pollinators are also particularly sensitive to

56   anthropogenic disturbance[12,13], which poses a threat to the pollination service they

57   provide[4]. Furthermore, restoring pollinator assemblages may be essential for

58   ecosystem restoration. A key unanswered question is whether the common practice

59   of restoring plant communities also leads to the restoration of pollinator assemblages

60   and the benefits they deliver. Here we report results of a study of isolated, rocky

61   mountaintops (inselbergs) in the Seychelles in which we experimentally assessed

62   the effects of vegetation restoration on pollinator assemblages and their services. In

63   particular, we quantified pollination networks and plant reproduction in both restored

64   and unrestored communities to assess structural and functional changes in plant-

65   pollinator communities as a response to vegetation restoration. We tested two main

66   questions: (1) Does vegetation restoration through exotic species removal increase

67   network interaction diversity? If so, (2) Does increase in interaction diversity in turn

68   restore pollination function and, thus, increase reproductive output of the plant

69   communities?

70

71   These questions are embedded in the conceptual framework that species interaction

72   networks are key features of ecosystems[2], which makes them useful to assess the

73   efficacy of restoration by providing comprehensive quantitative information on

74   structure and function of communities[14]. Weighted network metrics allow us to tease

75   apart the influence of species abundance, diversity, generalisation, and functional

76   overlap (Supplementary Methods 2)[15].

77

78   To account for temporal and spatial variation across a long tropical flowering season,

79   we collected eight monthly pollination networks from eight dwarf-forest plant

80   communities on discrete, mid-altitude inselbergs (64 networks; Fig. 1; Extended Data

81   Table 1) on the tropical island of Mahé, Seychelles. On four of the inselbergs all

82   exotic plants (~39,700 woody plants) were removed, referred to as 'restoration'

83   throughout ('restored' sites; for site selection criteria see Methods and

84   Supplementary Methods 1). The four 'unrestored' sites contained a similar number of

85   exotic species that flowered during the study (range 2–5 spp.), accounting for 25.3 ±

86   15.1% of all inselberg plants. Prior to restoration, restored and unrestored sites

87   contained a similar proportion of exotic plants (0.29 ± 0.21 vs. 0.25 ± 0.15 SD; SD

88   hereafter unless specified otherwise; $t_6 = 0.30$, $P = 0.78$; Extended Data Table 1).

89   After restoration, pollinators of all woody flowering plant species (38 spp.) were

90   scored for a total of 1525 observation hours, during which we recorded 581 species-

91   species interactions (links) and 12,235 pollinator visits to flowers. Pollinators

92   included bees and wasps (Hymenoptera: 25 spp.), flies (Diptera: 59 spp.), beetles

93   (Coleoptera: 38 spp.), moths and butterflies (Lepidoptera: 17 spp.), two bird species

94   (Nectariniidae, Pycnonotidae), and three lizard species (Gekkonidae, Scincidae).

95

96   Restoration markedly changed pollinator numbers, behaviour, performance, and

97   network structure in inselberg communities. Six to 14 months after restoration,

98   number of pollinator species was on average 21.6% higher across the four restored

99   compared to the unrestored inselbergs (Fig. 2). Monthly pollination networks showed

100 higher interaction richness and interaction diversity (a combined measure of

101 interaction richness and evenness) in restored networks, while interaction evenness

102 (a measure of the uniformity of the frequency of interactions) was similar between

103 treatments (Fig. 2, Table1). Overall, restored networks were more generalised than

104 unrestored networks (H_2', Fig. 2).

105

106 The observed network responses to restoration were mirrored by the plant

107 communities. Most native plants were more generalised in restored than unrestored

108 networks (d'_{pl}; Fig. 2; Extended Data Figure 1), attracting more pollinator species

109 ($\Delta_{poll} = 9.0 \pm 5.26$ pollinator spp. on 14 of 23 plants shared between treatments). At

110 restored sites, pollinator species were also more generalised in their partner

111 selection (d'_{poll}; Fig. 2, Table 1). This pattern was shaped by two super-generalist

112 and abundant pollinators, the native sweat bee *Lasioglossum mahense* (d'_{Lasio}

113 restored vs. unrestored: 0.17 ± 0.10 vs. 0.28 ± 0.23) and the exotic honey bee *Apis*

114 *mellifera* (d'_{Apis} restored vs. unrestored: 0.22 ± 0.18 vs. 0.40 ± 0.25; Extended Data

115 Table 2), which have both been previously shown to respond most strongly to exotic

116 plants on inselbergs[16]. Other pollinator species were also more generalised in the

117 restored habitats (e.g. d' of endemic flies, other bees and wasps, lizards and birds;

118 $F_{1,368.3} = 5.20$, $P = 0.023$), but their effect on overall network specialisation H_2'

119 without *Apis* and *Lasioglossum* was negligible due to their low relative abundances

120 (d' model without *Apis* and *Lasioglossum*: treatment effect $F_{1,61} = 0.17$, $P = 0.68$).

121 Competition between exotic and native plants for pollinators played a minor role as

122 exotics accounted for only 8.3 % (± 3.0 SE) of the total visitation frequency at

123 unrestored sites.

124 More generalised networks (H_2') and species (d') at restored sites indicate greater

125 functional redundancy and lower mutual dependencies in restored plant-pollinator

126 communities. Greater generalisation is also associated with larger niche

127 complementarity of pollinators and a 'sampling effect', which refers to the increased

128 likelihood of including highly effective pollinators in a plant's pollinator spectrum[17,18].

129 These responses address core aims of ecological restoration: elevated functional

130 redundancy enhances ecosystem resilience[19], lower mutual dependencies facilitate

131 functional robustness to local species loss or decline in populations of certain

132 pollinator species[20], and niche complementarity and sampling effect increase

133 functional performance of the pollinator community[9,18].

134

135 The observed changes in pollinator interaction behaviour and network structure had

136 implications for plant reproduction. Plants at restored sites produced 17.4% more

137 flowers (floral abundance: 0.27 ± 0.037 vs. 0.23 ± 0.037 SE, Table1) and attracted

138 22.9% more visits (6750 vs. 5490 visits; Fig. 2), which correlated with a larger total

139 fruit production (fruit crop) and higher fruit set (proportion of flowers producing fruit)

140 across the most common species (Fig. 3, Table 1). The three endemic palms

141 *Nephrosperma vanhoutteanum*, *Phoenicophorium borsigianum*, and *Roscheria*

142 *melanochaetes* were among the most abundant and generalised plant species

143 (Extended Data Table 3) and their fruit sets benefitted the most from the removal of

144 exotics (Extended Data Figure 2). A positive relationship between generalisation and

145 fruit production has also been observed in other island plant-pollinator

146 communities[17], supporting the importance of super-generalist mutualists on

147 islands[21].

148

149   The removal of exotic plants appeared to improve pollination, as flowers were more

150   frequently visited and native plants produced more fruit at restored sites. This

151   interpretation was supported by a positive relationship between fruit set and visitation

152   frequency (Table 1, Extended Data Figure 3). Plants at unrestored sites were likely

153   to be pollination limited, as fruit set was lower than at restored sites and increased as

154   a function of visitation, approaching similar levels of fruit set only at high visitation

155   rates (Fig. 3). Plants at restored sites had similar fruit set levels throughout the range

156   of visitation rates, possibly due to a saturating functional response of pollinators to

157   increasing floral abundance[22]. This result suggests a higher pollinator efficacy

158   compared to unrestored sites, despite the lower performance costs often associated

159   with generalist pollinator species[23]. Pollinator individuals, however, despite belonging

160   to generalist species in the networks, may respond to the higher purity of native floral

161   resources through changes in their foraging behaviour, which can result in higher

162   pollination quality[24]. Thus, one plausible explanation is that the removal of the dense

163   thickets of exotic plants enabled pollinators to detect and approach native flowers,

164   increasing visitation frequency to natives, interaction diversity, generalisation of

165   native networks and fruit set. Whether the structure and functioning of the restored

166   networks resemble those of undisturbed areas is, however, unknown, as no such

167   'reference' sites exist on Mahé.

168

169   The impact of anthropogenic habitat degradation on the structure of interaction

170   networks is well documented[25,26]. When exotic plants invade ecosystems,

171   subsequent declines in pollinator visitation, reproduction of native plants, and native

172   arthropod abundance and species richness are frequently reported[27,28]. Few studies,

173   however, have experimentally investigated community-level impacts of removing

174   exotic plants on biotic interactions (Supplementary Table 1). Two findings stand out:

175   removing exotic plants may disrupt indirect facilitation of native plants, albeit on a

176   small spatial scale, and the restoration of biotic interactions, especially of higher

177   trophic levels, is related to time since intervention (Supplementary Table 1).

178   Interestingly, network metrics in our study also changed over the 8-month period

179   (e.g. number of visits increased, and H_2', d'_{pl} and d'_{poll} decreased), which may be an

180   effect of season or time since restoration, indicated by significant main and

181   interaction effects, respectively (Table 1). Similarly, native species diversity and

182   abundance increased across multiple trophic levels two years after the removal of

183   exotic plants in the Azores[29].

184

185   Previous simulation studies on woodland restoration have indicated that plant-

186   pollinator networks undergo a succession of increasing functional redundancy and

187   complementarity following restoration[3]. Our experiments indicate that restoration

188   trajectories towards functionally more diverse (i.e. complementary) and robust (i.e.

189   redundant) plant-pollinator assemblages are established as early as the first post-

190   restoration flowering season. The prompt response to the removal of exotics may be

191   facilitated by high 'ecological memory' in inselberg communities[30], i.e., the

192   assemblage of functionally similar species, interactions and structures that facilitates

193   reorganisation of an ecosystem after disturbance[5], and spatial proximity to pollinator

194   source populations in the surrounding forest[8].

References

1   Butchart, S. H. M. *et al.* Global Biodiversity: Indicators of Recent Declines. *Science* **328**, 1164-1168, doi:10.1126/science.1187512 (2010).

2   McCann, K. Protecting biostructure. *Nature* **446**, 29-29 (2007).

3   Devoto, M., Bailey, S., Craze, P. & Memmott, J. Understanding and planning ecological restoration of plant–pollinator networks. *Ecol Lett* **15**, 319-328, doi:10.1111/j.1461-0248.2012.01740.x (2012).

4   Potts, S. G. *et al.* Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* **25**, 345-353, doi:10.1016/j.tree.2010.01.007 (2010).

5   Bengtsson, J. *et al.* Reserves, resilience and dynamic landscapes. *AMBIO: A Journal of the Human Environment* **32**, 389-396, doi:10.1579/0044-7447-32.6.389 (2003).

6   Oliver, T. H. *et al.* Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* **30**, 673-684, doi:http://dx.doi.org/10.1016/j.tree.2015.08.009 (2015).

7   Menz, M. H. M. *et al.* Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends Plant Sci.* **16**, 4-12, doi:DOI: 10.1016/j.tplants.2010.09.006 (2011).

8   Forup, M. L., Henson, K. S. E., Craze, P. G. & Memmott, J. The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. *Journal of Applied Ecology* **45**, 742-752 (2008).

9   Kaiser-Bunbury, C. N. & Blüthgen, N. Integrating network ecology with applied conservation: a synthesis and guide to implementation. *AoB Plants* **7**, plv076, doi:10.1093/aobpla/plv076 (2015).

219   10   Clewell, A. F. & Aronson, J. *Ecological restoration: principles, values, and*

220   *structure of an emerging profession*. 2nd edition edn, (Island Press, 2013).

221   11   Ollerton, J., Winfree, R. & Tarrant, S. How many flowering plants are

222   pollinated by animals? *Oikos* **120**, 321-326, doi:10.1111/j.1600-

223   0706.2010.18644.x (2011).

224   12   Traveset, A. & Richardson, D. M. Biological invasions as disruptors of plant

225   reproductive mutualisms. *Trends Ecol. Evol.* **21**, 208-216 (2006).

226   13   Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M. A. Plant reproductive

227   susceptibility to habitat fragmentation: review and synthesis through a meta-

228   analysis. *Ecol Lett* **9**, 968-980, doi:10.1111/j.1461-0248.2006.00927.x (2006).

229   14   Schleuning, M., Fründ, J. & García, D. Predicting ecosystem functions from

230   biodiversity and mutualistic networks: an extension of trait-based concepts to

231   plant–animal interactions. *Ecography* **38**, 380-392, doi:10.1111/ecog.00983

232   (2015).

233   15   Blüthgen, N., Menzel, F. & Blüthgen, N. Measuring specialization in species

234   interaction networks. *BMC Ecology* **6**, 9 (2006).

235   16   Kaiser-Bunbury, C. N., Valentin, T., Mougal, J., Matatiken, D. & Ghazoul, J.

236   The tolerance of island plant–pollinator networks to alien plants. *J. Ecol.* **99**,

237   202-213, doi:10.1111/j.1365-2745.2010.01732.x (2011).

238   17   Tur, C., Castro-Urgal, R. & Traveset, A. Linking plant specialization to

239   dependence in interactions for seed set in pollination networks. *PLoS ONE* **8**,

240   e78294, doi:10.1371/journal.pone.0078294 (2013).

241   18   Blüthgen, N. & Klein, A.-M. Functional complementarity and specialisation:

242   The role of biodiversity in plant-pollinator interactions. *Basic and Applied*

243   *Ecology* **12**, 282-291, doi:10.1016/j.baae.2010.11.001 (2011).

244 19 Walker, B. Conserving biological diversity through ecosystem resilience.

245   *Conserv Biol* **9**, 747-752, doi:10.2307/2386983 (1995).

246 20 Memmott, J., Waser, N. M. & Price, M. V. Tolerance of pollination networks to

247   species extinctions. *Proceedings of the Royal Society of London B* **271**, 2605-

248   2611 (2004).

249 21 Olesen, J. M., Eskildsen, L. I. & Venkatasamy, S. Invasion of pollination

250   networks on oceanic islands: importance of invader complexes and endemic

251   super generalists. *Diversity & Distributions* **8**, 181-192 (2002).

252 22 Morris, W. F., Vázquez, D. P. & Chacoff, N. P. Benefit and cost curves for

253   typical pollination mutualisms. *Ecology* **91**, 1276-1285, doi:10.1890/08-2278.1

254   (2010).

255 23 Larsson, M. Higher pollinator effectiveness by specialist than generalist

256   flower-visitors of unspecialized *Knautia arvensis* (Dipsacaceae). *Oecologia*

257   **146**, 394-403, doi:10.1007/s00442-005-0217-y (2005).

258 24 Araújo, M. S., Bolnick, D. I. & Layman, C. A. The ecological causes of

259   individual specialisation. *Ecol Lett* **14**, 948-958, doi:10.1111/j.1461-

260   0248.2011.01662.x (2011).

261 25 Hagen, M. *et al.* Biodiversity, species interactions and ecological networks in

262   a fragmented world. *Advances in Ecological Research* **46**, 89-210,

263   doi:http://dx.doi.org/10.1016/B978-0-12-396992-7.00002-2 (2012).

264 26 Tylianakis, J. M., Tscharntke, T. & Lewis, O. T. Habitat modification alters the

265   structure of tropical host-parasitoid food webs. *Nature* **445**, 202-205 (2007).

266 27 Morales, C. L. & Traveset, A. A meta-analysis of impacts of alien vs. native

267   plants on pollinator visitation and reproductive success of co-flowering native

268   plants. *Ecol Lett* **12**, 716-728, doi:doi: 10.1111/j.1461-0248.2009.01319.x

269   (2009).

270 28 van Hengstum, T., Hooftman, D. A. P., Oostermeijer, J. G. B. & van

271   Tienderen, P. H. Impact of plant invasions on local arthropod communities: a

272   meta-analysis. *J. Ecol.* **102**, 4-11, doi:10.1111/1365-2745.12176 (2013).

273 29 Heleno, R., Lacerda, I., Ramos, J. A. & Memmott, J. Evaluation of restoration

274   effectiveness: community response to the removal of alien plants. *Ecological*

275   *Applications* **20**, 1191-1203, doi:doi:10.1890/09-1384.1 (2010).

276 30 Thompson, J. N. *et al.* Frontiers of Ecology. *Bioscience* **51**, 15-24,

277   doi:10.1641/0006-3568(2001)051[0015:foe]2.0.co;2 (2001).

278 31 Fleischmann, K., Porembski, S., Biedinger, N. & Barthlott, W. Inselbergs in

279   the sea: vegetation of granite outcrops on the islands of Mahé, Praslin and

280   Silhouette (Seychelles). *Bulletin of the Geobotanical Institute ETH* **62**, 61-74

281   (1996).

282 32 Kaiser-Bunbury, C. N., Vázquez, D. P., Stang, M. & Ghazoul, J. Determinants

283   of the microstructure of plant-pollinator networks. *Ecology* **95**, 3314-3324

284   (2014).

285 33 Kaiser-Bunbury, C. N., Mougal, J., Valentin, T., Gabriel, R. & Blüthgen, N.

286   Herbicide application as a habitat restoration tool: impact on native island

287   plant communities. *Applied Vegetation Science* **18**, 650-660,

288   doi:10.1111/avsc.12183 (2015).

289 34 Ghazoul, J. Pollen and seed dispersal among dispersed plants. *Biological*

290   *Reviews* **80**, 413-443 (2005).

291 35 Kaiser-Bunbury, C. N., Memmott, J. & Müller, C. B. Community structure of

292   pollination webs of Mauritian heathland habitats. *Perspectives in Plant*

Ecology, Evolution and Systematics **11**, 241-254,

doi:10.1016/j.ppees.2009.04.001 (2009).

36   Kaiser-Bunbury, C. N., Muff, S., Memmott, J., Müller, C. B. & Caflisch, A. The

robustness of pollination networks to the loss of species and interactions: A

quantitative approach incorporating pollinator behaviour. *Ecol Lett* **13**, 442-

452 (2010).

37   Gibson, R. H., Knott, B., Eberlein, T. & Memmott, J. Sampling method

influences the structure of plant–pollinator networks. *Oikos* **120**, 822-831,

doi:10.1111/j.1600-0706.2010.18927.x (2011).

38   Vázquez, D. P., Blüthgen, N., Cagnolo, L. & Chacoff, N. P. Uniting pattern and

process in plant–animal mutualistic networks: a review. *Annals of Botany* **103**,

1445-1457, doi:10.1093/aob/mcp057 (2009).

39   Legendre, P. & Legendre, L. *Numerical ecology*. 2nd edn, Vol. 20 (Elsevier

Science, 1998).

40   Proctor, M., Yeo, P. & Lack, A. *The natural history of pollination*. 1 edn,

(Timber Press, 1996).

41   Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. *Mixed

Effects Models and Extensions in Ecology with R*. (Springer, 2009).

42   Burnham, K. P. & Anderson, D. R. *Model selection and multimodel inference:

a practical information-theoretic approach*. Second edn, (Springer New York,

2002).

43   Guisan, A. & Zimmermann, N. E. Predictive habitat distribution models in

ecology. *Ecol. Model.* **135**, 147-186, doi:http://dx.doi.org/10.1016/S0304-

3800(00)00354-9 (2000).

317   44   Nakagawa, S. & Schielzeth, H. A general and simple method for obtaining R2

318   from generalized linear mixed-effects models. *Methods in Ecology and*

319   *Evolution* **4**, 133-142, doi:10.1111/j.2041-210x.2012.00261.x (2013).

320

321   Supplementary Information is linked to the online version of the paper at

322   www.nature.com/nature.

323

332

333   **Author Contribution**

334   C.N.K.-B. conceived the ideas, led the experiments, collected and analysed the data

335   and wrote the manuscript. J.M. contributed to project implementation and restoration.

336   T.V. and R.G. conducted the restoration and collected data. A.E.W. identified

337   pollinators. J.M.O and N.B. contributed conceptually during the planning and

338   implementation phase. N.B. assisted with data analysis. J.M., A.E.W., J.M.O, and

339   N.B. commented on the manuscript.

340

Figure legends

Figure 1| The island of Mahé with study sites and pollination networks. At each of the

four restored (black circles) and unrestored (empty circles) sites we collected eight monthly

networks. The webs depict bipartite quantitative networks of interactions (wedges) between

plants (bottom bar) and pollinators (top bar). Each block represents a species, the width of a

block reflects its relative abundance, and the width of the wedges shows the interaction

frequency between pollinators and plants. Teal: Skinks and geckos, light blue: birds, dark

blue: beetles, green: flies, red: wasps and bees; yellow: moths and butterflies.

Figure 2| Treatment effects on pollinator communities and network structure. Number

of pollinator species ($N = 8$ sites; Welch's $t_4 = 3.14$, $P = 0.035$; means ± SD; data in

Extended Data Table 1) and network metrics ($N = 64$ networks; data in Supplementary Table

2) in unrestored (U) and restored (R) plant-pollinator communities. Metrics include number of

visits (Visits), number of interactions (I), interaction evenness (IE), interaction diversity (ID),

network specialisation (H_2'), and plant (d'_{pl}) and pollinator (d'_{poll}) specialisation. Boxplots

depict the median and ± 5%, 10%, 25% percentiles; statistics are shown in Table 1. *$P <$

0.05, **$P < 0.01$, ***$P < 0.001$, ns = not significant.

Figure 3| Fruit set increased with visitation rate at unrestored sites. Visitation rates

(square-root transformed; $N = 810$ displayed seven most common species across all sites)

368　of >1.5 visits flower^{-1} hour^{-1} were only observed at restored sites. Mean fruit set was higher

369　at restored sites than unrestored sites (see Table 1 for statistics of all 10 species). Shown

370　are lines of best fit (solid) with 95% CI (dotted).

371

372　**Table 1 | Effects of vegetation restoration on plant-pollinator communities and**

373　**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	Network-level specialisation [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

374

(B)

Model type	Random effect	Predictor	β	t	P
LMM	Crossed: Pollinator species, site	Pollinator specialisation [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 × Treatment	0.021	2.997	0.003

LMM	Crossed: Plant species, site	Plant specialisation [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 × 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} = 1035; $N_{branch:indiv}$ = 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} = 1035; $N_{branch:indiv}$ = 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) × 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) × treatment	0.358	6.229	< 0.001

375

376 Presented are statistics of the best minimal adequate models. We also showed alternative

377 models if ΔAICc < 0.5. Full models included main and interaction effects of the predictors

378 'month' and 'treatment' (A; d'_{poll} and d'_{pl}), only 'treatment' (floral abundance and fruit crop and

379 set), or 'visitation frequency/rate' and 'treatment' (fruit set). Model selection was based on

380 AICc, and ΔAICc indicate the difference between the best and next best model. Given are

381 also AICc weights (AICcWt) showing model probabilities. (A) Models are based on the

382 number of networks (N = 64), assuming largely spatial and temporal independence in

383 network parameters (see Methods). (B) Structurally more complex models with replicated

384 sampling across species or individuals at each site include 'site' as random effect. Month

385   was not fitted for response variables that span the entire season (floral abundance, fruit crop

386   and set). Coefficients of determination: adjusted R^2 (LM), D^2 (the amount of deviance

387   accounted for by the model; GLS), and marginal and conditional $R^2_{(G)LMM}$ (R^2-equivalent for

388   mixed models; LMM and GLMM). Restored sites were used as reference level of the factor

389   treatment. LM = linear model; GLS = generalised least square (variance structure weighted

390   by treatment); LMM = linear mixed model; GLMM = generalised linear mixed model; d'_{pl} = 29

391   native species; d'_{poll} = only bees and wasps, flies, birds and lizards with origin information.

392   Fruit crop refers to the number of fruit produced by the plant community at each site

393   (conservation relevance), and fruit set describes the proportion of flowers that set fruit

394   (ecological relevance). To assess the relationship between fruit set and pollinator visitation,

395   we modelled two measures of visitation: weighted visitation rate (see Methods) and visitation

396   frequency. Visitation rate (visits flower^{-1} hour^{-1}) represents the number of visits of a pollinator

397   individual to observed flowers, i.e., a per-capita measure of pollination. Visitation frequency,

398   calculated as visitation rate multiplied by the floral abundance of the visited plant species

399   (see Methods), assesses the effect of community-wide floral abundance on the relationship

400   between fruit set and pollinator behaviour.

401

402

403

404

Methods

Study sites

We collected interaction network data from eight discrete 'inselberg' (steep-sided

monolithic outcrops) plant communities on the granitic island of Mahé, Seychelles,

Indian Ocean (Fig. 1; Western Indian Ocean Biodiversity Hotspot) for eight

consecutive months between September 2012 and May 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

climate[31]. Selection criteria for inselberg study sites included elevation between 300

and 600m asl., approx. 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 wide-spread 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 compared to the

surrounding forest due to lower levels of human disturbance, harsh climatic, poor

soils 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

19

429   ecosystems[10]. Detailed descriptions of abiotic and biotic site characteristics are given

430   elsewhere[16,32].

431   To investigate the effect of vegetation restoration on plant-pollinator networks,

432   we removed all alien plants from four inselbergs between 15 November 2011 and 10

433   February 2012 by cutting stems close to the ground and applying systemic herbicide

434   to the cut stumps[33]. Treatment sites were selected to equally represent low and high

435   degree of invasion, with each two sites per invasion level and treatment (Extended

436   Data Table 1). Control and treatment sites were similar in plant (adonis: R^2 = 0.054,

437   P = 0.95, Supplementary Methods 1) and pollinator communities (R^2 = 0.187, P =

438   0.59, data from 2007/08[16]) prior to the removal of the exotic plant species. There was

439   no correlation between the spatial distance between sites and plant and pollinator

440   community compositions (Mantel tests; pre-removal: plants r = 0.165, P = 0.29;

441   pollinator r = 0.197, P = 0.32; post-removal: pollinators r = 0.231, P = 0.16),

442   indicating no site-related inherent bias and spatial-autocorrelation between treatment

443   levels (see also Supplementary Methods 2, Extended Data Table 4). The mean

444   number of native plant species across sites was similar between treatments (15.0 ±

445   1.8 vs. 16.0 ± 2.5; Student's t_6 = -0.63, P = 0.55). Cut plant material was compiled

446   and left to rot on site. Exotic plant removal is a widely used method in ecological

447   restoration following the assisted natural regeneration approach[10]. This approach

448   alters plant communities in two fundamental ways: 1) markedly reduced plant density

449   with swaths of open habitat shortly after intervention; and 2) increased availability of

450   resources due to reduced competition for nutrients, water and space between native

451   and alien plants. Both alterations can affect plant-pollinator interactions directly as

452   flowers are more easily detectable across the landscape without changes to the

453 effective distance between conspecifics[34], and native plants can allocate more

454 available resources to flowers and fruit.

455   To ensure long-term sustainability of the restoration efforts, local authorities

456 have committed to maintaining the management of exotic plants at the experimental

457 sites and incorporate inselberg habitat restoration into a national conservation

458 strategy to protect native biodiversity.

459

460 *Plant-pollinator networks*

461 To compile 64 plant-pollinator networks (8 sites × 8 months, Supplementary Table

462 2), we used established sampling protocols for focal point observations of plant-

463 pollinator interactions in heterogeneous vegetation[16,35]. Binary networks consist of

464 bars (plant and animal species) and links (interactions), in which the width of the

465 bars and links represents the abundance of flowers and animals and a measure of

466 visitation strength, respectively (Fig. 1). Flower visitors (hereafter 'pollinators'; total

467 144 spp; Supplementary Table 3) were recorded if they touched sexual parts of

468 flowers (Supplementary Methods 2). We observed all woody flowering species (38

469 spp.; Extended Data Table 3), each for 3.03 ± 0.62 hours per network. Flowers were

470 recorded monthly in 1×1×1m cubes placed stratified, randomly along several

471 transects spanning the extent of the inselbergs[16] (Extended Data Table 1). Floral

472 abundance was expressed as the number of flowers per sample cube. Pollinator

473 abundance was determined by the total number of visits of each pollinator taxon to

474 flowering plants in a network. To determine the links between plants and pollinators,

475 we calculated the *visitation frequency* between an animal species i and a plant

476 species j as mean visitation rate of animal species i multiplied by the floral

477 abundance of plant species j visited by i[35,36]. Visitation frequency was used to

478   calculate all network-level metrics (interaction richness, evenness, and diversity, H_2',

479   d'; Supplementary Methods 2). The observation methods used here reduce the risk

480   of under-sampling[16,37], all metrics are fully quantitative and H_2', d' are robust to

481   sampling bias, which is pervasive in pollination network studies[38].

482   We calculated two distance indices to test for qualitative and quantitative

483   differences in plant–pollinator communities within and across sites and months.

484   Specifically, we used the Jaccard (binary) and Bray-Curtis (quantitative) indices[39] to

485   determine species overlap and similarities in visits among networks, respectively.

486   Species in monthly networks within sites were unique to each network by 82% (± 4.6

487   SD; pollinators only: 67± 4.3%; plants only: 57 ± 10.7%), and these values were

488   similar to species uniqueness in networks across sites in given months (85 ± 1.4 %;

489   Welch's $t_{8.4}$ = 1.88, P = 0.095; pollinators only: 68± 3.3%, Welch's $t_{12.9}$ = 0.42, P =

490   0.685; plants only: 64 ± 6.5%, Welch's $t_{11.5}$ = 1.58, P = 0.140). Likewise, pollinator

491   and flower communities were highly variable across sites and equally variable across

492   months (mean Bray-Curtis distance ± SD of relative number of visits; Pollinators/site:

493   0.43 ± 0.09, pollinators/months: 0.46 ± 0.06, Welch's $t_{12.7}$ = 0.64, P = 0.533;

494   flowers/site: 0.59 ± 0.06, flowers/months: 0.63 ± 0.07, Welch's $t_{13.8}$ = 1.17, P =

495   0.262). The 64 networks are therefore temporally and spatially largely disconnected,

496   which implies a high degree of ecological independence of each network. Finally,

497   because plant communities harboured slightly different species, we conducted all

498   relevant analyses without native plant species that occurred only in one treatment (8

499   spp. marked with 'np' in Extended Data Table 3). We fitted the same models as with

500   the full data set (see below), and the results were qualitatively equivalent and

501   quantitatively slightly stronger than those of the entire plant communities

502   (Supplementary Table 4).

503

Reproductive performance

505 We measured reproductive performance of native plants as the number of fruit

506 produced at each site (fruit crop), and the proportion of flowers that set fruit (fruit

507 set). We monitored fruit crop and set of ten native species, which occurred at two or

508 more sites per treatment in sufficient numbers of individuals (>3 flowering females)

509 for between-treatment comparison. Increasing total fruit crop is a restoration

510 objective, and changes in fruit set indicate functional changes driven by pollinator

511 behaviour and/or nutrient availability[40]. We determined fruit set of 37,898 buds on

512 1035 branches or inflorescences nested in 346 plants. All ten species depend mostly

513 on pollen vectors for reproduction, as six species are dioecious or consecutively

514 monoecious and four are self-incompatible hermaphrodites[16]. Further, eight of ten

515 species produced fruits with one or always two seeds (*Timonius flavescens* and

516 *Nepenthes pervillei* contained multiple seeds per fruit), thus fruit set closely

517 corresponded with seed set.

518

Analyses

520 Analyses were conducted in R 3.1.1 (R Development Core Team; http://www.R-

521 project.org), using the libraries *bipartite*, *vegan, lmer*, *nlme, lmerTest* and *MuMIn*. To

522 test the response of network metrics to restoration (Supplementary Methods 2), we

523 fitted two types of models: (1) linear (LM) and generalised least square (GLS)

524 models without random effects, and (2) linear mixed models (LMM) with nested

525 random terms. Network-level response variables without replication across species

526 or individuals within a site (i.e. number of visits, number of interactions, IE, ID, and

527 *H2'*) were fitted with LM or GLS (Table 1A), depending on the variance structure.

528 When heterogeneity was detected we used the *varIdent* function with GLS models to

529 assign weight to the variance by the treatment stratum[41]. We analysed species-

530 specific responses of plant (d'_{pl}) and pollinator specialisation (d'_{poll}) and floral

531 abundance to treatment with linear mixed models (LMM). These response variables

532 contain data on within-site variation across species, we thus fitted species and sites

533 as crossed random effects, and month (only *d'*) and treatment (all) as fixed effects

534 (Table 1B). LM and GLS were based on the number of networks ($N = 64$), treating

535 each network independently. The following rationale warrants the analytical

536 approach: eight study sites may be considered statistically too low to detect

537 ecologically meaningful results despite the extent of the ecosystem-level field

538 experiment. To avoid an inflated 'type I error', we repeatedly sampled highly dynamic

539 interaction networks over time. We showed that the composition of plant and

540 pollinator communities in the networks was highly variable within and among sites

541 and months (see above), suggesting a low degree of overlap between networks from

542 the same site and month. Further, each observation session focussed on a different

543 plant individual, which ensured within-site spatial separation between consecutively

544 observed interactions. Finally, support for our approach comes from the visual

545 inspection of partial residual plots, which depict treatment effect after removing the

546 effects of time (fixed effect) and site (random effect in LMM; Extended Data Figure

547 4). We therefore considered networks independently for structurally simpler models

548 on network metrics (number of visits, number of interactions, IE, ID, and *H2'*, Table

549 1A) and fitted LM and GLS models with the fixed main effects month and treatment

550 and the interaction between month and treatment. The best model was selected

551 with the *dredge* function (package: *MuMIn*) based on AICc. AICc weights are

552 presented to indicate the level of support for selecting the most parsimonious among

553   a set of models. ΔAICc assesses the support of the best and second best models,

554   and alternative models were shown only when ΔAICc < 0.5 (Table 1). Given are also

555   AICc weights (AICcWt) showing model probabilities[42]. We computed the adjusted R^2

556   D^2, and marginal and conditional $R^2_{(G)LMM}$ as goodness-of-fit metrics for linear,

557   generalised least square, and mixed models, respectively. D^2 is the amount of

558   deviance accounted for by the model[43], and marginal and conditional $R^2_{(G)LMM}$ are

559   coefficients of determination for mixed models describing the proportion of variance

560   explained by the fixed factors only (marginal $R^2_{(G)LMM}$) and by both the fixed and

561   random effects (conditional $R^2_{(G)LMM}$)[44]. To test the influence of seasonality we ran

562   models initially with each one of three time effects: linear across months, a quadratic

563   term to reflect a hump-shaped seasonality, and a factor with eight levels. All models

564   showed a poorer (> AICc) fit of the quadratic term and the factor compared to the

565   linear fit. We therefore fitted in all models the linear time effect.

566   Treatment effects on total fruit crop and fruit set were tested with generalised

567   mixed models (GLMM) with Poisson and binomial distributions, respectively. To

568   account for unbalanced data and spatial and within-species dependencies, we used

569   species (in the model containing all species), plant and branch identity as nested and

570   site as crossed random effects. In the binomial models, we also weighted sample

571   sizes by the number of flowers recorded on each plant to calculate fruit set (*cbind*

572   function). Fruit set was also tested for each species separately (Supplementary

573   Methods 3, Extended Data Figure 2). To assess the functional relationship between

574   fruit set as a proxy for plant reproductive performance and pollinator behaviour, we

575   calculated weighted visitation rate and used a reduced fruit data set containing only

576   those species that were visited by pollinators in a given network (N = 975). Visitation

577   rate represent the number of visits of a pollinator individual to observed flowers,

578   expressed as rate of visits flower^{-1} hour^{-1}. Weighting was achieved in two steps: first,

579   because dioecious palms attracted a large proportion of visitors to either male or

580   female flowers, we considered the distribution of pollinator species between sexes in

581   a weighted visitation rate (VR) as follows:

$$VR = \sum_i v_i \cdot \frac{2 \cdot \min(m_i, f_i)}{m_i + f_i} flower^{-1} h^{-1}$$

582   where v_i is the total number of visits of pollinator i; m_i and f_i are the number of visits

583   to male and female flowers, respectively, visited by i in the network. This approach

584   ensures that pollinators with equal visits to male and female flowers are fully

585   weighted (ratio = 1) whereas pollinators that only visit one sex are not considered

586   (ratio = 0). The second step incorporated the importance of a pollinator species for a

587   plant species by dividing weighted visitation rate by the total sum of all visits. The

588   same steps were repeated with visitation frequency to assess the influence of

589   community-wide floral abundance on the relationship between fruit set and pollinator

590   behaviour (Extended Data Figure 3).

591   **References Methods**

592

593

Extended Data tables

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

Extended Data Table 2 | Results of full-factorial linear mixed model. Comparison of species-level specialisation d'_{poll} (log-transformed) between species (the exotic honey bee *Apis mellifera* vs. the native sweat bee *Lasioglossum mahense*) and treatments (restored vs. 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

* The following species were recently 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. ‡ across all networks [sum of number of flowers/cube across the eight sites]; § Equals 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. Numbers in bold are significant at $\alpha \leq 0.05$.

Extended Data figures

Extended Data Figure 1| Level of specialisation (d'_{pl}) of the 10 most common flowering plant species across all networks. Asterisks (*) indicates a significantly higher level of specialisation (mean ± SE) in the unrestored compared to the restored networks. For full

621 species names see Table 3. Linear mixed model: *P. bibracteata* $t = 2.836$, $P = 0.036$; *P.*

622 *lancifolia* $t = 2.644$, $P = 0.038$; *E. sechellarum* (variance structure weighted by treatment) $t =$

623 3.141, $P = 0.020$. Site was entered as random effect in all models. All other species $P >$

624 0.05.

625

626 **Extended Data Figure 2| Fruit set of the ten most abundant plant species.** The species

627 occurred at ≥ 2 sites per treatment (*Nepenthes, Mimusops*), seven sites (*Roscheria,*

628 *Timonius*), and eight sites (all others). The reproductive systems included dioecy (*Pyrostria,*

629 *Nepenthes, Timonius*), monoecy with temporally separated male and female flowers

630 (*Roscheria, Phoenicophorium*, *Nephrosperma*) and protandrous hermaphrodite flowers

631 (*Erythroxylum, Memecylon, Mimusops, Paragenipa*). The three palm species *Roscheria,*

632 *Phoenicophorium* and *Nephrosperma* had higher fruit set at the restored sites (GLMM:

633 *Nephrosperma* $N = 120$, $z = 2.54$, $P = 0.011$, *Phoenicophorium* $N = 120$, $z = 2.66$, $P = 0.008$,

634 *Roscheria* $N = 108$, $z = 2.29$, $P = 0.022$), the other species showed no clear species-specific

635 pattern. The boxes depict the median and 25th and 75th percentiles, whiskers show 1.5 ×

636 interquartile range of the data, and open circles indicate outliers.

637

638 **Extended Data Figure 3| Fruit set increased with visitation frequency at unrestored**

639 **sites**. Square-root-transformed visitation frequency ($N = 810$, displayed seven most

640 common species across all sites) of >1.5 visits flower^{-1} hour^{-1} × floral abundance were only

641 observed at restored sites. Mean fruit set was higher at restored sites than unrestored sites

642 (see Table 1 for statistics for statistics of all 10 species included in reproductive performance

643 analysis). Shown are lines of best fit (solid) and 95% CI (dotted).

644 **Extended Data Figure 4| Partial residual plots of network metrics**. Box plots of partial

645 residuals show the effect of treatment after removing the effect of month and site. Partial

646 residuals were calculated from linear mixed models with month and treatment as fixed main

647   and interaction effects and site as random effect. Shown are partial residuals plus intercept.

648   Boxplots depict the median and ± 5%, 10%, and 25% percentile.

649