

1 **Shifts from non-obligate generalists to obligate specialists in simulations**
2 **of mutualistic network assembly**

3 Authors: Timo Metz^{1,*}, Nico Blüthgen², Barbara Drossel¹

4 ¹ Institute for Condensed Matter Physics, Technical University of Darmstadt,
5 Hochschulstraße 6, 64289 Darmstadt, Germany

6 ² Ecological Networks Lab, Technical University of Darmstadt,
7 Schnittspahnstraße 3, 64287 Darmstadt, Germany

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9 **Abstract**

10 Understanding ecosystem recovery after perturbation is crucial for ecosystem
11 conservation. Mutualisms contribute key functions for plants such as pollination
12 and seed dispersal. We modelled the assembly of mutualistic networks based on
13 trait matching between plants and their animal partners that have different degrees
14 of specialization on plant traits. Additionally, we addressed the role of non-obligate
15 animal mutualists, including facultative mutualists or non-resident species that
16 have their main resources outside the target site. Our computer simulations show
17 that non-obligate animals facilitate network assembly during the early stages,
18 furthering colonization by an increase in niche space and reduced competition.
19 While non-obligate and generalist animals provide most of the fitness benefits to
20 plants in the early stages of the assembly, obligate and specialist animals dominate
21 at the end of the assembly. Our results thus demonstrate the combined occurrence
22 of shifts from diet, trait, and habitat generalists to more specialised animals.

23 **1 Introduction**

24 While ecosystems are degraded or destroyed at a high rate due to habitat
25 conversion, they are also able to recover on abandoned land (Chazdon, 2014;
26 FAO, 2020; Poorter *et al.*, 2021). Such secondary succession of communities and
27 ecosystems is globally widespread today and depends on the availability of species
28 pools in the surrounding landscape, much like primary succession of new islands or
29 habitats. Recovering ecosystems, such as secondary forests, play an increasingly
30 important role for biodiversity conservation (Chazdon, 2014; Moreno-Mateos *et al.*,
31 2020; Strassburg *et al.*, 2020). Therefore, it is crucial to understand the process
32 of ecosystem recovery after disturbance. Traditionally, the recovery of ecosystems
33 has been measured through rather simple parameters, such as species richness.
34 This, however, disregards much of an ecosystem's complexity, which is not only
35 based on the presence of species, but also on their interactions (Moreno-Mateos
36 *et al.*, 2020). Mutualistic interactions are ubiquitous in nature and are important
37 for sustaining terrestrial biodiversity. In mutualism, species provide a service or
38 a resource to other species with little costs to themselves (Bronstein, 2015). In
39 terrestrial ecosystems, it is often an animal guild which provides a service (such
40 as seed dispersal, pollination or protection) and a plant guild which provides
41 resources (such as fruits, nectar or pollen) (Bronstein, 2021). Mutualisms can
42 either be obligate, whenever a population goes extinct without its mutualistic
43 partners, or facultative, when a population is also able to survive on its own
44 (Bronstein, 2015). The dependence of many species on mutualistic interactions
45 makes the investigation of these interactions especially important in the context
46 of ecosystem recovery. Many plant species are obligate mutualists as they depend
47 highly on animal services for reproduction and establishment (Chazdon, 2014).
48 For pollination mutualism, it is estimated that 87.5 % of flowering plants globally

49 and 94% of flowering plants in the tropics are animal pollinated (Ollerton *et al.*,
50 2011). For seed-dispersal mutualism, animals are important dispersal agents for
51 a considerable proportion of plants, in the case of tropical rainforests for around
52 90% (Jordano *et al.*, 2014).

53 The ability of animal mutualists to successfully colonize a recovering site
54 depends on the vegetation structure (e.g. due to the availability of nesting, food
55 and shelter sites) which changes during succession. Animal mutualist pioneers
56 therefore are often highly mobile, flying taxa (Chazdon, 2014; Öckinger *et al.*,
57 2018; Woodcock *et al.*, 2012), which can provide reproductive services (pollination
58 or seed dispersal) to plants in the regenerating site but rely also on resources
59 that can be found in the surrounding environment (Dunning *et al.*, 1992). For
60 instance, frugivorous bats may defaecate seeds during flight (Gorchov *et al.*, 1993;
61 Hodgkison *et al.*, 2003; Muscarella & Fleming, 2007); birds that are diet and
62 habitat generalists perch in recovering sites, depositing seeds and speeding up
63 recovery Carlo & Morales (2016); Carlo & Yang (2011). Other authors also find
64 that many animal pioneers are generalists with respect to habitat (Bowman *et al.*,
65 1990; Chazdon, 2014; Chazdon *et al.*, 2009; Liebsch *et al.*, 2008; Pinotti *et al.*,
66 2015) and diet (May, 1982). Furthermore, studies with pollinating bees suggested
67 that animal pioneers are generalists with respect to the traits of their mutualistic
68 partners (Chazdon, 2014). While animal mutualists fulfilling these different
69 concepts of generalism dominate early stages of recovery, animal species with
70 more specialized requirements for habitat, diet, or specific mutualistic partners
71 are expected to increase in number with time (Bowman *et al.*, 1990; Chazdon,
72 2014; May, 1982; Pinotti *et al.*, 2015).

73 A way to understand the emergence of structural features in networks, such as
74 the degree of specialization, is the theoretical study of network assembly, usually

75 by computer simulations, which has in the past largely focused on food webs
76 (Valdovinos, 2019). Such assembly simulations are interpreted as modelling the
77 recovery of a destroyed habitat or the formation of a new habitat, for instance
78 when a new volcanic island emerges from the ocean. Colonization of a destroyed
79 or new habitat is modelled by immigration of species from a species pool, and the
80 colonization of the habitat is in these models due to successful immigration events.

81 To our knowledge, Campbell *et al.* (2011) introduced the first model to assemble
82 mutualistic plant-pollinator networks. This model is based on trait matching, with
83 the survival of a species being determined by the number of beneficial versus the
84 number of detrimental links it has. The focus of that study is on the diversity of
85 assembly trajectories and outcomes. A recently introduced model by Becker *et al.*
86 (2022) adds realism by including a niche width for animals and by determining
87 species survival based on explicit simulation of population dynamics, including
88 demographic noise. The assembly process in this model leads to networks where
89 specialists and generalists coexist. However, since all species of the model are
90 obligate mutualists, the initial stages of the assembly process are very slow.

91 In this paper we study a model that includes mutualistic animals that are not
92 necessarily dependent on the resources provided by the mutualistic partner plants
93 in the recovering site. These could represent highly mobile non-resident animals
94 such as birds or bats that only occasionally forage in or fly over a recovering site
95 as they rely also on adjacent undisturbed habitats for nesting or foraging. The
96 model would also suit facultative mutualists that do not feed exclusively on the
97 resources provided by their plant partner, or capital breeders that live in the larval
98 stadium as herbivores and can feed in their adult stadium on nectar to increase
99 reproduction (Davis *et al.*, 2016). We use in the following the term "non-obligate"
100 mutualists for these species. Other features of the model are similar to those

101 of (Becker *et al.*, 2022), in particular all plant species in our model are obligate
102 mutualists.

103 With our model, we will identify the influence of non-obligate animal mutualists
104 on network assembly, especially during the early stages when only few resources
105 and mutualistic partners are available in the recovering site. We investigate the
106 idea that animal pioneers with a high degree of generalism can play a key role
107 during assembly. Furthermore, we explore how their influence changes during
108 network assembly as species richness increases. At last, we study how the
109 non-obligate animal mutualists affect the time evolution of the structural features
110 of the network, in particular the degree of specialisation of the obligate animal
111 mutualists. Taken together, our results will provide a unified view and show
112 the combined action of the observed trends from more generalist animals (with
113 respect to habitat, diet, or trait spectrum of their plant partners) to more specialist
114 animals.

115 **2 Materials and Methods**

116 The building blocks of our model are trait-based network assembly and
117 deterministic as well as stochastic population dynamics for plants and animals
118 that interact in a service-for-resource mutualism.

119 **2.1 Trait-based network architecture**

120 Each plant and each animal in the network is assigned a trait t_{A_i} (for animals)
121 and t_{P_i} (for plants), and in case of animals also a niche width s_j . We assume that
122 this trait represents all the animal and plant properties that determine interaction
123 and competition between species. The scale of trait values is chosen such that
124 they lie in the interval $[0,1]$. Animal niche widths are chosen from the interval $(0,$

125 0.275], such that the model includes specialists with a narrow niche width as well
 126 as generalists that cover a considerable part of the trait space. Plants have a fixed
 127 niche width of $\xi = 0.1$ that determines their competition. The interaction between
 128 animals and plants is obtained from trait matching according to

$$129 \quad \alpha_{ij}(t_{P_i}, t_{A_j}, s_j) = \frac{A}{s_j} \cdot e^{\left(\frac{-(t_{A_j} - t_{P_i})^2}{s_j^2}\right)} \quad (1)$$

130 with $A = \sqrt{2\pi}^{-1}$, so that the area under the function is normalized to $1/\sqrt{2}$.
 131 Species P_i and A_j interact only if $\alpha_{ij} > 0.05$. According to Eq. (1), generalist
 132 animals with a high value of s_j (broad niche width) interact weakly, while specialist
 133 animals with a low value of s_j (narrow niche width) interact strongly.

134 2.2 Population dynamics equations

135 The dynamics for the population densities of plants p_i and animals a_j are given
 136 by the equations

$$137 \quad \dot{p}_i = r \left(1 - \sum_j u_{ij} p_j \right) \left(\frac{\sum_j \alpha_{ji} a_j p_i}{r + \sum_j \alpha_{ji} a_j} \right) - \mu_p p_i \quad (\text{plants}) \quad (2)$$

$$138 \quad \dot{a}_j = \lambda \left(\sum_i \frac{\alpha_{ji} a_j p_i}{r + \sum_m \alpha_{mi} a_m} \right) - \mu_a a_j \quad (\text{obligate animals}) \quad (3)$$

$$139 \quad \dot{a}_j = \lambda \left(\sum_i \frac{\alpha_{ji} a_j p_i}{r + \sum_m \alpha_{mi} a_m} \right) + \beta a_j \left(1 - \frac{a_j}{K} \right) - \mu_a a_j \quad (\text{non-obligate a.}) \quad (4)$$

140 with the maximum plant growth rate r , an energy conversion efficiency of animals
 141 λ/r , the mortality rates of animals μ_a and plants μ_p . For the non-obligate animals,
 142 there is a logistic growth term with the growth rate β and the carrying capacity K .
 143 This growth term makes sure that these animals are able to grow also in absence
 144 of a suitable mutualistic partner in the network (i.e., if all $p_i = 0$). The first two

145 of these equations have been derived from a more extensive model that includes
146 an equation for resource dynamics (Revilla, 2015), and they have also been used
147 by Becker *et al.* (2022).

148 The plant competition coefficient u_{ij} is given by

$$149 \quad u_{ij}(t_{P_i}, t_{P_j}) = u + (w - u) \cdot e^{-\left(\frac{t_{P_i} - t_{P_j}}{\xi}\right)^2} \quad (5)$$

150 with the intraspecific competition strength w , the interspecific competition
151 strength u , and the plant niche width ξ . For animals, competition for plant
152 provided resources is implemented implicitly by a limitation of the total growth
153 rate of all animals,

$$154 \quad \sum_j \dot{a}_{j,growth} = \sum_j \lambda \left(\sum_i \frac{\alpha_{ji} a_j p_i}{r + \sum_m \alpha_{mi} a_m} \right) \underset{\alpha_{ji} a_j \gg r}{\approx} \sum_i p_i. \quad (6)$$

155 The cumulative animal population growth rate is of the order of the cumulative
156 population density of plants, which in turn is proportional to the total amount of
157 nectar or fruits.

158 Obligate animals and plants are assigned extinction thresholds θ_a and θ_p ,
159 respectively. If the population density of a population falls below this threshold
160 during the simulation, it is removed from the network.

161 These population dynamics equations can be used for any type of mutualism
162 where plants provide resources and animals provide a service necessary for plant
163 population growth.

164 **2.3 Adding demographic noise to the population dynamics**

165 Additionally to deterministic population dynamics, plant and pollinator
166 population densities are subject to demographic noise, which is particularly

167 relevant for small population sizes. The change in population sizes during the
168 small time increment dt then becomes

$$169 \quad dp_i \equiv p_i(t + dt) - p_i(t) = \dot{p}_i(t) dt + \sigma \sqrt{p_i(t)} dW_i(t) \quad (7)$$

$$170 \quad da_j \equiv a_j(t + dt) - a_j(t) = \dot{a}_j(t) dt + \sigma \sqrt{a_j(t)} dW_j(t). \quad (8)$$

171 The strength of demographic noise is set via σ , which is 0 in the deterministic case
172 and 0.1 in the simulations with demographic noise. dW is a random number that
173 is taken from a normal distribution with mean 0 and standard deviation $(dt)^{1/2}$.
174 We scale the demographic noise with the square root of the population density
175 because theoretical calculations of demographic noise through stochastic birth
176 and death processes typically show that the variation coefficient of the population
177 density scales with the inverse of the square root of the population density itself
178 (Kot, 2001). In the computer simulations, time evolution was calculated using
179 the Euler-Maruyama method (Higham, 2001), which is a method to numerically
180 integrate stochastic equations. The time increment dt was set to 0.1 for all
181 simulations, which is small compared to the time interval between immigration
182 events.

183 **2.4 Assembly simulations**

184 The main aim of this study is to assess the influence of non-obligate animal
185 populations on mutualistic network assembly. Therefore, we compare two versions
186 of the same assembly model, namely one version with non-obligate animals, the
187 other version without them. In the first version, we include a fixed number of
188 non-obligate animal species from the beginning, because we assume that they are
189 able to visit and forage in a recovering habitat even in the absence of mutualistic

190 plant partners. During the course of the simulation, for both versions, obligate
191 animals and plants were added to the network with equal probability at a rate
192 μ . They were assigned a small initial population density just above the respective
193 extinction thresholds θ_p and θ_a , and a random trait and niche width, which are
194 taken from a uniform distribution. The assembly was run until the long-term
195 behavior of the system became visible.

196 For the model version with non-obligate animals, we initiated the assembly
197 with 5 non-obligate animals with random traits and niche widths. This number
198 is sufficient to cover a considerable part of the trait space, but still not too large
199 to competitively exclude obligate animal species from entering. As starting point
200 of the assembly, we added one plant species that was capable of surviving in the
201 presence of the non-obligate animal species and had an initial population density
202 of $5 \cdot \theta_p$. The initial population density of the non-obligate animals was set to the
203 carrying capacity K , which was 0.2 or 2 for different sets of runs. The two different
204 values were chosen because a value of 0.2 leads to significantly lower and a value
205 of 2 to similar population densities of non-obligate animals compared to obligate
206 animals. No new non-obligate animals were introduced during the course of the
207 simulation, and non-obligate animals could not go extinct since we assume that
208 their populations are sustained by the surrounding unperturbed environment (or
209 by other factors not included explicitly in the model).

210 For the simulations with only obligate mutualists, we generated initially one
211 plant-animal pair with random traits and niche widths (provided they had a
212 sufficiently strong interaction strength of $\alpha_{ij} > 3$) to start off the network assembly.
213 In this way, we accelerated the first step of the assembly, which consists in waiting
214 for the almost simultaneous immigration of a pair that can interact with each
215 other. The initial population densities were $5 \cdot \theta_p$ (plants) and $10 \cdot \theta_a$ (animals). In

216 the rare case that all obligate animals and plants went extinct during the course of
217 the assembly process, the assembly was restarted and the time counter was reset
218 to 0.

219 2.5 Data analyses and evaluated quantities

220 For every parameter set, we calculated the number of plant and animal species
221 in the network over time as well as the cumulative population densities of plants
222 and animals (that is the sum over all population densities of plants and animals
223 currently in the network at that specific time). We averaged over 100 simulation
224 runs. Furthermore, we quantified the immigration success by keeping track of
225 the proportion of immigrants with initial growth rate > 0 after immigration
226 according to Eq. (2) and (3) and took averages over 500 simulation runs. To assess
227 the importance of non-obligate animal mutualists, we evaluated the reproductive
228 service provided by them. This was done by first evaluating their contribution to
229 the growth term of each plant separately

$$230 \quad \dot{p}_{i,growth} = \underbrace{\left(\frac{\sum_{j=1}^{j=5} \alpha_{ji} a_j p_i}{r + \sum_j \alpha_{ji} a_j} \right)}_{\text{non-obligate repr. service}=A_i} + \underbrace{\left(\frac{\sum_{j>5} \alpha_{ji} a_j p_i}{r + \sum_j \alpha_{ji} a_j} \right)}_{\text{obligate repr. service}=B_i} = A_i + B_i \quad (9)$$

231 and then evaluating the relative contribution of non-obligate animals to the
232 cumulative growth of all plants:

$$233 \quad \text{Reproductive service} = \frac{\sum_i A_i}{\sum_i A_i + \sum_i B_i}. \quad (10)$$

234 Additionally, we evaluated the reproductive service provided only by the most
235 generalized and most specialized animals (lowest and highest 18% of the niche
236 width interval) of each class (obligate or non-obligate).

237 The results displayed below are averages over 100 simulation runs.

238 **3 Results**

239 **3.1 Communities assemble faster with non-obligate animal mutualists**

240 Compared to the assembly simulations with only obligate mutualists, the
241 simulations with non-obligate animals show a much faster increase of cumulative
242 population densities and of species richness for both plants and obligate animals,
243 see Fig. 1. The generality of this trend is confirmed by the fact that there is not
244 much difference between the simulations with high and low carrying capacities
245 (and thereby population densities) of non-obligate animals (compare the upper
246 and middle rows of Fig. 1). The overall trends are similar for both model versions
247 and agree with the findings reported in Becker *et al.* (2022): While the cumulative
248 population densities of animals and plants increase monotonously from an initial
249 value of 0 to a constant, maximum value for all investigated parameter sets,
250 the species richness of obligate animal mutualists and of plants shows a peak at
251 intermediate assembly stages and then decreases slightly towards its asymptotic
252 value (see Fig. 1 upper and middle row) when population dynamics is deterministic.
253 In the presence of demographic noise, the intermediate peak of species richness
254 vanishes for the chosen parameter values (see Fig. 1 last row).

255 Total animal cumulative population densities in the model with non-obligate
256 animal mutualists are higher than in the model with only obligate mutualists.
257 Species richness of obligate animals at the maximum is lower in the model with
258 non-obligate animal mutualists compared to the model with only obligate animal
259 mutualists. However, at the final stage of the assembly, we find similar numbers
260 of obligate animal species in both model versions.

261 **3.2 Immigration success of both mutualistic partners is enhanced by**
262 **the presence of non-obligate animal mutualists**

263 The faster increase of obligate species richness and total population densities in the
264 simulations with non-obligate animals is caused by a higher immigration success
265 in the presence of non-obligate animals, see Fig. 2. This increase in immigration
266 success is higher for plants than for animals. Again, there is little difference
267 between the simulations with high and low carrying capacities (i.e. population
268 densities) of non-obligate animals. At later assembly stages, the immigration
269 success decreases towards zero in the simulations with deterministic population
270 dynamics, but it stabilizes at a non-zero value in the presence of demographic
271 noise (see Fig. 2. This asymptotic value is affected only very weakly by the
272 presence of non-obligate animals.

273 **3.3 Trait space is covered faster in the presence of non-obligate**
274 **animal mutualists, but the final network structure remains highly**
275 **specialized**

276 The assembly simulations with only obligate mutualists start from one interacting
277 pair and expand from there into the adjacent trait space. The assembly process
278 in the presence of non-obligate animals, on the other hand, allows plants (and
279 subsequently animals) to immigrate at multiple points in trait space already at
280 early assembly stages, as can be seen in Fig. 3 when comparing the second and
281 third row with the first row.

282 Even in the presence of non-obligate animals, the simulation leads to a
283 specialized obligate network, with each plant and each obligate animal having one
284 link. The only animal generalists present at the end are non-obligate animals,
285 as their composition does not change according to our model rules. Again, the

286 population densities of non-obligate animal mutualists has no clearly visible effect
287 on the findings. In the presence of demographic noise, species numbers are smaller,
288 and at the final stage of the assembly obligate generalist and specialist species can
289 coexist. In contrast to the deterministic case, some plants are only connected to a
290 non-obligate animal.

291 **3.4 The main reproductive service of animals to plants shifts during** 292 **assembly from generalist to specialist and from non-obligate to** 293 **obligate animals**

294 At early assembly stages, plants depend fully on the non-obligate animals for
295 reproduction, and the reproductive service (defined in Eq. (10)) provided by these
296 mutualists is initially 100% (see Fig. 4). Among them, the generalists with large
297 niche width ($0.225 < s_j < 0.275$) contribute considerably more to pollination
298 than the specialists with small niche width ($0 < s_j < 0.05$). With time, the
299 reproductive service of non-obligate animals decreases asymptotically towards a
300 smaller value, which is zero in the simulations with deterministic population
301 dynamics and non-zero with demographic noise. When the carrying capacity of
302 the non-obligate animals is higher, the decrease of their reproductive service is
303 slower, and the asymptotic value reached in the presence of demographic noise
304 is higher. This is not surprising as population sizes of non-obligate animals are
305 higher when their carrying capacity is higher, and so is their contribution to the
306 mutualistic service.

307 Over time, when the reproductive service by non-obligate animal mutualists
308 decreases, generalist obligate animal mutualists show a peak in reproductive service
309 at intermediate stages, but are gradually replaced by specialist obligate animal
310 mutualists. These specialist obligate animal mutualists provide the major part of

311 reproductive service in the long term in the case with deterministic population
312 dynamics. However, with demographic noise, the reproductive service provided by
313 specialist obligate animal mutualists becomes lower, at a value of approximately
314 40% for our parameter values. These trends are similar with high and low carrying
315 capacities of non-obligate animal mutualists.

316 **4 Discussion**

317 We investigated the assembly of service-for-resource mutualistic networks, using
318 a mathematical model where interactions between species are based on trait
319 matching between plants and animals. Animals in the model may depend
320 exclusively on their plant partners (i.e., they are obligate mutualists), or may have
321 other resources not included in the model (i.e., they are non-obligate mutualists),
322 and both types of animals may be trait specialists that interact strongly with
323 plants within a narrow trait range or trait generalists that interact moderately
324 with plants within a wider trait interval. Our most important findings are that (i)
325 assembly is more rapid if non-obligate animals are present than without them,
326 and (ii) there is a change in species traits during assembly towards a higher
327 degree of specialization, with non-obligate and generalist animals providing the
328 main reproductive service during early stages, and obligate and specialist animals
329 during the late stages. Non-obligatism and generalism thus act in combination
330 to facilitate network assembly. When stochastic effects due to demographic noise
331 are taken into account, the contribution of non-obligate and generalist obligate
332 animals to reproductive service remains non-zero even for long times.

333 The insights provided by our model have broad implications as the model is not
334 restricted to a specific type of mutualism or animal group, and as the non-obligate
335 animals can be viewed either as facultative mutualists (e.g. flies, butterflies and

336 wasps in pollination mutualism) that rely on resources not included in the model,
337 or as non-resident animals (e.g. mobile pollinating or seed-dispersing birds, bats or
338 insects) that occasionally visit the investigated site but also depend on structures
339 and resources in the surrounding landscape. The observed facilitation effect due to
340 non-obligate animals is supported by empirical observations which report habitat
341 and diet generalist seed-dispersing birds (which correspond to non-obligate animals
342 in our model) to promote tropical forest regeneration Carlo & Morales (2016). Our
343 model suggests that this keystone role of non-obligate animals at early assembly
344 stages is not restricted to plant-seed disperser mutualism, but a feature of any
345 type of service-for-resource mutualism.

346 The shift in traits of animal mutualists over time observed with our model
347 (see Fig. 4) agrees with general insights of succession theory that early pioneer
348 species differ in their properties from climax species (Chazdon, 2014). Habitat or
349 diet generalists prevail in young forests, while forest specialists or obligate animal
350 mutualists (i.e. diet specialists) dominate in mature forests (Bowman *et al.*, 1990;
351 May, 1982; Pardini *et al.*, 2009; Pinotti *et al.*, 2015). In contrast to our model,
352 each of these studies focuses on specific animal groups (e.g. birds and butterflies),
353 or on a certain type of mutualism (e.g. seed dispersal). Furthermore, the studies
354 consider different types of generalism, namely habitat generalism, diet generalism
355 (when, e.g., a bird eats insects and nectar), or trait generalism (when, e.g., bees
356 visit a broad range of flowers). Our theoretical approach connects these different
357 observations by suggesting that the shift from generalists to specialists occurs in
358 a correlated manner for all three concepts of generalism.

359 Since the facilitation of assembly by non-obligate animals is similarly enhanced
360 in the case with high and with low population density of non-obligate animals,
361 our model suggests that non-obligate animal mutualist population density is not

362 important for facilitating the network assembly. This finding appears empirically
363 relevant as one can expect the population density of animals in recovering sites to
364 be relatively low in the beginning, due to a lower abundance of resources (Chazdon,
365 2014).

366 We could ascribe the facilitation effect to a significantly increased immigration
367 success of plants and animals (Fig. 2). A closer look at snapshots of the network
368 assembly in Fig. 3 revealed that assembly with non-obligate animals can proceed at
369 multiple places in trait space from the beginning, compared to an initially narrow
370 trait range in the absence of non-obligate animals. This means that a higher
371 fraction of immigrating species can establish a link to a species already present in
372 the network, and hence can grow and survive. Additionally, in the network with
373 only obligate species newly entering species are necessarily ecologically similar to
374 species already present in the network, which means that their growth is hampered
375 by competition for resources and for mutualists. By enabling immigration of plants
376 over a wide range of traits, non-obligate animals lead to decreased interspecific
377 competitive pressure but have a competitive disadvantage themselves, and they
378 are replaced by obligate animals during succession.

379 Immigration success of animals is also enhanced, despite the presence of
380 non-obligate animals with similar traits. We explain this with the relatively
381 low competition between obligate and non-obligate animals in our model. As
382 we assume food to be the limiting resource for animals, non-obligate animals can
383 always rely on their other nutrition source apart from the one provided by their
384 interaction partners in the recovering habitat, leaving more of these resources to the
385 obligate animals. In this way, the competition between obligate animal mutualists
386 is decreased because they share less plant partners in the early stage compared to
387 the model version with only obligate species.

388 One might argue that the increased immigration success in the presence of
389 non-obligate animals is due to a wider range of trait space being available,
390 increasing the chance of an immigrating species to establish a link. To test this
391 hypothesis, we also made a simulation where each immigrating species is chosen
392 such that it has at least one link upon entry into the network. We found that in
393 this case immigration success is still higher in the model version with non-obligate
394 animal mutualists than without (see Figure S1 in Supporting Information). This
395 means that the availability of niches alone cannot fully explain the increased
396 immigration success, but the reduced competition also plays an important role.

397 Non-obligate animals lead in our model to functional redundancy and therefore
398 to a more robust network structure during later assembly stages: whenever the
399 obligate partner animal of a plant goes extinct, the non-obligate partner might
400 save it. Higher robustness due to functional redundancy is supported by empirical
401 observations (Biggs *et al.*, 2020). With demographic noise, the non-obligate animal
402 mutualists provide a non-negligible proportion of reproductive service even in
403 the long term, due to the continuous extinction risk of obligate animals and
404 the subsequent necessity of plants to rely on their non-obligate partners. Hence
405 non-obligate partners stabilize the mutualism against reproductive failure and
406 co-extinction.

407 In conclusion, our model provides a unifying framework and a mechanistic
408 understanding of different empirical observations concerning the role of diet,
409 habitat, and trait generalists during early stages of ecosystem recovery and the
410 shift towards a higher degree of specialism at later stages. It demonstrates that
411 these shifts occur in combination, suggesting a broader empirical exploration
412 of pioneer and climax species' traits to corroborate and refine our mechanistic
413 findings. Ultimately, this can show ways for accelerating ecosystem restoration.

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Var.	Description	Value	Dimension
t_{P_i}	Plant niche value	$\in [0,1]$	
t_{A_j}	Animal niche value	$\in [0,1]$	
s_j	Animal niche width	$\in (0,0.275]$	
ξ	Plant niche width	0.1	
p_i	Density of plant population i		[individuals/area]
a_j	Density of animal population j		[individuals/area]
r	Per capita growth rate of plants	1	[1/time]
λ	Per capita growth rate of animals	0.8	[1/time]
w	Intraspecific competition coeff. of plants	0.8	[area/individuals]
u	Interspecific competition coeff. of plants	0.2	[area/individuals]
μ_p	Per capita mortality rate of plants	0.002	[1/time]
μ_a	Per capita mortality rate of animals	0.1	[1/time]
K	Carrying capacity	0.2, 2	[area/individuals]
β	Logistic growth rate	2	[1/time]
σ	Strength of demographic noise	0, 0.1	$[\sqrt{\frac{\text{individuals}}{\text{area}\cdot\text{time}}}]$
μ	Immigration rate	0.1	[1/time]
θ_p	Extinction threshold of plants	10^{-2}	[individuals/area]
θ_a	Extinction threshold of animals	10^{-4}	[individuals/area]
	Initial population density of plants	$(1+10^{-4})\cdot\theta_p$	[individuals/area]
	Initial population density of animals	$(1+10^{-4})\cdot\theta_a$	[individuals/area]
dt	Step size for numerical integration	0.1	[time]

Table 1: List of all parameters and variables that were used in the simulations, including a description, the used values and respective dimensions.

501 Figure 1: Cumulative population density and species richness of plants (left) and
502 animals (right) over time for deterministic population dynamics ($\sigma = 0$) and
503 population dynamics with demographic noise ($\sigma = 0.1$), and for high ($K = 2$) and
504 low ($K = 0.2$) carrying capacity of non-obligate animals. Full lines correspond
505 to cumulative population density (left y-axis), dashed lines to species richness
506 (right y-axis). For species richness, only obligate animal and plant numbers are
507 shown. For the cumulative population density, obligate and non-obligate animals
508 are pooled together. Computer simulations of the model with only obligate
509 animals (lighter colour) and the model with additional non-obligate animals
510 (darker colour) are shown together. Vertical black dotted lines refer to times
511 when network plots of Fig. 3 were created. The immigration rate was set to $\mu = 0.1$.

512

513 Figure 2: Immigration success of plants (left) and animals (right) over time
514 for deterministic population dynamics ($\sigma = 0$) and population dynamics with
515 demographic noise ($\sigma = 0.1$), and for high ($K = 2$) and low ($K = 0.2$) carrying
516 capacity of non-obligate animals. Computer simulations of the model with only
517 obligate animals (lighter colour) and the model with additional non-obligate
518 animals (darker colour) are shown together. The immigration rate was set to $\mu =$
519 0.1.

520

521 Figure 3: Snapshots of the network assembly after 5 (left), 500 (middle),
522 and 500,000 (right) immigration events. We compare the model with only
523 obligate animals (top row) with the one with non-obligate animals (three
524 bottom rows), the model with deterministic population dynamics ($\sigma = 0$) to
525 the one with demographic noise ($\sigma = 0.1$), and simulations with high ($K = 2$)
526 and low ($K = 0.2$) carrying capacity of non-obligate animals. Light blue

527 squares correspond to non-obligate animal mutualists, dark blue to obligate
528 animal mutualists. The circles represent plants. The size of squares and circles
529 corresponds to the population density of the respective species.

530

531 Figure 4: Reproductive service of obligate and non-obligate animal mutualists
532 over time according to Eq. (10). Species with a niche width $s_j \in [0.225, 0.275]$ or
533 $s_j \in (0, 0.05]$ were labeled generalists (dashed line) and specialists (dotted line),
534 respectively. Full lines correspond to total non-obligate/obligate reproductive
535 service, where the reproductive service of generalist, specialist and intermediate
536 ($s_j \in [0.05, 0.225]$) animal mutualists is added up.

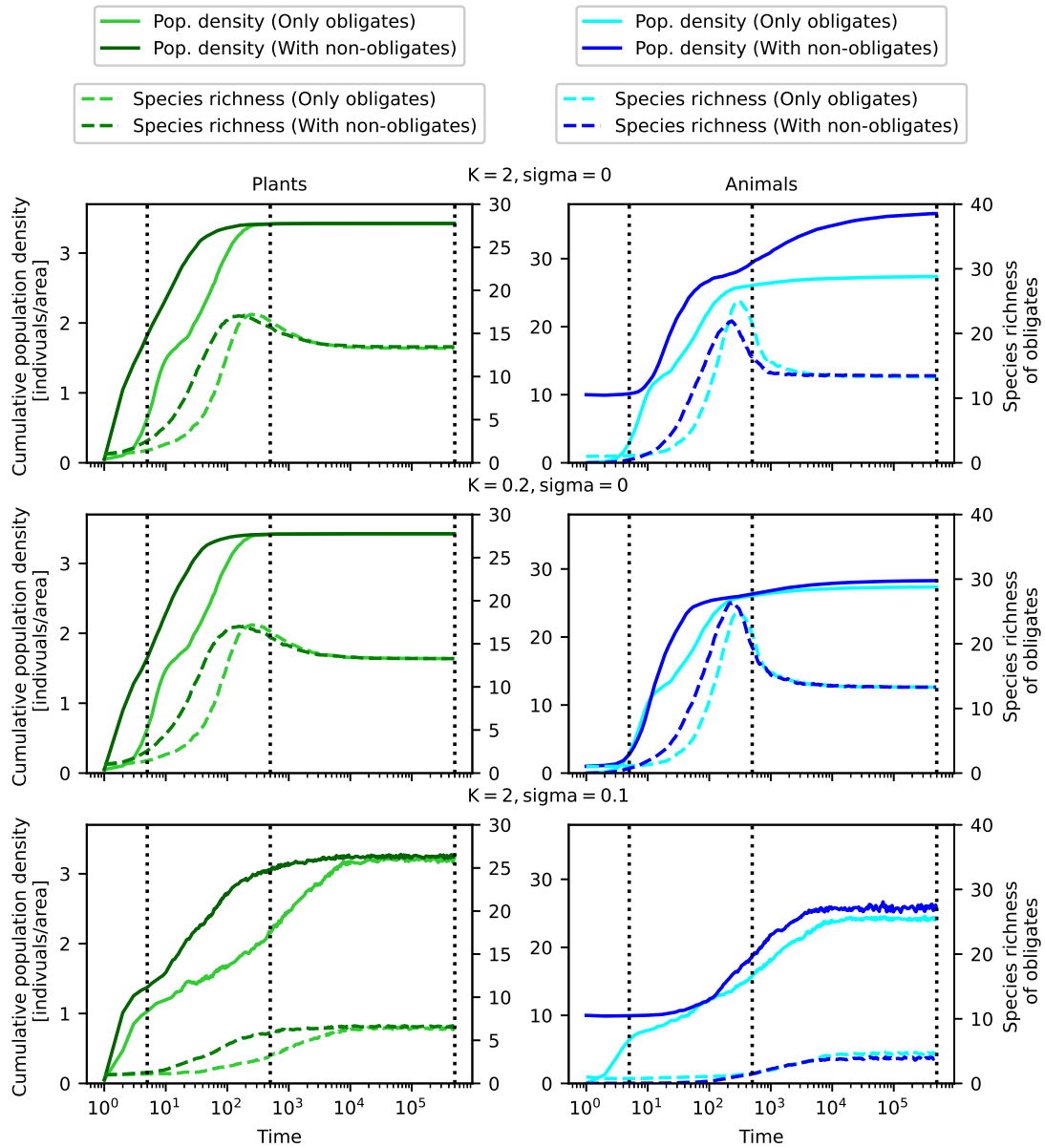


Figure 1

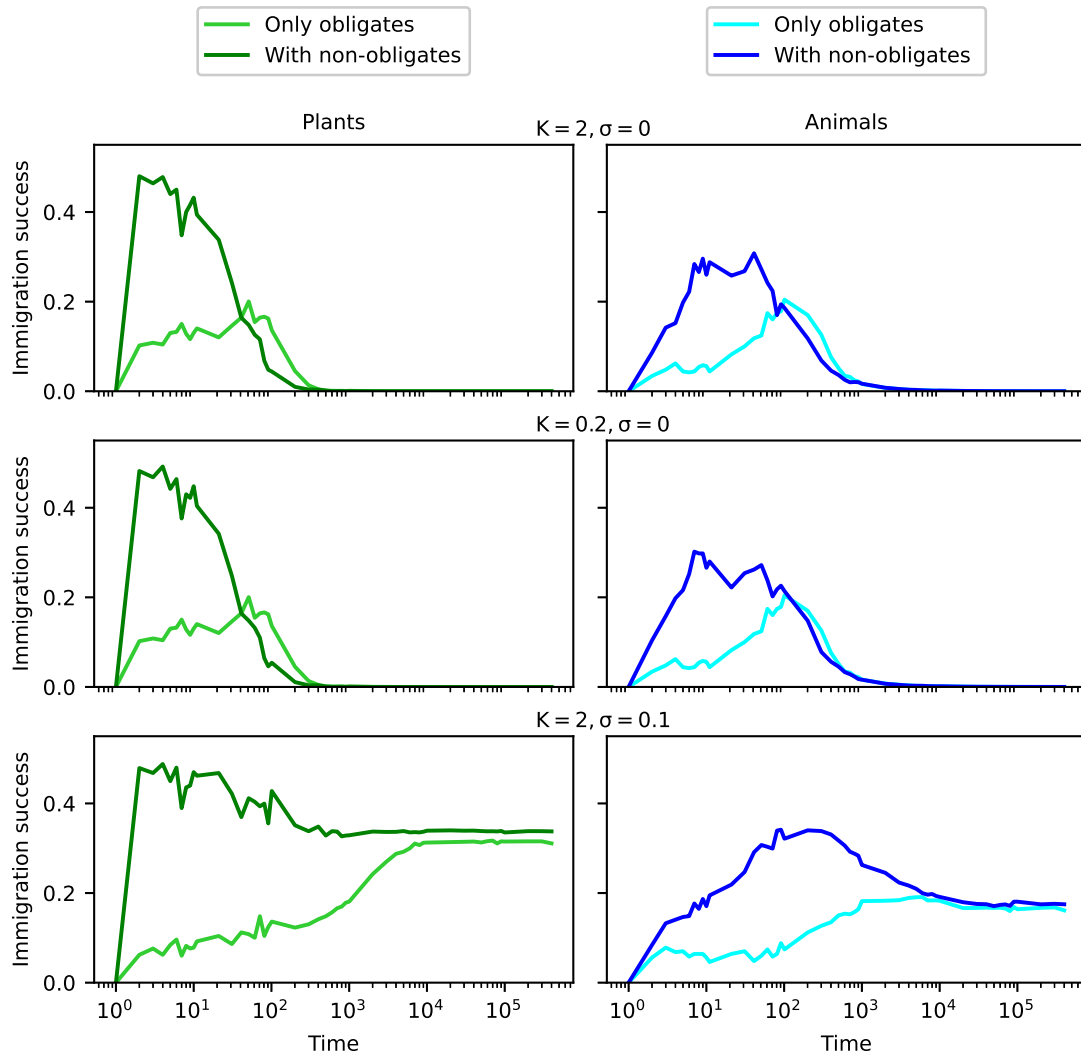


Figure 2

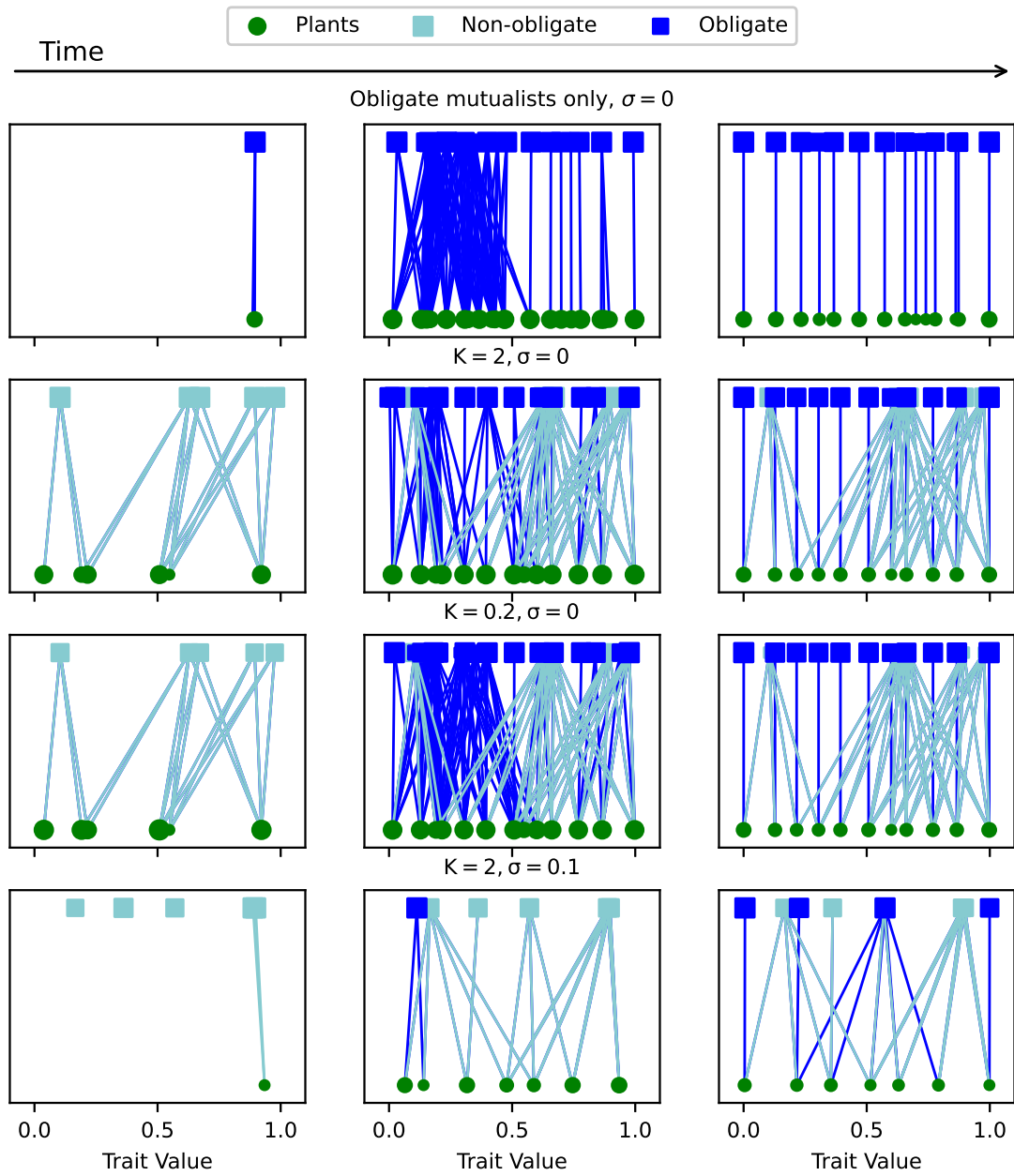


Figure 3

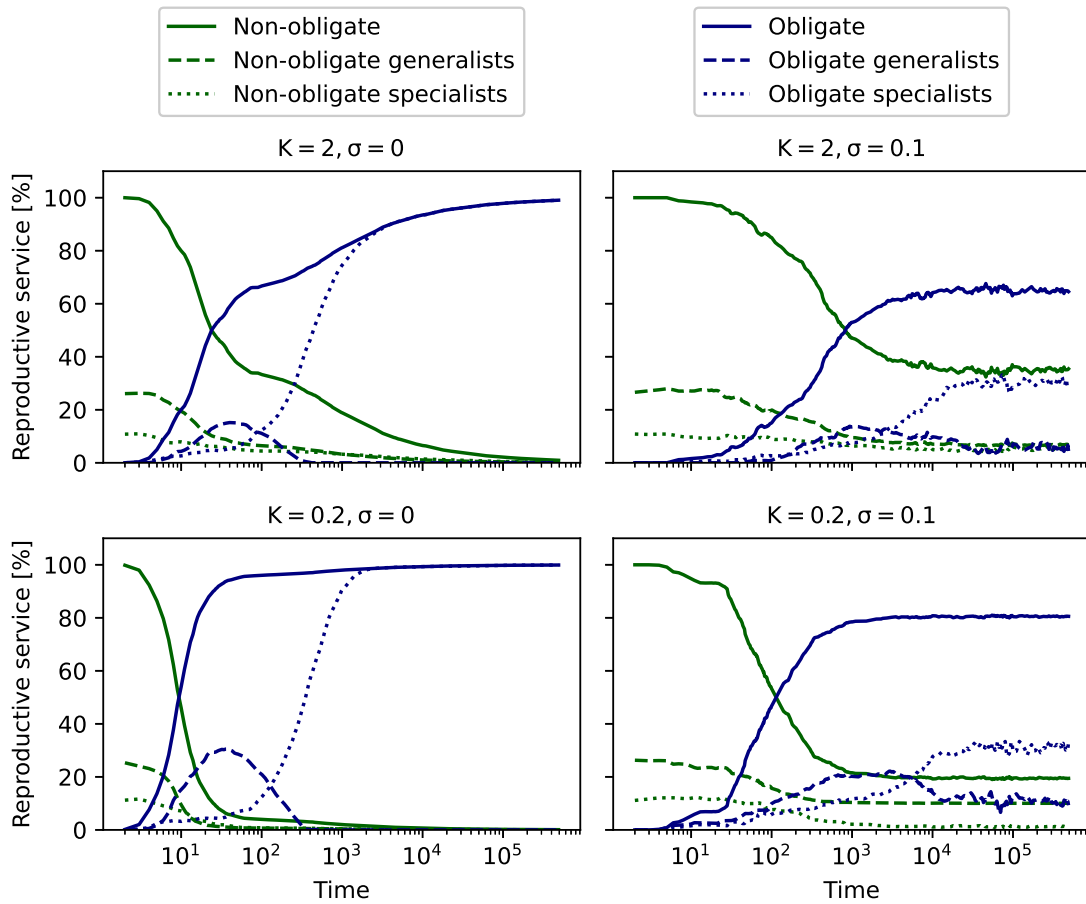


Figure 4