

3 **Ecosystem restoration strengthens pollination network resilience**
4 **and function**

6 Christopher N. Kaiser-Bunbury¹, James Mougai², Andrew E. Whittington³, Terence
7 Valentin², Ronny Gabriel², Jens M. Olesen⁴, and Nico Blüthgen¹

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

17 Abstract

18 Land degradation results in declining biodiversity and disruption of ecosystem
19 functioning worldwide, particularly in the tropics¹. 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 scarce³. Pollination is an important ecosystem function, and global pollinator
24 declines attenuate the resistance of natural areas and agro-environments to
25 disturbances⁴. 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 process⁷. 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 effects¹⁰. 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

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 reproduction¹¹. Pollinators are also particularly sensitive to
56 anthropogenic disturbance^{12,13}, which poses a threat to the pollination service they
57 provide⁴. 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 ecosystems², which makes them useful to assess the
73 efficacy of restoration by providing comprehensive quantitative information on
74 structure and function of communities¹⁴. 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 $25.3 \pm$
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 inselbergs¹⁶. 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 resilience¹⁹, lower mutual dependencies facilitate
131 functional robustness to local species loss or decline in populations of certain
132 pollinator species²⁰, 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 communities¹⁷, supporting the importance of super-generalist mutualists on
147 islands²¹.

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 abundance²². This result suggests a higher pollinator efficacy
158 compared to unrestored sites, despite the lower performance costs often associated
159 with generalist pollinator species²³. 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 quality²⁴. 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 Azores²⁹.

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 restoration³. 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 communities³⁰, i.e., the
192 assemblage of functionally similar species, interactions and structures that facilitates
193 reorganisation of an ecosystem after disturbance⁵, and spatial proximity to pollinator
194 source populations in the surrounding forest⁸.

195 References

- 196 1 Butchart, S. H. M. *et al.* Global Biodiversity: Indicators of Recent Declines.
197 *Science* **328**, 1164-1168, doi:10.1126/science.1187512 (2010).
- 198 2 McCann, K. Protecting biostructure. *Nature* **446**, 29-29 (2007).
- 199 3 Devoto, M., Bailey, S., Craze, P. & Memmott, J. Understanding and planning
200 ecological restoration of plant–pollinator networks. *Ecol Lett* **15**, 319-328,
201 doi:10.1111/j.1461-0248.2012.01740.x (2012).
- 202 4 Potts, S. G. *et al.* Global pollinator declines: trends, impacts and drivers.
203 *Trends Ecol. Evol.* **25**, 345-353, doi:10.1016/j.tree.2010.01.007 (2010).
- 204 5 Bengtsson, J. *et al.* Reserves, resilience and dynamic landscapes. *AMBIO: A*
205 *Journal of the Human Environment* **32**, 389-396, doi:10.1579/0044-7447-
206 32.6.389 (2003).
- 207 6 Oliver, T. H. *et al.* Biodiversity and resilience of ecosystem functions. *Trends*
208 *Ecol. Evol.* **30**, 673-684, doi:<http://dx.doi.org/10.1016/j.tree.2015.08.009>
209 (2015).
- 210 7 Menz, M. H. M. *et al.* Reconnecting plants and pollinators: challenges in the
211 restoration of pollination mutualisms. *Trends Plant Sci.* **16**, 4-12, doi:DOI:
212 10.1016/j.tplants.2010.09.006 (2011).
- 213 8 Forup, M. L., Henson, K. S. E., Craze, P. G. & Memmott, J. The restoration of
214 ecological interactions: plant-pollinator networks on ancient and restored
215 heathlands. *Journal of Applied Ecology* **45**, 742-752 (2008).
- 216 9 Kaiser-Bunbury, C. N. & Blüthgen, N. Integrating network ecology with applied
217 conservation: a synthesis and guide to implementation. *AoB Plants* **7**, plv076,
218 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., Mougat, 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., Mougai, 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*

- 293 *Ecology, Evolution and Systematics* **11**, 241-254,
294 doi:10.1016/j.ppees.2009.04.001 (2009).
- 295 36 Kaiser-Bunbury, C. N., Muff, S., Memmott, J., Müller, C. B. & Caflisch, A. The
296 robustness of pollination networks to the loss of species and interactions: A
297 quantitative approach incorporating pollinator behaviour. *Ecol Lett* **13**, 442-
298 452 (2010).
- 299 37 Gibson, R. H., Knott, B., Eberlein, T. & Memmott, J. Sampling method
300 influences the structure of plant–pollinator networks. *Oikos* **120**, 822-831,
301 doi:10.1111/j.1600-0706.2010.18927.x (2011).
- 302 38 Vázquez, D. P., Blüthgen, N., Cagnolo, L. & Chacoff, N. P. Uniting pattern and
303 process in plant–animal mutualistic networks: a review. *Annals of Botany* **103**,
304 1445-1457, doi:10.1093/aob/mcp057 (2009).
- 305 39 Legendre, P. & Legendre, L. *Numerical ecology*. 2nd edn, Vol. 20 (Elsevier
306 Science, 1998).
- 307 40 Proctor, M., Yeo, P. & Lack, A. *The natural history of pollination*. 1 edn,
308 (Timber Press, 1996).
- 309 41 Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. *Mixed*
310 *Effects Models and Extensions in Ecology with R*. (Springer, 2009).
- 311 42 Burnham, K. P. & Anderson, D. R. *Model selection and multimodel inference:*
312 *a practical information-theoretic approach*. Second edn, (Springer New York,
313 2002).
- 314 43 Guisan, A. & Zimmermann, N. E. Predictive habitat distribution models in
315 ecology. *Ecol. Model.* **135**, 147-186, doi:[http://dx.doi.org/10.1016/S0304-](http://dx.doi.org/10.1016/S0304-3800(00)00354-9)
316 [3800\(00\)00354-9](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

324 **Acknowledgements**

325 We thank the Seychelles National Parks Authority, the Ministry of Environment,
326 Energy and Climate Change and the Seychelles Bureau of Standards for permission
327 to conduct the work and administrative assistance. Sabrina van de Velde and Paola
328 Acuña helped with data collection. Jaboury Ghazoul, Nancy Bunbury, Lindsay
329 Turnbull, Diego Vázquez, and Jeff Ollerton provided comments on earlier versions
330 and Carsten Dormann, Andy Hector, and Matthias Schleuning advised on statistics.
331 CNK-B was funded by the German Research Foundation (KA 3349/2-1).

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

341 **Author Information** Data is available from the Interaction Web Database IWDB at
342 <https://www.nceas.ucsb.edu/interactionweb/>. Reprints and permissions information is
343 available at www.nature.com/reprints. The authors declare no competing financial
344 interests. Readers are welcome to comment on the online version of the paper.
345 Correspondence and requests for materials should be addressed to C.N.K.-B.
346 (c.kaiserbunbury@gmail.com).

347

348 **Figure legends**

349 **Figure 1| The island of Mahé with study sites and pollination networks.** At each of the
350 four restored (black circles) and unrestored (empty circles) sites we collected eight monthly
351 networks. The webs depict bipartite quantitative networks of interactions (wedges) between
352 plants (bottom bar) and pollinators (top bar). Each block represents a species, the width of a
353 block reflects its relative abundance, and the width of the wedges shows the interaction
354 frequency between pollinators and plants. Teal: Skinks and geckos, light blue: birds, dark
355 blue: beetles, green: flies, red: wasps and bees; yellow: moths and butterflies.

356

357 **Figure 2| Treatment effects on pollinator communities and network structure.** Number
358 of pollinator species ($N = 8$ sites; Welch's $t_4 = 3.14$, $P = 0.035$; means \pm SD; data in
359 Extended Data Table 1) and network metrics ($N = 64$ networks; data in Supplementary Table
360 2) in unrestored (U) and restored (R) plant-pollinator communities. Metrics include number of
361 visits (Visits), number of interactions (I), interaction evenness (IE), interaction diversity (ID),
362 network specialisation (H_2'), and plant (d'_{pl}) and pollinator (d'_{poll}) specialisation. Boxplots
363 depict the median and \pm 5%, 10%, 25% percentiles; statistics are shown in Table 1. * $P <$
364 0.05, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

365

366 **Figure 3| Fruit set increased with visitation rate at unrestored sites.** Visitation rates
367 (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, $D^2 = 0.14$, $\Delta AICc = 1.72$			
	Month	0.068	2.94	0.005
	Treatment	-0.305	-2.42	0.019
LM	Number of interactions			
	Best model, AICcWt = 0.51, Adj. $R^2 = 0.05$, $F_{1,62} = 4.16$, $P = 0.046$, $\Delta AICc = 1.95$			
	Treatment	-5.500	-2.039	0.046
LM	Interaction evenness			
	Best model, AICcWt = 0.44, Adj. $R^2 = 0.11$, $F_{1,62} = 8.94$, $P = 0.004$, $\Delta AICc = 0.24$			
	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. $R^2 = 0.09$, $F_{2,61} = 3.96$, $P = 0.024$, $\Delta AICc = 1.31$			
	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, $D^2 = 0.27$, $\Delta AICc = 1.84$			
	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, $R^2_{LMM(m)} = 0.04$, $R^2_{LMM(c)} = 0.22$, $\Delta AICc = 5.74$			
		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	Plant specialisation [d'_{pl}] ($N_{obs} = 440$; $N_{plants} = 29$; $N_{sites} = 8$) Best model, AICcWt = 0.77, $R^2_{LMM(m)} = 0.07$, $R^2_{LMM(c)} = 0.46$, $\Delta AICc = 3.01$	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 ($N_{obs} = 1035$; $N_{branch:indiv} = 159$; $N_{indiv:plants} = 53$; $N_{plants} = 10$; $N_{sites} = 8$) 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) \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

375

376

377

378

379

380

381

382

383

384

Presented are statistics of the best minimal adequate models. We also showed alternative models if $\Delta AICc < 0.5$. 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 $\Delta AICc$ indicate 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 more complex models with replicated 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

405 **Methods**

406 *Study sites*

407 We collected interaction network data from eight discrete ‘inselberg’ (steep-sided
408 monolithic outcrops) plant communities on the granitic island of Mahé, Seychelles,
409 Indian Ocean (Fig. 1; Western Indian Ocean Biodiversity Hotspot) for eight
410 consecutive months between September 2012 and May 2013 (the full flowering
411 season; Extended Data Table 1). The eight sites constitute the majority of mid-
412 altitude, highly diverse inselbergs on Mahé. All study sites were surrounded by steep
413 cliffs on at least three sides of the inselberg, separating typical inselberg vegetation
414 on the plateau from the surrounding forest, and creating comparable inselberg
415 climate³¹. Selection criteria for inselberg study sites included elevation between 300
416 and 600m asl., approx. 1 ha in size, flat-topped, similar native plant communities and
417 accessibility. Inselbergs harbour endemic dwarf-forest consisting almost entirely of
418 perennial shrubs and small trees, forming refuges of formerly widespread woody
419 species (Extended Data Table 3). Many inselbergs experience ecosystem
420 degradation by encroaching exotic plant species. The most dominant exotic plants
421 are woody perennial shrubs and trees, which are wide-spread invaders of island
422 ecosystems, including *Psidium cattleianum*, *Chrysobalanus icaco*, *Cinnamomum*
423 *verum* and *Alstonia macrophylla*. The establishment and subsequent spread of these
424 plants on inselbergs have, however, been more gradual compared to the
425 surrounding forest due to lower levels of human disturbance, harsh climatic, poor
426 soils and the steep cliffs that provide a natural barrier against plant invasion.
427 Ecological restoration, including the removal of exotic plants, is considered a suitable
428 tool to mitigate the threat by exotic species to the long-term viability of native

429 ecosystems¹⁰. 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 stumps³³. 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 2007/08¹⁶) 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 ($15.0 \pm$
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 approach¹⁰. 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 conspecifics³⁴, 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 inselbergs¹⁶ (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 studies³⁸.

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) indices³⁹ 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: $67 \pm 4.3\%$; plants only: $57 \pm 10.7\%$), and these values were
488 similar to species uniqueness in networks across sites in given months ($85 \pm 1.4 \%$;
489 Welch's $t_{8,4} = 1.88$, $P = 0.095$; pollinators only: $68 \pm 3.3\%$, Welch's $t_{12,9} = 0.42$, $P =$
490 0.685 ; plants only: $64 \pm 6.5\%$, 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 \pm 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

504 *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 availability⁴⁰. 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 hermaphrodites¹⁶. 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

519 *Analyses*

520 Analyses were conducted in R 3.1.1 (R Development Core Team; [http://www.R-](http://www.R-project.org)
521 [project.org](http://www.R-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 stratum⁴¹. We analysed species-
530 specific responses of plant (d'_{pi}) 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 $\Delta\text{AICc} < 0.5$ (Table 1). Given are also
555 AICc weights (AICcWt) showing model probabilities⁴². 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 model⁴³, 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 ($> \text{AICc}$) 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:

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

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

594 **Extended Data tables**

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

597

598 **Extended Data Table 2 | Results of full-factorial linear mixed model.** Comparison of
599 species-level specialisation d'_{poll} (log-transformed) between species (the exotic honey bee
600 *Apis mellifera* vs. the native sweat bee *Lasioglossum mahense*) and treatments (restored vs.
601 unrestored). Site was entered as a random effect. Numbers in bold are significant at $\alpha \leq$
602 0.05.

603

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

605 * The following species were recently renamed: *Diospyros boiviniana* = *Maba seychellarum*;
606 *Polyscias crassa* = *Gastonia crassa*; *Pyrostria bibracteata* = *Canthium bibracteatum*;
607 *Peponidium carinatum* = *Canthium carinatum*; † LC = least concern, NT = near threatened,
608 VU = vulnerable, EN = endangered, CR = critically endangered; - = exotic species, not listed.
609 ‡ across all networks [sum of number of flowers/cube across the eight sites]; § Equals
610 number of interactions, na = not applicable, np = not present; || R = restored sites; U =
611 unrestored sites; bold font indicates species included in reproductive performance analysis
612 (fruit crop and fruit set)

613

614 **Extended Data Table 4 | Spatial auto-correlation coefficients of community and**
615 **network parameters across the study sites.** Numbers in bold are significant at $\alpha \leq 0.05$.

616

617 **Extended Data figures**

618 **Extended Data Figure 1| Level of specialisation (d'_{pl}) of the 10 most common flowering**
619 **plant species across all networks.** Asterisks (*) indicates a significantly higher level of
620 specialisation (mean \pm 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 $1.5 \times$
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 \times 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 \pm 5%, 10%, and 25% percentile.

649