Title: Population turnover reverses classic island biogeography predictions in river-like landscapes

Running Head: Biodiversity in river-like landscapes.

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Statement of authorship: EH, IG, EAF and FA designed the research; IG and EAF designed the model; IG programmed and ran the model, analyzed the simulation data with support from EAF and produced the figures; EH conducted the lab experiment with support from IG, EAF and FA, processed the experimental data with support from IG, and carried out the analysis of experimental data; all authors participated in results interpretation; EH wrote the first draft of the manuscript; All authors significantly contributed to further manuscript revisions. EH and IG contributed equally to this work.

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Background

Motivated by the global biodiversity crisis, ecologists have spent the last decades identifying biodiversity hotspots. While these global analyses of biodiversity show recurrent patterns of spatial distributions worldwide, unveiling specific drivers remains logistically challenging. Here, we investigate the processes underlying biodiversity patterns in dendritic, river-like landscapes, iconic examples of highly diverse but threatened ecosystems. Combining theory and experiments, we show that the distribution of biodiversity in these landscapes fundamentally depends on how ecological selection is modulated across the landscape: while uniform ecological selection across the network leads to higher diversity in confluences, this pattern can be inverted due to patch size-dependent population turnover. Higher turnover in small headwater patches can slow down ecological selection, increasing local diversity in comparison to large confluences. Our results provide a way forward in the long-standing debate regarding the distribution of diversity in river-like landscapes within a single, experimentally validated conceptual framework.

Local species diversity in dendritic, river-like landscapes is generally expected to be higher in larger, more connected confluences than in headwaters[1–5]. Previous theoretical, comparative and experimental studies have all emphasized the importance of dispersal along the network structure of the landscape as a key driver of this diversity pattern, regardless of the specific dominant local drivers of community dynamics (such as ecological drift[3,6] or ecological selection[7]). The pattern of lower local diversity in upstream habitats compared to downstream confluences (hereafter 'classical pattern'), however, is not ubiquitous in natural river systems: recent empirical studies[8,9] have documented that diversity patterns can be completely reversed, with higher diversity upstream rather than downstream (hereafter 'reversed pattern'). These contrasting empirical patterns, especially the reversed one, and the transition from one to the other remain insufficiently understood and are currently not accounted for by any theoretical or experimental work. Given that river ecosystems support roughly 10% of all animal species on only 0.01% of the globe surface[10], it is surprising and disturbing that we are still lacking a general understanding of the processes driving diversity patterns and the transition between seemingly opposed empirical patterns of diversity in these ecosystems. A better understanding of the dominant mechanisms generating contrasting diversity patterns is essential if we hope to counter current trends of erosion of biodiversity and ecosystem services in river ecosystems worldwide[11–13].

River-like landscapes are structured by spatial flows of organisms and resources. They also inherently display strong environmental gradients, both in terms of resources (habitat size / land use influence) and perturbations (current flow, erosion)[1,14]. While previous theoretical work has primarily focused on dispersal-related mechanisms[3,15,16], the latter

61 intrinsic characteristics might be key to explaining contrasting diversity patterns in such
62 spatially structured landscapes where habitat size scales with position in the landscape[4,17]:
63 While small headwater patches can be found across a wide range of landscape
64 connectivity, the fewer and larger downstream patches are inherently more connected[14].
65 The Theory of Island Biogeography[18,19] ('TIB') provides explanation for one of the most
66 established and universal ecological patterns stating that smaller and more isolated
67 patches suffer higher extinction rates and lower immigration rates eventually leading to
68 lower diversity than in larger and more connected patches[18–22]. In such a scenario,
69 competitive exclusion due to ecological selection occurs more rapidly in small headwater
70 communities because, in finite populations, extinction thresholds are reached earlier.
71 Consequently, all else being equals, at equilibrium density, smaller patches should always
72 contain lower diversity. In that context the 'reversed pattern' can only occur if (i) all else
73 is not equal and smaller headwater patches contain higher environmental heterogeneity or
74 (ii) equilibrium density is reached more slowly in smaller patches. The former represents
75 the obvious case where headwater patches might contain higher proportion of micro-
76 habitats providing higher niche dimensionality and/or *refugia* from competition and
77 predation. Here we focus on the latter case, where perturbations maintain smaller patches
78 away from their community equilibrium state. This is an especially likely and
79 increasingly widespread scenario in the context of global change[23]. However, due to
80 multiple interacting factors and lack of replication, it is highly challenging to be directly
81 test in the field. To get a causal understanding, we thus develop first a general
82 mathematical model, and then test the main predictions in well-established ecological
83 microcosms.

84 Perturbations and associated increased population turnover are often seen as a major
85 driver of community dynamics by slowing down competitive exclusion and ultimately
86 favouring species coexistence[24–26]. If perturbations impact smaller patches more strongly
87 than larger patches, it will generate higher population turnover in smaller patches that, in
88 turn, can potentially lead to higher species richness in smaller headwater patches than in
89 larger downstream patches. Thus, in the classical biodiversity pattern, competitive
90 exclusion by ecological selection is expected to occur faster in smaller patches because of
91 finite population sizes, while in the presence of perturbations higher population turnover
92 in smaller patches should slow down competitive exclusion making selection slower in
93 smaller patches thus potentially reversing biodiversity pattern in the landscape.

94 Indeed, beyond the structural properties of river-like landscapes, specific
95 characteristics of headwaters also suggest that they are naturally more prone to
96 perturbations[27] and thus to higher population turnover rates. For instance, headwaters
97 exhibit higher benthic surface area to water volume ratio[28] and thus are more sensitive to
98 minor changes to their surrounding environment[29,30]. Furthermore, they expand into
99 higher elevations, which are experiencing harsher and more variable environmental
100 conditions[31]. Eventually, this asymmetry in population turnover between upstream and
101 downstream patches due to perturbations may generate higher diversity upstream
102 compared to downstream patches.

103 To resolve the apparent inconsistency in our understanding of local diversity patterns
104 in river-like landscapes[3,8,9,16,32], we here investigate the processes underlying the
105 distribution of biodiversity and specifically focus on characteristic patch size distributions
106 and population turnover. In natural riverine landscapes, patch size distribution, network

107 configuration and perturbations are intrinsically linked, and cannot be disentangled in a
108 causal approach (see also [4,14,33]). We thus used a general model reproducing river-like
109 networks properties to disentangle spatial patterns of population turnover from other
110 drivers of biodiversity. We then also validated the predicted turnover-induced reversed
111 biodiversity pattern with a simple experiment. We first show theoretical results from a
112 spatially explicit Lotka-Volterra competition metacommunity model. The model includes
113 dispersal along dendritic networks, demographic stochasticity, and patch size-dependent
114 turnover, that is, higher mortality in smaller patches (see full details in Methods). We
115 secondly corroborated experimentally the model's main prediction on population
116 turnover effects, using dendritic protist microcosm landscapes[34] of the same network
117 topologies (see Methods and Fig. 1). Patch size-dependent turnover was experimentally
118 reproduced by sampling, killing and pouring back (no change in biomass) a fixed volume
119 of each community, which resulted in a gradient of population turnover from smaller
120 upstream to larger downstream microcosms (13%, 8%, 4%, and 2% mortality). This
121 mortality gradient implementing an inverse relationship between population turnover and
122 patch size, can be seen as a general effect of environmental perturbation (perturbation-
123 induced turnover).

124

125 **Results**

126 **Classical diversity pattern.** In the simulations without perturbation-induced population
127 turnover, the highest diversity levels are found in the large downstream patches (Fig. 1
128 and 2a). Contrastingly, the smaller, mostly upstream patches have lower diversity levels.

129 This differences in diversity unfolded with smaller patches supporting smaller population
130 sizes (Fig. 3a), which are then more sensitive to stochastic extinctions relative to
131 populations in larger patches (Fig. 3b).

132 **Reversed diversity pattern.** In the simulations with a gradient of perturbation-induced
133 population turnover, highest diversity levels are found in upstream patches (Fig. 1 and
134 2b) consistently across all the different community (different species traits) and landscape
135 (different spatial networks) replicates. The same pattern was found in the context of our
136 experiment with an aquatic protist community (Fig. 1 and 2c): As in the simulations
137 (Supplementary Fig. 1), the biodiversity pattern appeared progressively over time with no
138 apparent effects of patch size at the first sampling day (experiment day 7, 7.4 ± 0.67
139 species in smallest vs. 7.1 ± 0.70 species in largest patches, mean ± sd, Supplementary
140 Fig. 2 and Table 1) compared to the final experimental day 29, when there was a clear
141 and significant decline in local diversity with patch size (4.7 ± 1.3 species in smallest
142 patches vs. 2.5 ± 1.5 species in largest patches, mean ± sd, Fig.1, 2b and Supplementary
143 Table 1). The simulations show that, overall, patch size-dependent population turnover
144 slows down ecological dynamics (ecological selection; Fig. 3a), but does more so in
145 smaller patches (Fig. 3a), which is then increasing the time to extinction of less
146 competitive species (Fig. 3b).

147 **Persistence of diversity patterns in river-like landscapes.** Our model predicts both
148 diversity scenarios to occur within specific parts of the parameter space defined by the
149 magnitude of dispersal and the strength of patch size-dependent population turnover (i.e.,
150 slope of the relationship between patch size and population turnover rate, see Methods for
151 details; Fig. 4): weak patch size-dependent population turnover generates the classical

152 diversity pattern, while intermediate to high strengths of patch size-dependent population
153 turnover generate the reversed diversity pattern until population turnover is so high in
154 smaller relative to larger patches that all species upstream go extinct, leading to a return
155 to the classical diversity pattern. As expected, regardless of the strength of patch size-
156 dependent population turnover, increasing dispersal blurs diversity patterns by
157 homogenizing diversity in the landscape (Fig. 4).

158

159 **Discussion**

160 Testing the impact of perturbation-induced population turnover on the distribution of
161 biodiversity in river-like landscapes, we found that turnover can alter the classical
162 biodiversity pattern of higher diversity in larger downstream patches predicted by the
163 TIB[3,6,18]: the classical pattern persists only until a certain level of population turnover, at
164 which point asymmetry in turnover between smaller upstream and larger downstream
165 patches will reverse the pattern completely. Such a reversed diversity pattern has been
166 observed in case studies from multiple natural systems[8,9] and has challenged the idea of
167 one overarching and universal diversity pattern to be expected in river-like landscapes (as
168 proposed by some studies[3,16,35,36]). However, this reversal has hitherto neither been
169 understood mechanistically nor predicted by current theory. Here, we provide a clear
170 mechanistic explanation based on theoretical considerations, which we then successfully
171 validated experimentally.

172 Dispersal and the landscape context are key factors in driving metacommunity
173 dynamics[37]. Here we showed that specific characteristics of river-like landscapes, namely

174 a combination of the spatial distribution of patch sizes and an associated population
175 turnover gradient, can also play a dominant role in driving diversity patterns. Higher
176 population turnover in smaller headwater patches keeps communities away from their
177 equilibrium state and thus reduces the strength of local ecological selection. This leads to
178 the coexistence of more species for longer periods of time in comparison to larger
179 patches, in which turnover is not strong enough to prevent competitive exclusion. This
180 effect will be especially pronounced in communities with strong competitive asymmetries
181 and even enhanced in systems with competition-colonization trade-offs, as few strong
182 competitors with low dispersal rates, would lead to strong selection in the absence of
183 turnover.

184 Our work suggests that there may be general mechanisms responsible for the naturally
185 observed diversity patterns including the reversal of diversity patterns. Perturbation-
186 mediated slowing down of competitive exclusion is a well-understood ecological
187 mechanism affecting population dynamics[25,38–40]. Here we show that this mechanism can
188 generate a specific signature in terms of biodiversity patterns when applied over a spatial
189 gradient in perturbation, which are a common feature of river-like landscape. For
190 instance, headwaters in river systems are naturally more prone to higher levels of
191 population turnover because of their higher benthic surface area to water volume ratio
192 compared to larger downstream patches[28]. Headwaters are also more exposed to changes
193 in their surrounding environment, such as natural fire dynamics, potentially leading to
194 more frequent flooding events, higher erosion levels and a decline in terrestrial subsidy
195 (leaf input) on which they are energetically more dependent than larger downstream
196 patches[29,41]. They are on average also located at higher elevation, and thus experiencing

197 stronger variations in temperature and weather conditions. Human-induced perturbations
198 in pristine headwaters are increasingly common[30] and the general mechanisms
199 demonstrated by our study suggest that these anthropogenic impacts can have unexpected
200 large-scale consequences by inverting biodiversity patterns. This is especially true if
201 perturbations occur in combination with invasive species, which is a common scenario[42].
202 Thereby, size-dependent population turnover leads to species-poor and highly invasion-
203 prone communities at downstream sections of the river network, whereas species-rich
204 upstream sections may be more resilient due to slower competitive exclusion In
205 conclusion, we show that patch size-dependent turnover, which is intrinsic to river-like
206 landscapes, and its effect on ecological selection can be a key mechanisms responsible
207 for shaping the distribution of biodiversity distribution in river-like landscapes.

208

209 **Methods**

210 **Simulation experiment.** To investigate the mechanisms underlying biodiversity
211 distribution in dendritic, river-like networks in relation to their intrinsic non-random
212 patch connectivity/size pattern, we first used general simulations of a Lotka-Volterra
213 competition model for 10 species, in which the temporal variation of species *i* density in
214 patch *x*, N_{ix} is described by:

215 $$\frac{dN_{ix}}{dt} = r_i N_{ix}\left(1 - \frac{\sum_{j=1}^{n} \alpha_{ij} N_{jx}}{K_i V_x}\right) - \frac{d}{V_x}\sum(N_{ix} - N_{iz}) - m_x N_{ix} + a * \rho\sqrt{N_{ix}}$$

216 where r_i is the intrinsic growth rate, α_{ij} the per capita effect of species *j* on species *i*
217 (interaction coefficient), K_i the carrying capacity, which is scaled with the size of the

patch V_x, d_i the dispersal rate and m_i the patch size-dependent mortality rate (population turnover). In the last term we model demographic stochasticity as in Giometto et al.[43]. At each time step, a proportion a times ρ of the square root of population density is being either added or removed from each species population in each patch; the parameter a modulating the magnitude of this drift is set to 0.25 in all simulations; the random factor ρ is sampled for each species within a patch at each time step from a Gaussian distribution of mean $\mu = 0$ and variance $\sigma = 0.1$. Species traits were parameterized in a very simple and general way, independent of our experimental organisms, to preserve the generality of our model predictions. To limit sources of variations, r, K and d are the same for all species in all patches and we implement species differences via interaction coefficients only. Interaction coefficients are drawn from a Gaussian distribution ($\mu = 2, \sigma = 0.25$) with all negative coefficients multiplied by -1 to obtain a purely competitive community; r and K were set to 0.25 and 2000 respectively in all simulations. The dispersal term is a sum function of the population density differences between patch x and each patch z to which it is connected according to the specific topology of the dendritic landscape. We scale dispersal rates with patch size to make it comparable to the experimental set-up where exchanging a constant volume between two patches was the most feasible dispersal mode. However, the results are robust to change in dispersal mode, using a constant rate either per vertex or per patch. As a minimal assumption to implement patch size dependency in turnover rates, we make mortality rates follow a linear relationship with patch size (see sensitivity analysis below for the values).

For the landscapes, we use river-like networks generated from five different space-filling optimal channel networks[44] known to reproduce the scaling properties observed in real river systems[4,45]. In order to also be able to use the same landscapes in the experiments, a coarse-graining procedure is used to reduce the 5 generated constructs to equivalent 6x6 patch networks, preserving the characteristics of the original three-dimensional basin (see Fig.1, for details see appendix A in Carrara et al.[4]), but having a total node size that was experimentally feasible. These 6x6 patch networks contained 36 patches of four different volumes (V) respecting river system scaling properties: 7.5, 13, 22.5, and 45 mL (see Fig.1). These volume values are used for patch sizes V_x in the model.

Using these simulation settings, we test the effect of patch size-dependent population turnover on biodiversity patterns by contrasting simulations with and without turnover. We have two levels of replication: we replicate our simulations over the 5 different dendritic landscapes to assess the independence of the results from specific network topologies, and 10 random realisations of the interaction matrix (replicate communities), leading to 50 simulations total per scenario (turnover settings at a given dispersal rate). Simulations always start with all species already present in all patches and with same absolute density set to 200 individuals. The results are robust to starting conditions with same relative density (scaled to patch size). Simulations are run until 400 time steps, which is sufficient to observe competitive exclusion (see Fig. 3 and Supplements Figure 1 for examples of dynamics). A species for which density falls below 10^{-3} is considered extinct and its density set to 0. The results are robust to the decline or suppressing of this threshold but we keep it to optimize the computation time.

In addition, we explore the persistence of the different observed diversity patterns as a function of the magnitude of dispersal and the strength of the turnover *vs*. patch size relationship (slope of the relationship, see Fig. 4). We explore 6 levels of dispersal with $d \in \{0, 0.05, 0.1, 0.25, 0.5, 1\}$ and 21 mortality rate combinations between the largest and the smallest patches, that is all combinations with $m \in \{0, 0.01, 0.05, 0.1, 0.25, 0.5\}$ with mortality in smallest patches being higher or equal to in largest patches (Supplementary figure 3). This results in 14 different slopes of the relationship between turnover (mortality rate) and patch size, ranging from 0 to −1.33. For each parameter combination we run 50 simulations (i.e., 5 replicate landscapes x 10 replicate communities) resulting in a total of 6,300 simulations.

Experimental validation. To empirically validate the main finding from our simulations, that is, patch size-dependent population turnover leading to a reversal of the 'classical' biodiversity pattern in dendritic network, we conducted a protist meta-community experiment. We did not experimentally test for the diversity pattern without perturbations because it has already been empirically verified many times in the literature[2,3,7,27,46,47], and in the same experimental conditions[4,16]. Therefore, we focussed here on testing specific predictions from the simulations owing to patch-size dependent turnover and the occurrence of the predicted pattern of biodiversity under this scenario. In that context, the experiment constitutes a very conservative test of our much more general simulations. The experiment consisted of seven protist species interacting and dispersing for 29 days along 4 different dendritic networks of 36 patches (same than four of the five landscapes used in the simulations; see Fig. 1). Each landscape had 4 different patch size levels (7.5, 13, 22.5, and 45 mL) connected by dispersal along a dendritic network and

286 preserving the scaling properties observed in real river systems (see Fig. 1 and
287 Supplementary figure 4 for a photo, and section "simulation experiment" above,
288 following Carrara et al.[4]).

289 Our communities were composed of three bacteria species (*Serratia fonticola*, *Bacillus*
290 *subtilis* and *Brevibacillus brevis*) fed upon by seven bacterivorous protist and one rotifer
291 species (henceforth called "protists"): *Tetrahymena* sp., *Paramecium caudatum*,
292 *Colpidum striatum*, *Spirostomum* sp., and *Chilomonas* sp., *Blepharisma* sp. and the
293 rotifer *Cephalodella* sp. The latter two species can, next to feeding on bacteria, to a lesser
294 degree also predate on smaller protists. Prior to the beginning of the experiment, each
295 protist species was grown in monoculture in a solution of pre-autoclaved standard protist
296 pellet medium (Carolina Biological Supply, Burlington NC, USA, 0.46 g protist pellets 1
297 L^{-1} tap water) and 10% bacteria inoculum, until they reached carrying capacity (for
298 methodological details and protocols see Altermatt et al.[34]). Protist abundance and
299 diversity were measured by video recording combined with a trained algorithm to
300 differentiate each species based on their morphological traits (see below).

301 Each microcosm in our four landscapes consisted of a 50 mL polypropylene falcon
302 tube (VWR, Dietikon, Switzerland). At day 0, we pipetted an equal mixture of each of
303 the seven species into each microcosm to reach the corresponding volume (7.5, 13, 22.5
304 or 45 mL). Thus, protist communities were added at 15% of their carrying capacity and
305 were allowed to grow 24 hours before the first dispersal event. Dispersal and imposed
306 population turnover (see below) occurred two times per week, while sampling of the
307 communities for species count was done once a week (two dispersal events between each
308 sampling with always at least 48 hours between the last dispersal/turnover event and

309 sampling). Sampling events and counting were done at day 0, 7, 15, 21, 29 of the
310 experiment, while dispersal and turnover events occurred at day 1, 4, 8, 11, 16, 19, 22, 25
311 of the experiment.

312 Dispersal was done by pipetting a fixed volume per vertex (1 mL) to each of the
313 connected patches. Dispersal was bi-directional along each vertex (1 mL from a to b and
314 1 mL from b to a), which ensured the maintenance of the same volume in each patch
315 throughout the duration of the experiment. Other experiments in the same settings and
316 simulations have shown that directional dispersal tends to strengthen meta-population and
317 community patterns compared with bi-directional dispersal, but with no qualitative
318 differences in the observed patterns[4,16,48]. Thus, doing dispersal in this way is
319 conservative. For dispersal we used a mirror landscape (following methods developed in
320 Carrara et al.[16]): first, 1 mL was sampled for each vertex connecting a microcosm in the
321 real landscape and then pipetted to the recipient microcosm, but in the mirror landscape.
322 Once this was done for all microcosms, the content of each mirror microcosm was poured
323 to the same microcosm in the real landscape. It is noteworthy, however, that because we
324 started our simulations and experiment with species already assembled (all species were
325 present at start in all patches), we probably are underestimating the importance of
326 dispersal dynamics in the process of early assembly[49].

327 Patch size-dependent population turnover was experimentally reproduced by
328 sampling, killing and pouring back (no change in biomass) a fixed volume of each
329 community, which resulted in a gradient of turnover from smaller upstream to larger
330 downstream microcosms (13%, 8%, 4%, and 2%), and can be seen as the most general
331 type of disturbance. For each mortality event, 1 mL was sampled from each microcosm

and microwaved until boiling to turn all living cells into detritus[50]. After a 1-hour cooling period at ambient temperature (20 °C), the microwaved sampled had reached ambient temperature again and were poured back into the same microcosm.

At each measurement day, 0.4 mL was sampled from each microcosm for the protist density measurements. Protist density was measured by using a standardized video recording and analysis procedure[51,52] (for details see Supplementary appendix A). In short, a constant volume (34.4 μL) of each 0.4 mL sample was measured under a dissecting microscope connected to a camera for the recording of videos (5 s per video, see Supplementary appendix A for further details on this method). Then, using a customized version of the R-package bemovi[52], we used an image processing software (ImageJ, National Institute of Health, USA) to extract the number of moving organisms per video frame along with a suite of different traits for each occurrence (e.g., speed, shape, size) that could then be used to filter out background movement noise (e.g., particles from the medium) and to identify species in a mixture (see Supplementary appendix A).

Statistical analysis. To test for the effect of patch size on protist local diversity we used a two-way linear mixed effect model testing the interactive effects of patch size and continuous time on protist species richness. To control for temporal pseudo-replication, we added replicate and time as nested random factors. The model was fitted by maximizing the restricted log-likelihood ("REML", see [53]). The linear mixed effect model was conducted using the R-package NLME[53]. The complete results can be found in Supplementary Table 1.

355 **Data availability.** The main data and r-script to reproduce the experimental results

356 can be downloaded from Dryad (DOI:XX.XXXX/Dryad.XXXXXX).

357

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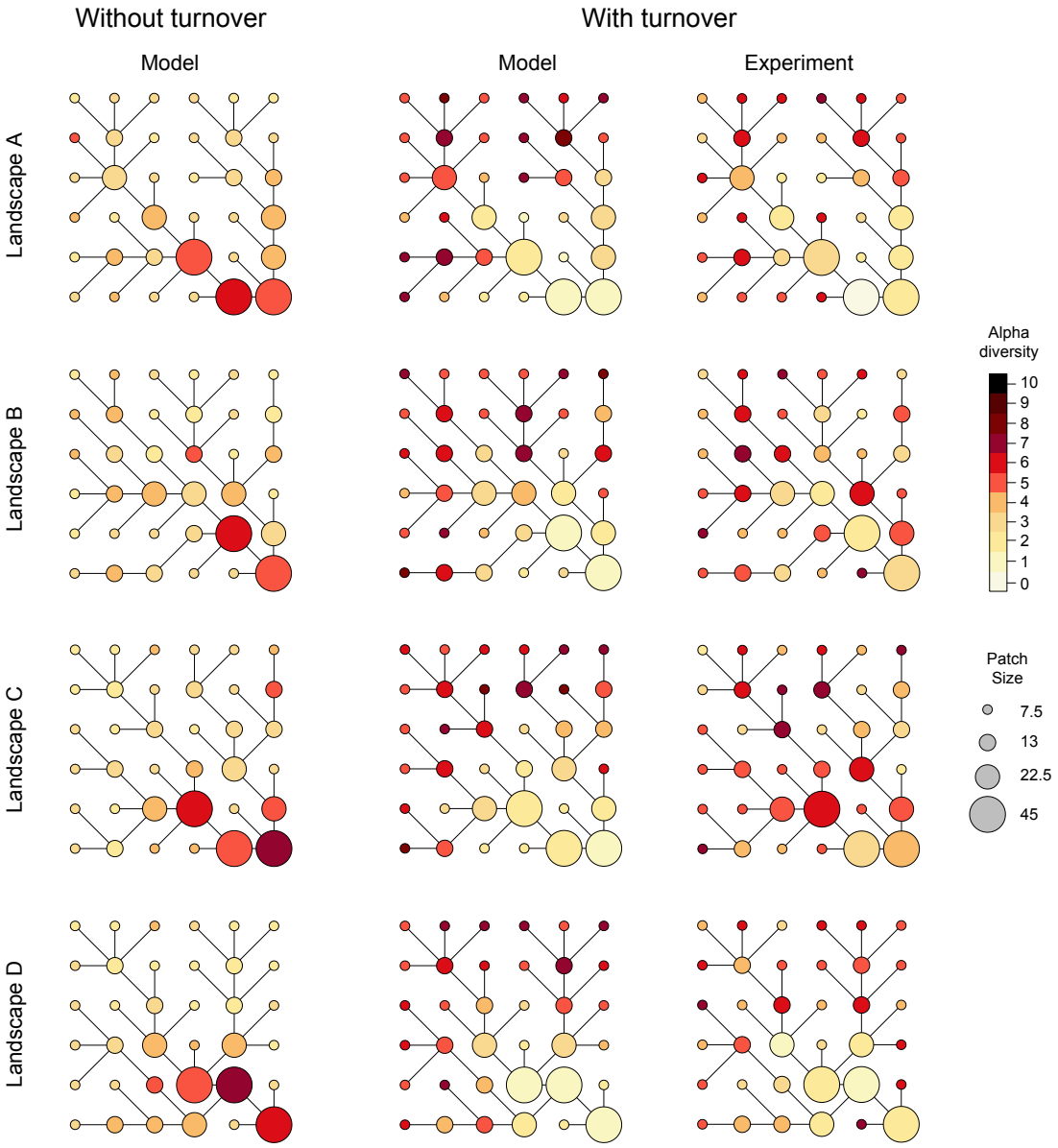
489 Figures

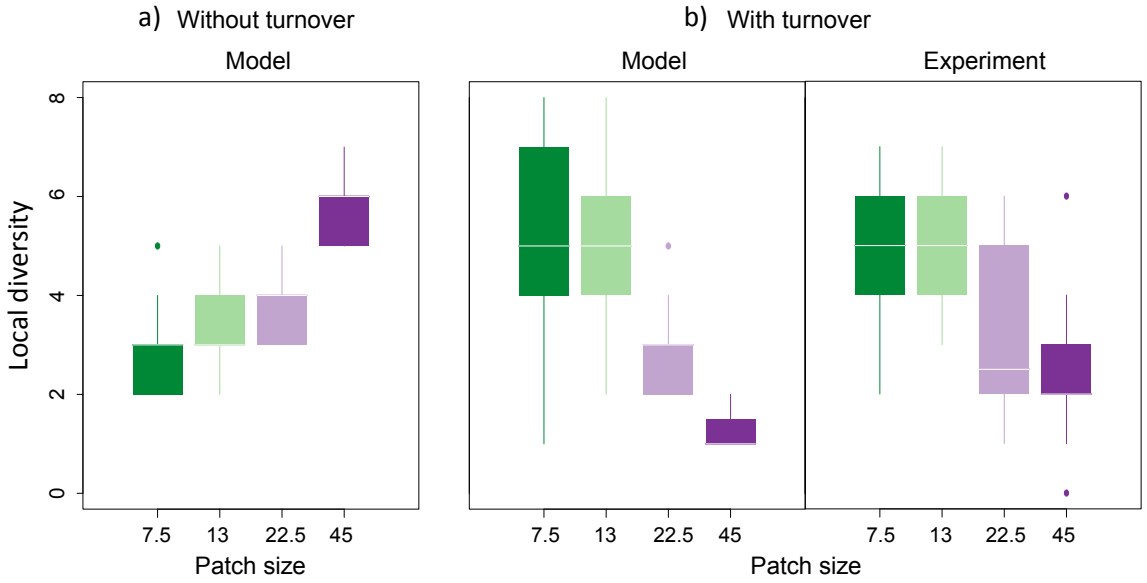


490

491 Figure 1. Diversity distribution (local species richness) in dendritic, river-like landscapes
492 with and without patch size-dependent population turnover. The 'Model' landscapes
493 displayed in this figure are example of simulations made with the same replicate
494 community. Results were qualitatively similar for each of the 10 replicate communities
495 randomly generated (see Supplementary Figure 1 for results with the different
496 communities; the community used in the present figure is community 7); model
497 parameters specific to these simulations are $d = 0.05$, patch size-dependent mortality
498 rates m are 0.1, 0.0864, 0.064 and 0.01 respectively from smaller to larger patches. For

499 network graphs based on experimental results, each graph represents local diversity
500 pattern for one of the four landscape replicates (A, B, C, and D). For illustration purpose,
501 all network graphs are depicted at snapshots of diversity patterns at time steps of
502 comparable local diversity: time steps 118.4 (simulations without population turnover;
503 faster dynamics), 168.1 (simulations with population turnover; slower dynamics), and at
504 experimental day 29 (last sampling day). See complete dynamics over time for model
505 simulations on Supplementary figure 1 and for experimental results on Supplementary
506 figure 2.

507



508

509 Figure 2. Diversity distribution in dendritic, river-like landscapes a) without and b) with
510 patch size- dependent population turnover. For the panels based on simulations, each
511 boxplot represents the distribution of diversity values across the 4 replicate landscapes
512 used in the experiment, and for one of the 10 replicate communities that were used in the
513 simulations (community 7 in Supplementary figure 1). Parameters and data are the same
514 as in Figure 1. The two largest patch sizes of 45 (N=11) and 22.5 mL (N=14) show
515 significant decline in local diversity compared to the smaller patch sizes of 13 (N=34)
516 and 7.5 mL (N=85) (see Supplementary Table 1 for complete linear mixed effect model
517 results).

518

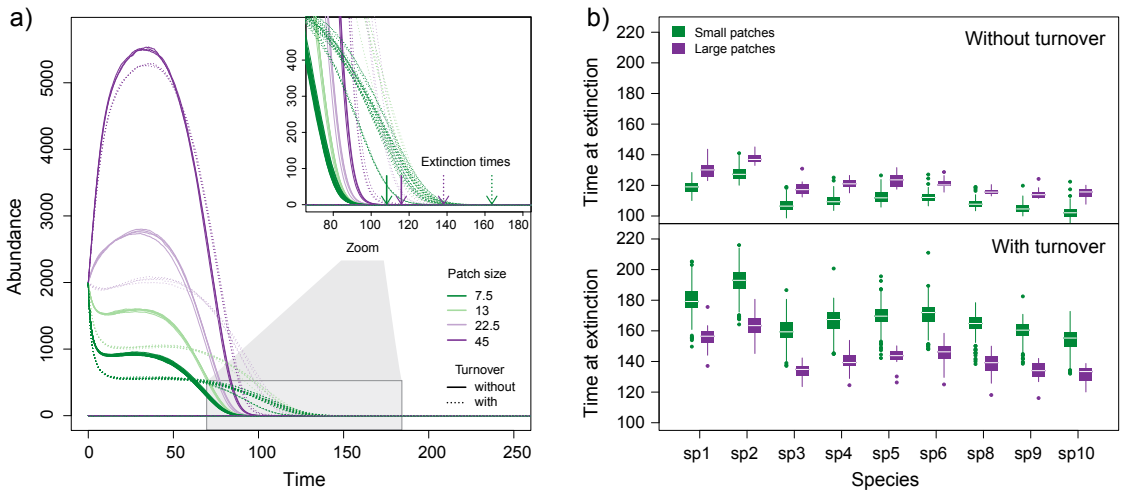
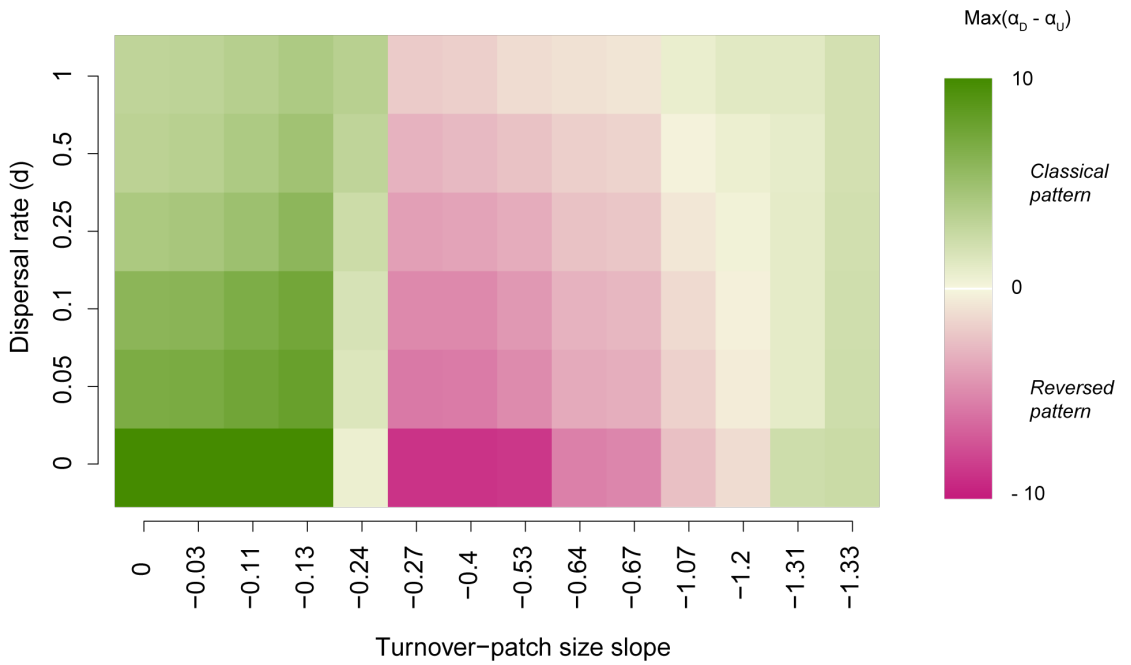


Figure 3. Time to extinction as a function of patch size-dependent turnover in the simulations. a) Temporal dynamics of one species with and without turnover (dotted and full lines respectively). Arrows indicate time at extinction for the smallest (green) and largest (purple) patches with and without turnover. b) Time at extinction for each species in the smallest and the largest patches with turnover (lower panel) or without turnover (upper panel). Each boxplot represents the distribution of values across the 4 replicate landscapes, and for one of the 10 different replicate communities that were used in the simulations (community 7 in Supplementary figure 1). Data and parameters are the same as in Figure 1. Temporal dynamics in a) are the ones of species 10 in community 7 in replicate landscape A.



531

532 Figure 4. Persistence of diversity patterns in dendritic, river-like landscapes. The figure
533 illustrates the parameter space within which each diversity pattern is found as a function
534 of the strength of patch size-dependent population turnover and the magnitude of
535 dispersal (for all mortality combinations see Supplementary figure 3). α_D–α_U corresponds
536 to the maximum observed difference, along the temporal dynamics, in richness between
537 largest and smallest patches. When α_D–α_U is positive (green colours) the classical pattern
538 emerges over the course of the dynamics, with higher diversity in large than in small
539 patches, while when the difference is negative (pink colours) it is the reversed pattern,
540 with higher diversity in small (i.e., headwarer) rather than in large patches.

541