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1 **Predictions of Taylor's power law, density dependence and pink**
2 **noise from a neutrally modelled time series**

3

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21

21 **Abstract**

22

23 There has recently been increasing interest in neutral models of biodiversity and their
24 ability to reproduce the patterns observed in nature, such as species abundance
25 distributions. Here we investigate the ability of a neutral model to predict phenomena
26 observed in single-population time series, a study complementary to most existing
27 work that concentrates on snapshots in time of the whole community. We consider
28 tests for density dependence, the dominant frequencies of population fluctuation
29 (spectral density) and a relationship between the mean and variance of a fluctuating
30 population (Taylor's power law). We simulated an archipelago model of a set of
31 interconnected local communities with variable mortality rate, migration rate,
32 speciation rate, size of local community and number of local communities. Our
33 spectral analysis showed 'pink noise': a departure from a standard random walk
34 dynamics in favor of the higher frequency fluctuations which is partly consistent with
35 empirical data. We detected density dependence in local community time series but
36 not in metacommunity time series. The slope of the Taylor's power law in the model
37 was similar to the slopes observed in natural populations, but the fit to the power law
38 was worse. Our observations of pink noise and density dependence can be attributed
39 to the presence of an upper limit to community sizes and to the effect of migration
40 which distorts temporal autocorrelation in local time series. We conclude that some of
41 the phenomena observed in natural time series can emerge from neutral processes, as
42 a result of random zero-sum birth, death and migration. This suggests the neutral
43 model would be a parsimonious null model for future studies of time series data.

44

45 **Key words:** random walk, spectral analysis, mean-variance scaling, stochasticity,
46 neutral theory of biodiversity, autocorrelation, 1/f noise

47

48

49 **Introduction**

50

51 The neutral theory of biodiversity (NTB; Hubbell, 2001; Chave, 2004; Alonso et al.,
52 2006; Leigh, 2007; Rosindell et al., 2010) has revolutionized the way we think about
53 species coexistence over the last decade. The assumptions of the theory are
54 controversial (Tilman, 2004; Leibold and McPeck, 2006) and some argue that there is
55 limited empirical support (McGill et al., 2006), but the theory still has huge potential
56 as a null model (Gotelli and McGill, 2006), serving as an essential first approximation
57 to reality and a base for more complex theories. Even with its apparently
58 oversimplified set of assumptions, the NTB is capable of predicting realistic species-
59 abundance distributions (Hubbell, 2001; Etienne, 2005) and species-area curves
60 (Rosindell and Cornell, 2007, 2009), as well as many other ecological patterns
61 (Herben, 2004, 2009). Most of the current research is focused on the community-level
62 predictions of a single snapshot in time at equilibrium (Chave et al., 2002; McGill,
63 2003; Turnbull et al., 2005; Volkov et al., 2005; Dornelas, et al. 2006). Dynamical
64 behaviour of populations in NTB has rarely been studied. Azaele et al. (2006) used
65 ratios of population sizes between two snapshots of time to estimate species turnover
66 rates and extinction times of trees in Barro Colorado Island, Panama. Mutshinda et al.
67 (2008) produced the only study (as far as we are aware) that examines sufficiently
68 long real-world time series from the perspective of NTB. They used the Bayesian
69 statistical framework and a neutral model of community dynamics (zero-sum

70 assumption relaxed) to show that sizes of natural communities fluctuate more than
 71 expected under neutrality. However, Mutshinda et al. (2008) focused only on the
 72 dynamics of local community size and they did not examine time series of individual
 73 species.

74 There are some characteristics of natural time-series that are often used as
 75 summary statistics and can be employed here in making comparisons with the time
 76 series produced by a neutral model. For example, natural time series have been shown
 77 to obey some degree of stabilizing density dependence (Woiwod and Hanski, 1992;
 78 Brook and Bradshaw, 2006; Sibly et al., 2007). Natural populations also follow a
 79 specific relationship between mean population size (m) and variance of population
 80 size (s^2) called Taylor's Power Law (TPL) (Taylor et al., 1983; Tokeshi, 1995;
 81 Ballantyne and Kerckhoff, 2007) which has the form $s^2 \propto m^b$. In natural populations,
 82 the exponent b of TPL is usually observed to satisfy $1 < b < 2$ (Kendal, 2004). Natural
 83 time series can be considered as being the net result of a number of independent
 84 fluctuations each with a distinct frequency and amplitude. The amplitude (or 'spectral
 85 density') $S(f)$ is a function of the frequency f and often satisfies $S(f) \propto 1/f^\gamma$
 86 (Halley, 1996). The exponent γ usually falls between 0 and 2 for natural time series
 87 (Arino and Pimm, 1995; Halley, 1996; Inchausti and Halley, 2001, 2002), a property
 88 known as 'pink noise'.

89 The null model for discrete population dynamics is an unbounded *random*
 90 *walk* of population size (N) and is described as

$$91 \quad \ln N_{t+1} = \ln N_t + e_t \quad (1)$$

92 where e_t varies at random according to a given distribution with zero mean and
 93 is independent on population size (Murdoch, 1994; Hanski et al., 1996). The model is
 94 a discrete first-order Markov chain in which all the information that can influence the

95 future state ($t+1$) is fully captured in the present state (t). Random walk time series are
96 often termed “brownian” or autocorrelated noise. Random walk is synonymous for a
97 completely density-independent process in ecology, it produces a slope of $b \approx 2$ in
98 Taylor’s power law and spectral scaling exponent of $\gamma \approx 2$.

99 Although the term random walk is sometimes used to describe the population
100 time series in neutral models (Hubbell, 2001; Alonso et al., 2006), there are reasons
101 why neutral models can behave differently from the random walk as defined above.
102 Firstly, there is usually a constraint on the total number of individuals (the ‘zero-sum’
103 rule) which imposes a clear upper limit to any population fluctuations (Hubbell, 2001;
104 Hubbell and Lake, 2003). Secondly, immigration of individuals into the local
105 community can cause a locally extinct species to reappear (zero is not necessarily
106 absorbing; Hubbell, 2001) and finally immigration can distort the temporal
107 autocorrelation of N_t (the number of individuals belonging to the species of interest in
108 a local community). In the presence of immigration, N_{t+1} for a given local community
109 does not depend solely on N_t for that community (as in the autocorrelated random
110 walk), it also depends on the N_t for all the other local communities (the
111 metacommunity).

112 In this paper we ask if a simple neutral model can produce time series that are
113 similar to natural time series. In particular, we show that populations in the neutral
114 model can produce realistic slopes of the Taylor’s power law, have spectral properties
115 similar to natural populations and seem to reveal density-dependency more frequently
116 than expected in a random walk. Additionally, we explore the influence of the NTB
117 parameters (size of local communities, number of local communities, mortality rate,
118 migration and mutation rate) on these properties of population time series.

119

120 **Methods**

121

122 *The simulation model*

123 Instead of the classic neutral model used by Hubbell (2001) and Volkov et al. (2003),
124 we simulate a *metacommunity* consisting of an archipelago of L isolated *local*
125 *communities* interconnected by migration at rate m (see Fig. 1 below and Volkov et
126 al., 2007). Each local community contains J individuals all of which behave in an
127 identical manner irrespective of the species to which they belong. The archipelago
128 model enabled us to obtain data on abundances and their variances for one species at
129 multiple local communities, which is necessary for the analysis of Taylor's Power
130 Law. We used the simulation approach because it enabled us to record the species
131 identity of every individual at each time step and across all local communities.

132 Furthermore, we wished to collect time series of limited lengths that are comparable
133 to those of empirically collected time series in order to accurately mimic any sampling
134 effects present in empirical data. This would be particularly difficult to approach
135 analytically. Our simulations were conducted using a 'forwards in time' approach. A
136 'backwards in time' or coalescence approach can be much faster (Rosindell et al.,
137 2008), but the main strengths of this approach are only present when collecting a snap
138 shot in time of a sample from a very large or infinite metacommunity. We are instead
139 collecting single species time series data and sampling all individuals from a
140 relatively small metacommunity: a scenario where coalescence is far less beneficial.

141 Four processes operate in the local community at each step: mortality (d ;
142 $0 < d < 1$), local replacement (l ; $0 < l < 1$), immigration from outside of the local
143 community (m ; $m = 1 - l$) and speciation (s ; $0 < s < 1$) in that order (Fig. 1, Table 1).

144 To model mortality, $J \times d$ individuals were randomly removed from each local

145 community in every time step with all individuals having an equal probability of
146 removal. These removed individuals were then replaced by offspring from others in
147 the local community and other local communities (immigration). Local replacement
148 was modeled by drawing individuals to reproduce at random from the
149 $J(1-d)$ individuals that survived mortality until $J \times d \times l$ offspring have been created.
150 The remaining $J \times d \times m$ dead individuals were replaced by immigration from all of
151 the other local communities. The probability of immigration of a species is given by
152 its relative abundance in the whole metacommunity (excluding the local community
153 in focus).

154 A local population can occasionally give rise to a new species (a speciation
155 event), this happens with a fixed probability at each time step for each local
156 population of a species. When speciation occurs, individuals of the given species in
157 the local community were randomly split into two parts, one of which forms the initial
158 abundance of a new species (a version of *random-fission* model; Hubbell, 2001;
159 Etienne and Haegeman, 2010; Haegeman and Etienne, 2010). Pilot testing of a *point*
160 *mutation* model (Hubbell, 2001) showed that the choice of a speciation model does
161 not affect the outcome of the simulations, this is not entirely surprising because for a
162 single species population time series, speciation can be regarded as another form of
163 mortality: individuals belonging to our focal species that switch to a new species
164 reduce the population of our focal species in the same way as dead individuals. Each
165 simulation was launched with only one species that occurred in all local communities
166 and was left running for 5000 steps which we found was always sufficient for the
167 system to reach a steady state. The last 100 steps of the simulation were then taken
168 and used for analyses.

169

170 ***Spectral analysis***

171 We performed 200 simulations for each combination of model parameters (Table 1).
172 From each simulation we randomly selected one species and from this species we
173 used two time series: (1) time series of population sizes within a randomly selected
174 *local community* and (2) time series of population sizes within the whole
175 *metacommunity*. In cases where the species went extinct in one or both time series we
176 randomly selected another one thereby conditioning the time series as being drawn
177 from a locally extant species. For these time series we conducted spectral analysis
178 (Halley, 1996; pages 680-681 in Legendre and Legendre, 2003) and estimated the
179 value of the exponent γ in $S(f) \propto 1/f^\gamma$ where $S(f)$ is spectral density at given
180 frequency f ($0 \leq f \leq f_{n/2}$; n is length of the time series). Values of $S(f)$ were obtained
181 through Fast Fourier Transform of the log-transformed time series data. The spectral
182 exponent γ was estimated as minus the regression slope of the $\log(S(f))$ versus
183 $\log(f)$. This procedure is exactly the same as used by Inchausti and Halley (2001)
184 and hence our estimates of γ are directly comparable to theirs (Fig. 2). The value of γ
185 can vary from $\gamma < 0$ ('blue noise') through $\gamma = 0$ ('white noise'), $\gamma \approx 1$ ('pink
186 noise') and $\gamma = 2$ ('brown noise' or random walk) to $\gamma > 2$ ('black noise'). We use
187 the term 'whitening' of the spectra for a deviation of γ from 2 towards 0.

188 To assess effects of the neutral model parameters on γ we fitted a multiple
189 ANOVA model with γ as the response variable and five explanatory variables:
190 mortality rate, migration rate, speciation rate, number of local communities and
191 number of individuals. Since we were dealing with simulated data we only report R^2 's
192 and do not report any P -values because these could be modified arbitrarily by
193 changing number of simulations. Comparisons were made with the values of γ
194 measured in natural populations taken from the Global Population Dynamics

195 Database (kindly provided by Pablo Inchausti; see also Inchausti and Halley, 2001,
196 2002).

197

198 *Testing for density dependence*

199 Using the same data, we conducted three distinct tests for density dependence in the
200 time series: Pollard's randomization test (Pollard et al., 1987), Dennis and Taper's
201 parametric bootstrap maximum likelihood test (PLBR; Dennis and Taper, 1994) and
202 Bulmer's test (Bulmer, 1974). The Pollard's test is a distribution-free likelihood ratio
203 randomization test in which a random walk (Eq. 1) or a random walk with trend are
204 density independent hypotheses, whereas the density dependent hypothesis is defined
205 as a first-order *linear* autoregression model (stochastic Gompertz model):

$$206 \quad \ln N_{t+1} = \ln N_t + r + \beta \ln N_t + e_t \quad (\beta \neq 1) \quad (2)$$

207 where r and β are model parameters. The Bulmer's test is a parametric
208 predecessor of the Pollard's test and has been criticized for weak performance in cases
209 where there was a trend in the data ($r \neq 0$). The PLBR test is a likelihood ratio test
210 which uses the first-order *non-linear* autoregression model (stochastic logistic model)
211 as the density dependent hypothesis:

$$212 \quad \ln N_{t+1} = \ln N_t + r + \beta N_t + e_t \quad (3)$$

213 All of these tests have been criticized for disputable performance when there is
214 a census error affecting the estimation of population abundance in the field (Shenk et
215 al., 1998; Freckleton et al., 2006), but this is not the case for our simulated data. All
216 three tests gave nearly identical results and we therefore only present the output from
217 Pollard's randomization test (Pollard et al., 1987) which is 'Pollard's P ': the
218 probability of observing the empirical data in the case of the density independent
219 hypothesis (Eq. 1). Following the approach of Woiwod and Hanski (1992) we

220 normalized the distribution of Pollard's P by logit transformation. To assess effects of
221 the neutral model parameters on Pollard's P we again fitted a multiple ANOVA
222 model in which we used the values of logit-transformed Pollard's P as the response
223 variable.

224

225 *Taylor's power law*

226 To test if populations in our model obey the Taylor's Power Law (TPL) we performed
227 50 simulations for each combination of parameters (Table 1). For each species in the
228 simulations we created a metapopulation matrix (MPM) of abundances in which rows
229 represent the last 100 time steps of the simulation and columns represent the
230 populations in different local communities. We excluded all MPMs in which the
231 species had gone globally extinct. We studied the TPL in its temporal context (Taylor
232 and Woiwod, 1982) which means that variances and means are calculated over each
233 column (one column is one local population) in the MPM – when plotted, each point
234 in the log-log plot therefore represents one local population. Using rows instead of
235 columns in the MPM would yield the TPL in a spatial context, but the temporal
236 context is more germane to this time series study. A linear regression was fitted in
237 each of the log-log plots and the TPL slope (parameter b ; Taylor, 1961; Tokeshi,
238 1995) and the coefficients of determination (R^2) were calculated. As with our other
239 results, the simulated values of TPL slopes and R^2 s were compared with empirically
240 observed values (taken from Taylor and Woiwod, 1980, 1982).

241

242 **Results**

243

244 *Spectral analysis*

245 Values of the scaling exponent γ estimated from our simulations are summarized in
246 Figure 2. For local communities, the median value of γ was 1.59 (2.5% and 97.5%
247 quantiles were 1.26 and 2.19 respectively). The value of γ was only influenced by
248 mortality rate and migration rate (Table 2, Fig. 3) with higher mortality and higher
249 migration each producing time series that were closer to pink noise ($\gamma < 2$) (Fig. 2).
250 On the metacommunity scale, the median of γ was 1.75 (2.5% and 97.5% quantiles
251 were 1.05 and 2.07 respectively). We did not detect any influence of the model
252 parameters on the value of γ at the metacommunity scale (Table 2, Fig. 3). Our
253 simulations produced γ values falling within a narrower interval than is generally
254 observed in nature (Fig. 2), however, they departed from 2 (the value for an
255 unbounded random walk) in the same direction as for natural populations.

256 In general, the population time series emerging from our neutral model had
257 lower γ than would be expected for an autocorrelated random walk ($\gamma = 2$). This
258 could partly be an artifact caused by the insufficient length of time series. It was
259 recently shown that random walks of length ~ 100 actually give estimates of between
260 1.5 and 1.8 instead of 2 because of the missing low-frequency fluctuations
261 (Miramontes and Rohani, 2002). Nevertheless, since empirically collected time series
262 are rarely longer than 100 sequential observations, our simulations of time series of
263 similar lengths are amply justified to purposefully include the effects of sampling over
264 a limited time scale. Since we also showed that the values of γ tended to be lower at
265 local scales when comparing time series of equal lengths, we can still conclude that
266 some whitening of spectra at local community scales is caused by more than just the
267 length of the sampled time series.

268

269 *Testing for density dependence*

270 On the scale of local communities the median of Pollard's P was 0.14 (2.5% and
271 97.5% quantiles were 0 and 0.82 respectively) indicating a distribution skewed
272 towards the lower values of Pollard's P . We also found that the values of Pollard's P
273 were dependent on mortality rate and migration rate (Table 2, Fig. 4). Similarly to
274 spectral analysis, simulations with higher mortality rate and higher migration rate
275 produced time series with lower values of Pollard's P (Fig. 4). On the
276 metacommunity scale the median value of Pollard's P was 0.5 (2.5% and 97.5%
277 quantiles being 0.01 and 0.97 respectively). This indicates no clear signal of density
278 dependence on the metacommunity scale. We did not detect any influence of the other
279 model parameters on the values of logit-transformed Pollard's P (Table 2, Fig. 4).
280 Pollard's P varied with relative abundance of species in local communities but not in
281 metacommunities (Fig. 6).

282

283 *Taylor's power law (TPL)*

284 The median slope of TPL was 1.73 (2.5% and 97.5% quantiles were 0.059 and 2.49
285 respectively). The coefficients of determination (R^2) of power law regressions varied,
286 following skewed, non-normal distributions (Figs. 2, 5), having generally lower
287 values to what has been observed in nature (Fig. 2). The effects of model parameters
288 on the slope of TPL was not as distinct as in spectral analysis and density dependence
289 analysis; we detected a weak influence of number of local communities and mortality
290 rate on the slopes of TPL (Table 2, Fig. 5). Both the slopes and R^2 's showed negative
291 dependence on the mean relative abundance of species (Fig. 7).

292

293 **Discussion**

294

295 *Spectral analysis and density dependence*

296 The observed whitening of spectra in our model is not what we would expect under
297 random walk dynamics. One possible reason for this is the effect of *migration* which
298 can cause the spectral whitening. A population in an isolated local community (low or
299 no immigration from outside) follows dynamics similar to an autocorrelated random
300 walk ($\gamma \approx 2$) in which there is little or no dependence on the abundances in other local
301 communities. However, after introducing immigration from outside of the local
302 community, the autocorrelative nature of the process is broken and the species
303 abundance in the whole metacommunity becomes important. The influence of single
304 local community dynamics on the metacommunity are likely to be small (inversely
305 proportional to the number of local communities), but in contrast the influence of the
306 metacommunity on local community dynamics can be substantial (proportional to the
307 migration rate). Hence, the migration causes the local time series to be whitened (non-
308 autocorrelated in time) while the metacommunity time series remains “brownian”
309 (autocorrelated in time). The *mortality* rate can also cause spectral whitening by
310 adding random population fluctuations at high frequencies, but not at low ones
311 subsequently lowering γ . We expect that this effect of mortality rate would not be
312 apparent in very long time series (> 400 time steps; Miramontes and Rohani, 2002).
313 However, such long time series are nearly never available in ecology and we wanted
314 to keep our time series comparably long to the real-world ones.

315 The spectral analysis results are mirrored by the results of the tests for density
316 dependence. Density dependence is modeled either as stochastic Gompertz (Eq. 2) or
317 stochastic logistic (Eq. 3) models in the tests we used (Shenk et al., 1998, see also
318 Methods).

319 It has been recognized for a long time (Eberhardt, 1970; Freckleton et al.,
320 2006) that a sequence of uncorrelated random numbers (“white noise”) tends to
321 follow a pattern consistent with density dependence. If you take white noise time
322 series and plot changes of ln population size ($\ln N_{t+1} - \ln N_t$) against $\ln N_t$ (where N_t
323 is the number of individuals at time t) you will get a linear negative relationship,
324 corresponding (spuriously) to the density dependent Gompertz model (Eq. 2) with
325 $\beta \approx -1$. Moreover, white noise can be very similar to the output of the stochastic
326 logistic model (Eq. 3) with $\beta < 0$. We have learned that the whitening of a spectra
327 means bringing it from $\gamma \approx 2$ down towards 0, which is white noise. We also know
328 that migration (by breaking the autocorrelation structure) and mortality rate (by
329 increasing spectral density at high frequencies in time series of limited length) cause
330 spectral whitening. The detection of density dependence can also be attributed to the
331 same mechanisms, although most ecologists would consider such density dependence
332 to be spurious (Freckleton et al., 2006).

333 Uncorrelated noise in the form of census error also causes spurious detection of
334 density dependence has long been known to population ecologists (Shenk et al., 1998;
335 Freckleton et al., 2006). Moreover, Freckleton et al. (2006) showed an example of a
336 population that follows a random walk but consists of two subpopulations each of
337 which apparently shows density dependence because there is random migration
338 between them. That immigration can cause time series to resemble a sequence of
339 uncorrelated random numbers was also noted by Anderson et al. (1982) and this is
340 indeed the case for our neutral model.

341 There should also be real density dependence in our model. In an isolated
342 community, the closer N_t gets to zero (extinction) or to J (monodominance) the lower
343 the probability of N_{t+1} differing from N_t will be. When a species almost fills the local

344 community, its probability of increasing its abundance in the next time step is small,
345 because it is unlikely that one of the few individuals belonging to a different species
346 will be selected for mortality. Similarly, when the abundance of a species is low, its
347 probability of reproducing is low because after mortality it is not likely to be selected
348 to reproduce. The highest rate of fluctuations and lowest incidence of density
349 dependence is then expected when a population has a relative abundance of 0.5
350 (Hubbell, 2001). We detected this form of density dependence only in local
351 communities at low relative abundances (Fig. 6). Species with high relative
352 abundances were rare in our simulations and hence we were unable to clearly show
353 the real density dependence for them (Fig. 6) even though in theory it must exist.

354

355 *Taylor's power law (TPL)*

356 The archipelago neutral model produced slopes of Taylor's Power Law with median
357 close to the range observed in natural populations ($1 < b < 2$), but with higher incidence
358 of low coefficients of determination. In order to explain this we need to summarize
359 the mean-variance scaling properties of simple stochastic models. If a species
360 undergoes an unrestricted random walk (Eq. 1), the TPL has a slope $b = 1$ at very low
361 population densities and gradually changes to $b = 2$ at a certain density (Anderson et
362 al., 1982; Tokeshi, 1995; Keeling, 2000). The population density at which b starts to
363 change from 1 to 2 depends on the relative magnitude of stochastic changes because
364 of the high incidence of extinctions at low population densities which lower the
365 variance. This effect can explain $b < 2$ at very low densities.

366 Hubbell (2001) shows what happens with the mean-variance scaling if the
367 stochastic population fluctuations are restricted by an upper boundary (the zero-sum
368 rule) and are fed by immigration, although Hubbell does not use the term Taylor's

369 power law. Hubbell (2001) predicts hump-shaped parabolic relationship between
370 abundance of species in a metacommunity and the variance of a local population size
371 undergoing the zero-sum ecological drift. He also hypothesizes that most of the
372 species in nature have low relative abundances and hence should occur in the left part
373 (relative abundance < 0.2) of the parabola which is nearly linear in the log-log space,
374 resembling the power-law with slope of 2. Although Hubbell's (2001) reasoning
375 focuses on the relationship between mean and variance in a set of species within one
376 community (one point in the mean-variance plot represents one species) it can apply
377 to the set of single-species local populations in our model: the mean relative
378 abundances of species in local communities were rarely higher than 0.2 in our
379 simulations and indeed, there is a much better fit of the TPL for species with low
380 abundances (Fig. 7). The poor fit at higher relative abundances is then a result of
381 fitting the linear TPL on the actually parabolic mean-variance relationship.
382 Consequently, as the mean relative abundance of species increases, the slope of the
383 TPL decreases (Fig. 7).

384

385 *Comparison with empirical data and conclusions*

386 Our model produces qualitatively similar patterns to those observed in nature. This is
387 perhaps surprising given the assumptions made by the neutral model, but it does again
388 highlight its use as a powerful null model.

389 There is a general agreement that natural time series are not "brownian" (Fig.
390 1; Arino and Pimm, 1995; Inchausti and Halley, 2001, 2002) – they clearly fall into
391 the whitened range of scaling exponents ($0 < \gamma < 2$; Fig. 2). Our simulations indicate
392 that neutral models have the potential to explain part of this observed whitening,
393 although this potential may be limited. Although higher migration rates can result in

394 time series with more realistic values of γ , our migration rates are similar (10%) or
395 much higher (30%) than what is usually observed in natural metacommunities (see
396 Volkov et al., 2003 and Mutshinda et al., 2008). Mutshinda et al. (2008) already
397 showed that sizes of local communities fluctuate more than is expected from neutral
398 theory. This resonates with our simulations of individual species time series which
399 show rather high values of γ (i.e. lower importance of high-frequency fluctuations)
400 when compared to empirical data. Recent progress in population ecology suggests that
401 a promising explanation for these high fluctuations of natural populations might be
402 environmental stochasticity (Lande et al., 2006; Mutshinda et al., 2009) which is
403 absent in neutral models, but not impossible to include in future and more general
404 versions of the original theory (Allen and Savage, 2007).

405 Realistic slopes of TPL can be produced by a number of different mechanisms
406 (Tokeshi, 1995; Keeling, 2000; Kendal, 2004; Ballantyne and Kerkhoff, 2007) and it
407 is therefore difficult to infer any definitive underlying mechanisms from its shape
408 (Mitzenmacher, 2003). Here we add neutral models to the list of possible mechanisms
409 that can produce realistic TPL slopes, although not necessarily realistic fits.

410 In conclusion, our results show that realistic slopes of Taylor's power law and
411 density dependence can emerge from a simple neutral model, whilst spectral colours
412 are less likely, but still possible to be reproduced by the neutral model. Still some
413 other natural phenomena remain unexplained by our model, such as the possibility for
414 very small γ closer to white noise. Our findings suggest the interesting possibility that
415 the properties of population time series observed in nature are in part due to simple
416 factors such as sampling effects and dispersal limitation, which would then represent
417 the most parsimonious explanation of observed patterns. The patterns of population
418 fluctuations observed in nature may not reflect resource-driven species-specific

419 dynamics but instead processes at the metacommunity scale, with an important effect
420 of stochastic mortality and random immigration of individuals into local communities.
421 The neutral model encompasses these factors without being overly complex and we
422 therefore suggest that neutral models make more powerful null models for time series
423 data compared to alternatives such as Brownian random walks.

424

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426

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436

437 **References**

438

- 439 Allen, A.P., Savage, V.M. 2007. Setting the absolute tempo of biodiversity dynamics.
440 *Ecol. Lett.* 10, 637–646.
- 441 Alonso, D., Etienne, R.S., McKane, A.J. 2006. The merits of neutral theory. *Trends*
442 *Ecol. Evol.* 21, 451–457., doi:10.1016/j.tree.2006.03.019.

- 443 Anderson, R.M., Gordon, D.M., Crawley, M.J., Hassell, M.P. 1982. Variability in the
444 abundance of animal and plant species. *Nature* 296, 245-296.
- 445 Arino, A., Pimm, S.L. 1995. On the nature of population extremes. *Evol. Ecol.* 9, 429-
446 443.
- 447 Azaele, S., Pigolotti, S., Banavar, J.R., Maritan, A. 2006. Dynamical evolution of
448 ecosystems. *Nature* 444, 926-928.
- 449 Ballantyne, F., Kerkhoff, A.J. 2007. The observed range for temporal mean-variance
450 scaling exponents can be explained by reproductive correlation. *Oikos* 116,
451 174-180.
- 452 Brook, B.W., Bradshaw, C.J.A. 2006. Strength of evidence for density dependence in
453 abundance time series of 1198 species. *Ecology* 87, 1445-1451.
- 454 Bulmer, M.G. 1974. A statistical analysis of the 10-year cycle in Canada. *J. Anim.*
455 *Ecol.* 43, 701-718.
- 456 Chave, J. 2004. Neutral theory and community ecology. *Ecol. Lett.* 7, 241-253.
- 457 Dennis, B., Taper, M.L. 1994. Density dependence in time series observations of
458 natural populations: Estimation and testing. *Ecol. Monogr.* 64, 205-224.
- 459 Dornelas, M., Connolly, S.R., Hughes, T.P. 2006. Coral reef diversity refutes the
460 neutral theory of biodiversity. *Nature* 440, 80-82.
- 461 Eberhardt, L.L. 1970. Correlation, regression and density dependence. *Ecology* 51,
462 306-310.
- 463 Etienne, R.S. 2005. A new sampling formula for neutral biodiversity. *Ecol. Lett.* 8,
464 253-260.
- 465 Etienne, R.S., Haegeman, B. 2010. The neutral theory of biodiversity with random
466 fission speciation. *Theor. Ecol.* 'in press'.

- 467 Freckleton, R.P., Watkinson, A.R., Green, R.E., Sutherland, W.J. 2006. Census error
468 and the detection of density dependence. *J. Anim. Ecol.* 75, 837-851.
- 469 Gotelli, N.J., McGill, B.J. 2006. Null versus neutral models: what's the difference?
470 *Ecography* 29, 793-800.
- 471 Haegeman, B., Etienne, R.S. 2010. Self-consistent approach for neutral community
472 models with speciation. *Phys. Rev. E* 81, 031911.
- 473 Halley, J.M. 1996. Ecology, evolution and 1/f-noise. *Trends Ecol. Evol.* 11, 33-37.,
474 doi:10.1016/0169-5347(96)81067-6.
- 475 Hanski, I., Foley, P., Hassell, M. 1996. Random walks in a metapopulation: how
476 much density dependence is necessary for long-term persistence? *J. Anim.*
477 *Ecol.* 65, 274-282.
- 478 Herben, T., Mandák, B., Bímová, K., Münzbergová, Z. 2004 Invasibility and species
479 richness of a community: a neutral model and a survey of published data.
480 *Ecology* 85, 3223–3233.
- 481 Herben, T. 2009. Invasibility of neutral communities. *Basic Appl. Ecol.* 10, 197–207.,
482 doi:10.1016/j.baae.2008.08.006.
- 483 Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography.
484 Princeton Univ. Press, Princeton.
- 485 Hubbell, S.P., Lake, J.K. 2003. The neutral theory of biodiversity an biogeography,
486 and beyond. In: Blackburn, T.M., Gaston, K.J. (Eds.), *Macroecology:*
487 *Concepts and Consequences.* Blackwell, Oxford, pp. 45-63.
- 488 Inchausti, P., Halley, J. 2001. Investigating long-term ecological variability using the
489 global population dynamics catabase. *Science* 293, 655-657.
- 490 Inchausti, P., Halley, J. 2002. The long-term temporal variability and spectral colour
491 of animal populations. *Evol. Ecol. Res.* 4, 1033-1048.

- 492 Keeling, M.J. 2000. Simple stochastic models and their power-law type behaviour.
493 Theor. Popul. Biol. 58, 21-31., doi:10.1006/tpbi.2000.1475.
- 494 Kendal, W.S. 2004. Taylor's ecological power law as a consequence of scale invariant
495 exponential dispersion models. Ecol. Complex. 1, 193-209.,
496 doi:10.1016/j.ecocom.2004.05.001.
- 497 Lande, R., Engen, S., Saether, B.-E. 2006. Stochastic population dynamics in ecology
498 and conservation. Oxford. Univ. Press, Oxford.
- 499 Legendre, P., Legendre L. 2003. Numerical Ecology. Elsevier, Amsterdam.
- 500 Leibold, M.A., McPeck, M.A. 2006. Coexistence of the niche and neutral perspectives
501 in community ecology. Ecology 87, 1399-1410.
- 502 Leigh, E.G. 2007. Neutral theory: a historical perspective. J. Evolution. Biol. 20,
503 2075-2091.
- 504 McGill, B.J. 2003. A test of the unified neutral theory of biodiversity. Nature 422,
505 881-885.
- 506 McGill, B.J., Maurer, B.A., Weiser, M.D. 2006. Empirical evaluation of neutral
507 theory. Ecology 87, 1411-1423.
- 508 Miramontes, O., Rohani, P. 2002. Estimating $1/f^\alpha$ scaling exponents from short time-
509 series. Physica D 166, 147-154., doi:10.1016/S0167-2789(02)00429-3.
- 510 Mitzenmacher, M. 2003. A brief history of generative models for power laws and
511 lognormal distributions. Internet Mathematics 1, 226-251.
- 512 Murdoch, W.W. 1994. Population regulation in theory and practice. Ecology 75, 271-
513 287.
- 514 Mutshinda, C.M., O'Hara, R.B.O., Woivod, P. 2008. Species abundance dynamics
515 under neutral assumptions: a Bayesian approach to the controversy. Funct.
516 Ecol. 22, 340-347.

- 517 Mutshinda, C.M., O'Hara, R.B.O., Woiwod, P. 2009. What drives community
518 dynamics? *P. Roy. Soc. B-Biol. Sci.* 276, 2923-2929.
- 519 Pollard, E., Lakhani, K.H., Rothery, P. 1987. The detection of density-dependence
520 from a series of annual censuses. *Ecology* 68, 2046-2055.
- 521 Rosindell, J., Cornell, S.J. 2007. Species-area relationships from a spatially explicit
522 neutral model in an infinite landscape. *Ecol. Lett.* 10, 586-595.
- 523 Rosindell, J., Cornell, S.J. 2009. Species-area curves, neutral models, and long-
524 distance dispersal. *Ecology* 90, 1743-1750.
- 525 Rosindell, J., Cornell, S.J., Hubbell, S.P., Etienne, R.S. 2010. Protracted speciation
526 revitalizes the neutral theory of biodiversity. *Ecol. Lett.* 'in press'.
- 527 Rosindell, J., Wong, Y., Etienne, R.S. 2008. Coalescence models for spatial neutral
528 ecology. *Ecol. Inform.* 9, 1743-1750., doi:10.1016/j.ecoinf.2008.05.001.
- 529 Shenk, T.M., White, G.C., Burnham, K.P. 1998. Sampling-variance effects on
530 detecting density dependence from temporal trends in natural populations.
531 *Ecol. Monogr.* 68, 445-463.
- 532 Sibly, R.M., Barker, D., Hone, J., Pagel, M. 2007. On the stability of populations of
533 mammals, birds, fish and insects. *Ecol. Lett.* 10, 970-976.
- 534 Taylor, L.R., Woiwod, I.P. 1980. Temporal stability as a density-dependent species
535 characteristic. *J. Anim. Ecol.* 49, 209-224.
- 536 Taylor, L.R., Woiwod, I.P. 1982. Comparative synoptic dynamics. I. Relationships
537 between inter- and intra-specific spatial and temporal variance/mean
538 population parameters. *J. Anim. Ecol.* 51, 879-906.
- 539 Taylor, L.R., Taylor, R.A.J., Woiwod, I.P., Perry, J.N. 1983. Behavioural dynamics.
540 *Nature* 303, 801-804.

- 541 Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic
542 theory of resource competition, invasion, and community assembly. *P. Natl.*
543 *Acad. Sci. USA* 101, 10854-10861.
- 544 Tokeshi, M. 1995. On the mathematical basis of the variance-mean power
545 relationship. *Researches on Population Ecology* 37, 43-48.
- 546 Turnbull, L.A., Manley, L., Rees, M. 2005. Niches, rather than neutrality, structure a
547 grassland pioneer guild. *P. Roy. Soc. B-Biol. Sci.* 272, 1357-1364.
- 548 Volkov, I., Banavar, J.R., Hubbell, S.P., Martian, A. 2003. Neutral theory and relative
549 species abundance in ecology. *Nature* 424, 1035-1037.
- 550 Volkov, I., Banavar, J.R., He, F., Hubbell, S.P., Maritan, A. 2005. Density
551 dependence explains tree species abundance and diversity in tropical forests.
552 *Nature* 438, 658-661.
- 553 Volkov, I., Banavar, J.R., Hubbell, S.P., Maritan, A. 2007. Patterns of relative species
554 abundance in rainforests and coral reefs. *Nature* 450, 45-49.
- 555 Woiwod, I.P., Hanski, I. 1992. Patterns of density dependence in moths and aphids. *J.*
556 *Anim. Ecol.* 61, 619-629.
- 557

557 **Figure legends**

558

559 **Figure 1** Schematic illustration of the “archipelago” model. Note that we performed
560 our simulations using much larger numbers of local communities than illustrated here.
561 See the methods for detailed description of the model.

562

563 **Figure 2** Some aspects of real-world populations and those produced by our neutral
564 model. Empirical slopes of Taylor’s Power Law and coefficients of determination of
565 TPL of 429 species of aphids, moths and birds were taken from Taylor & Woiwod
566 (1980, 1982). Empirical values of scaling exponent γ of power spectra of 544 time
567 series were taken from the Global Population Dynamics Database (GPDD, kindly
568 provided by Pablo Inchausti; see also Inchausti and Halley, 2001, 2002). Box and
569 whisker plots show medians, quartiles and outliers.

570

571 **Figure 3** Results of the spectral analysis of population time series produced by a
572 neutral model. γ is the scaling exponent in $S(f) \propto 1/f^\gamma$ where $S(f)$ is spectral density
573 and f is frequency. Displayed are the effects of the neutral model’s parameters (Tab.
574 1) on γ as a box and whisker plot with median and quartiles. A random walk of
575 sufficient length would have $\gamma = 2$.

576

577 **Figure 4** Results of the testing for density dependence in population time series
578 produced by neutral model as a box and whisker plot with median and quartiles.
579 Pollard’s P is the probability of obtaining the data in case of density independence
580 (Eq. 1; Pollard et al., 1987).

581

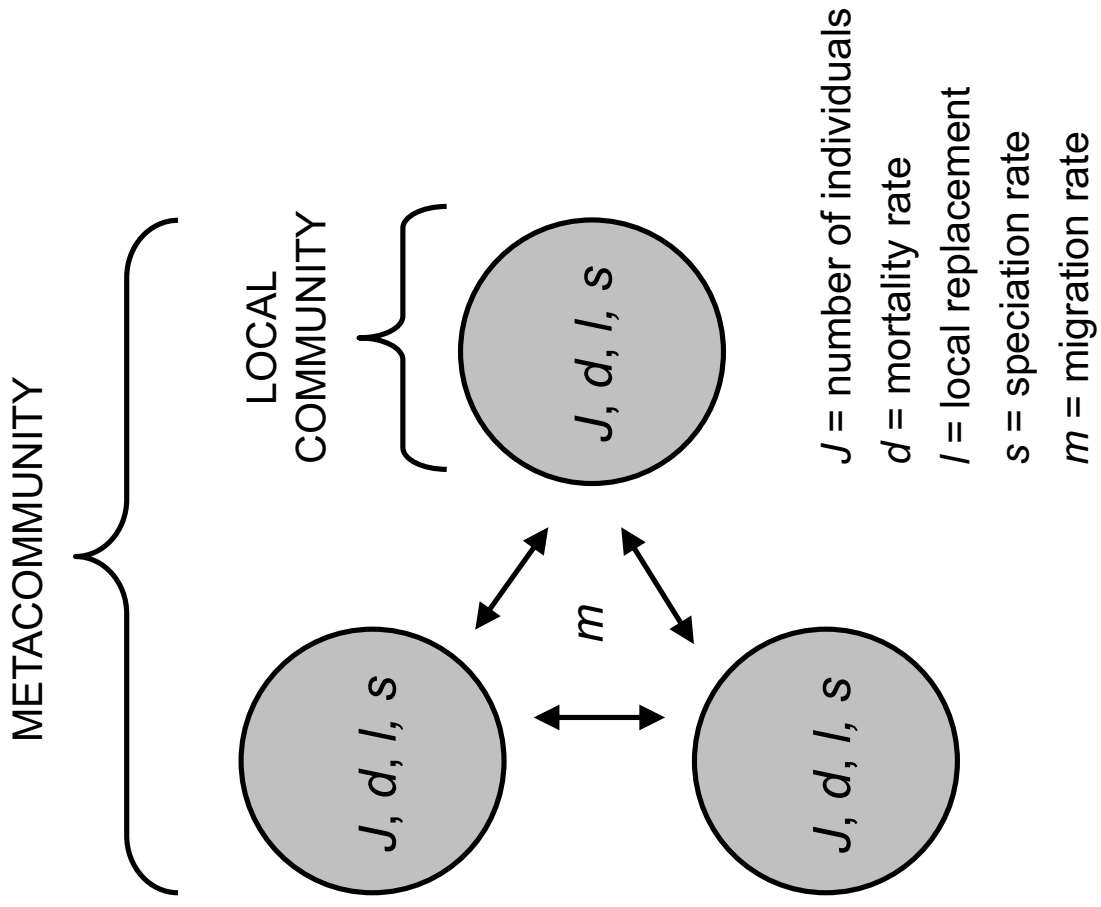
582 **Figure 5** The slopes of temporal Taylor's power law (TPL) as produced by neutral
583 models with various levels of model parameters. Solid horizontal lines delimit the
584 range observed in natural populations. Shown as a box and whisker plot with median
585 and quartiles shown, outliers are not displayed.

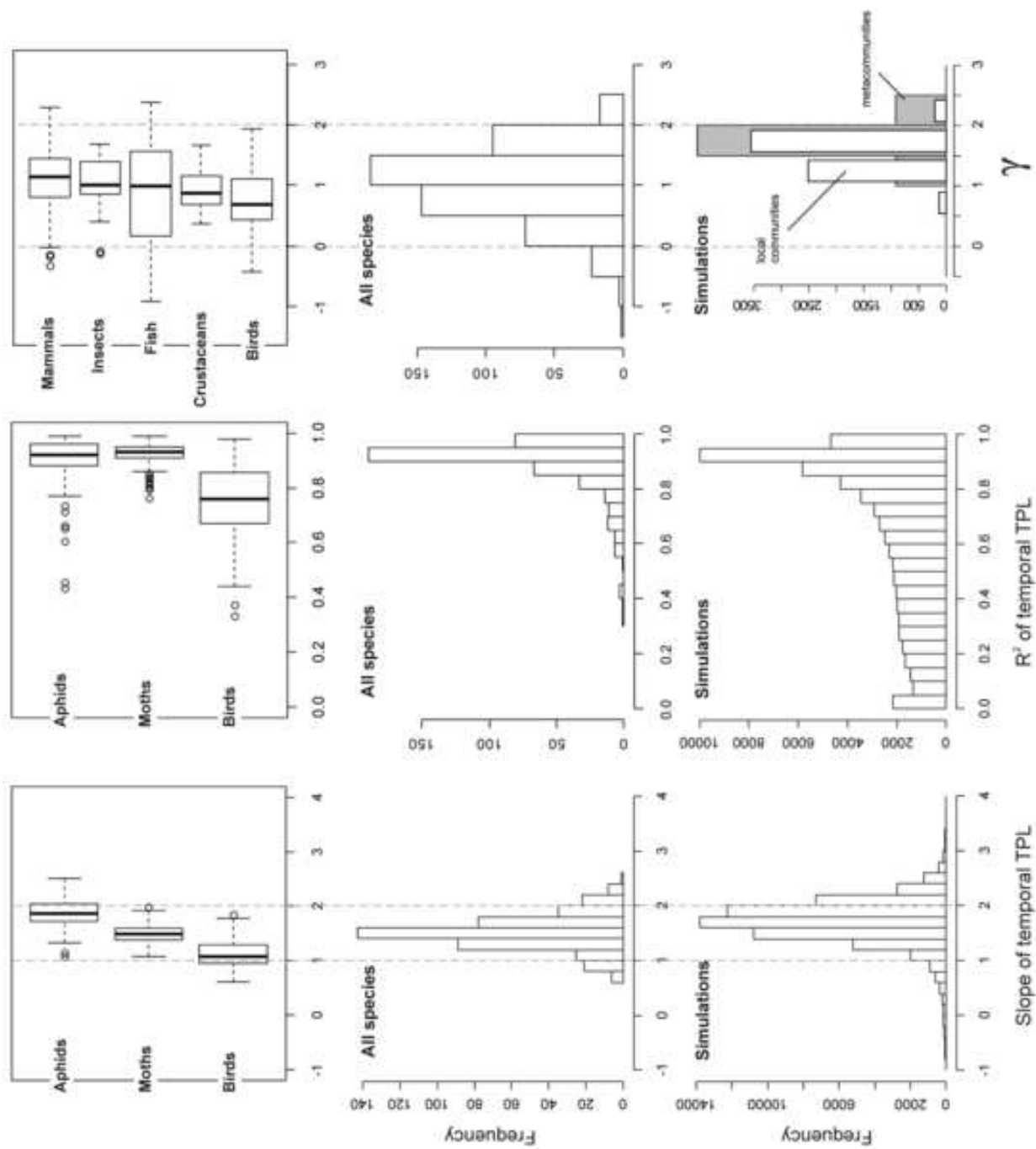
586

587 **Figure 6** Dependence of Pollard's P on relative abundance of species in local
588 communities and in metacommunities. Shades of grey represent density of points in
589 hexagonal bins.

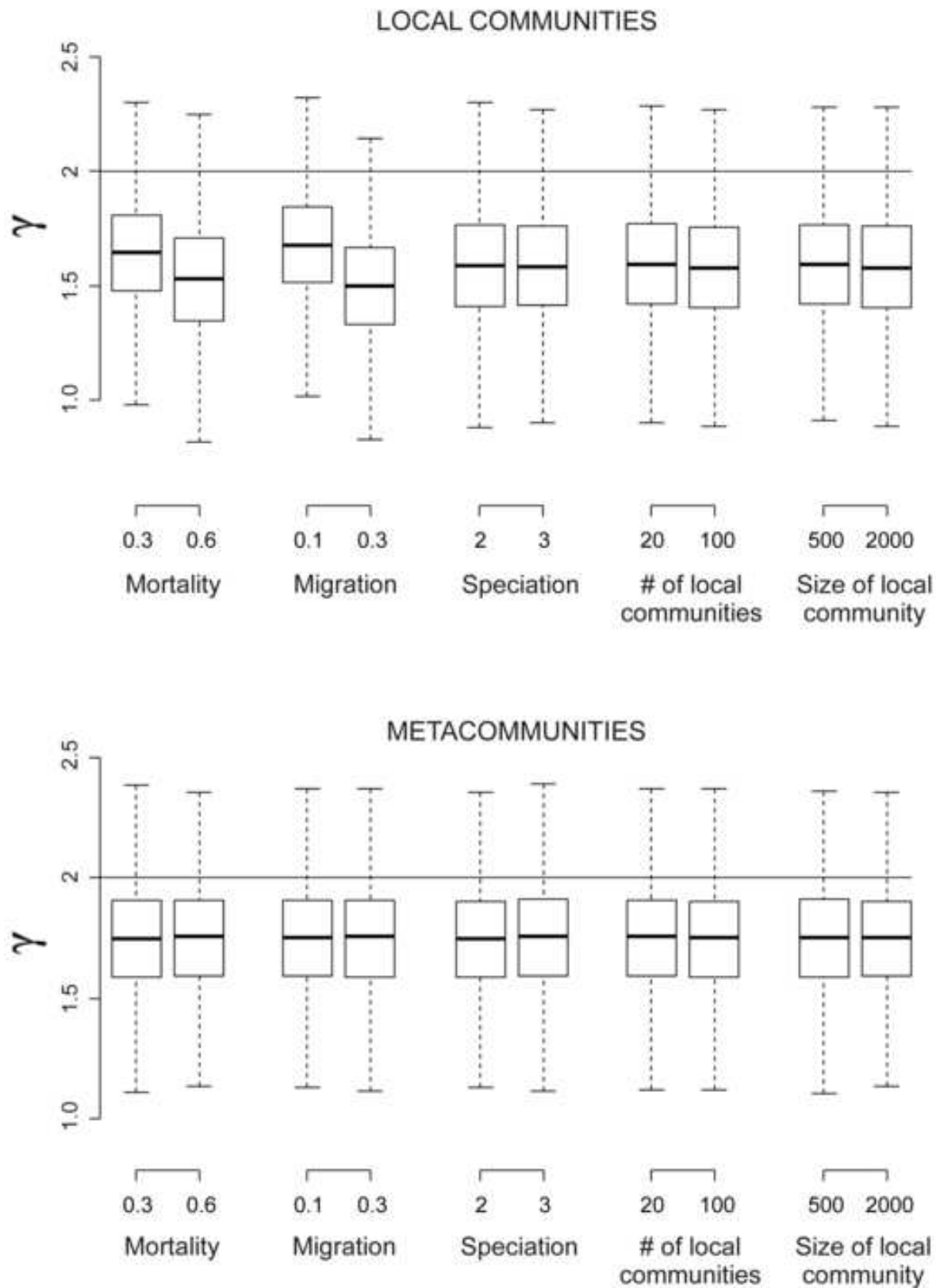
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591 **Figure 7** Dependence of slope and coefficient of determination (R^2) of Taylor's
592 Power Law on mean relative abundance of species in local communities. Shades of
593 grey represent density of points in hexagonal bins.

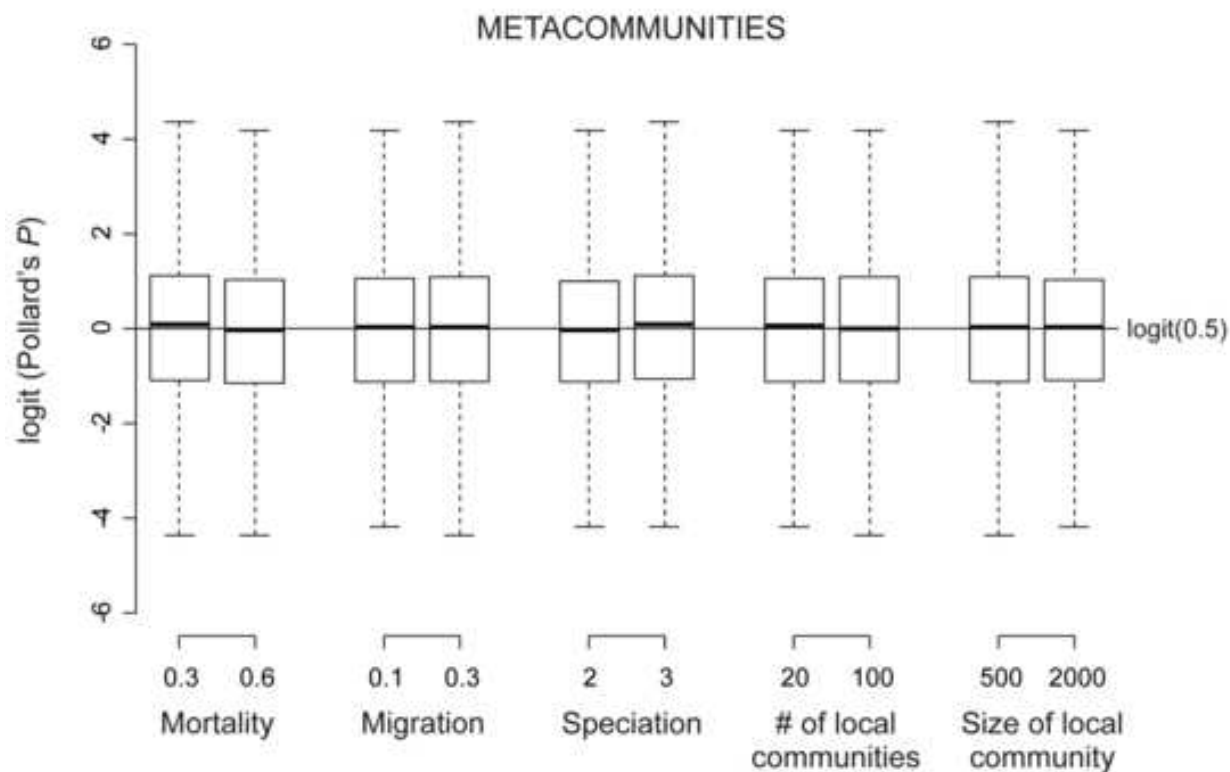
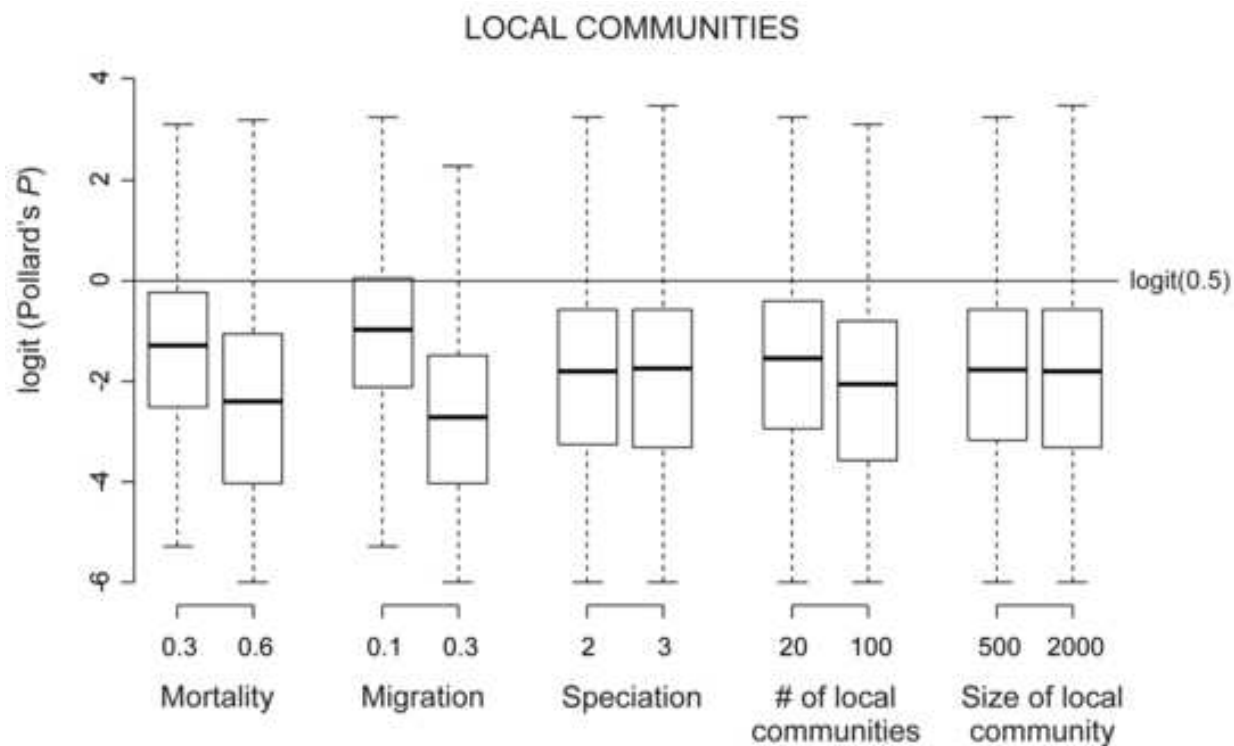


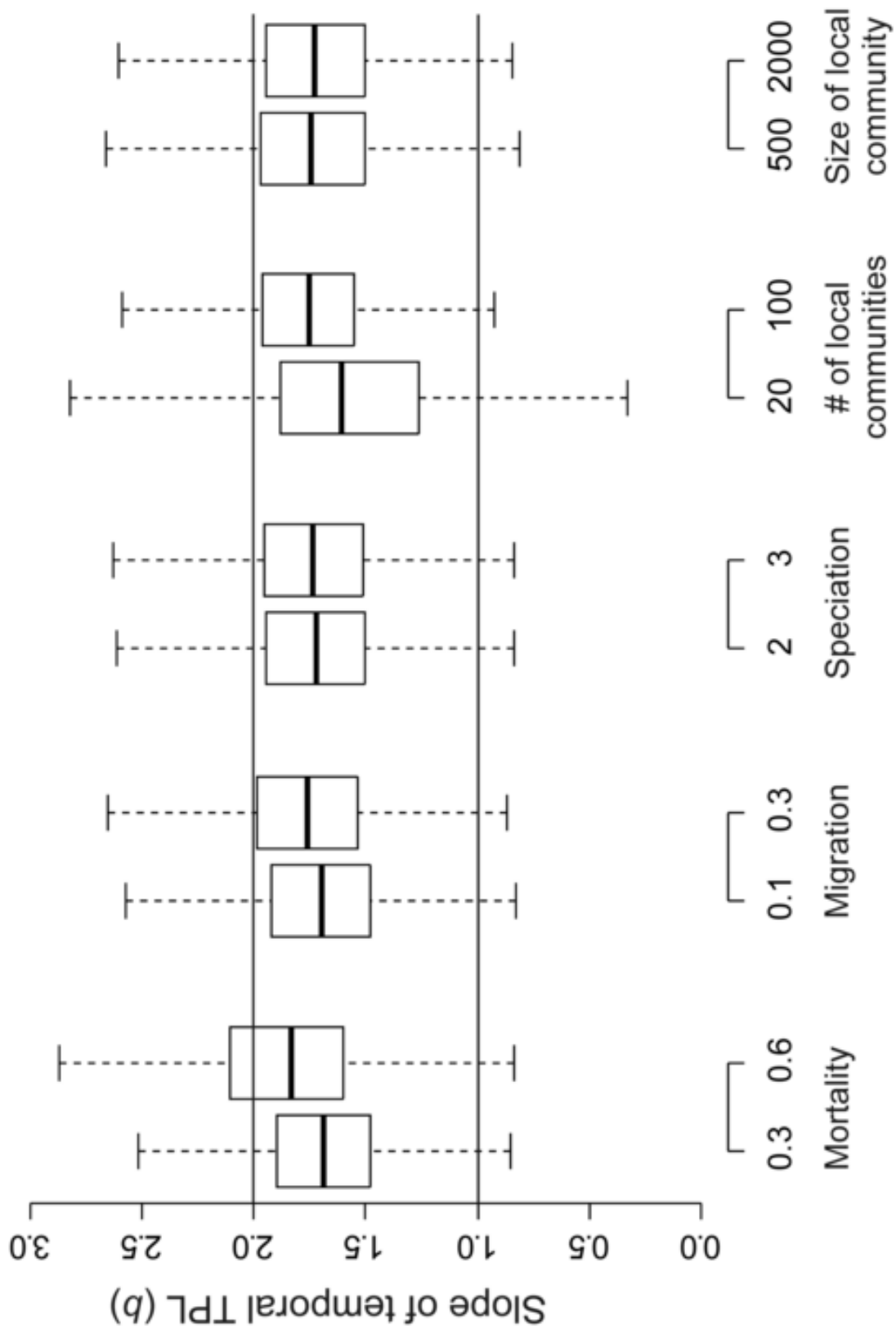


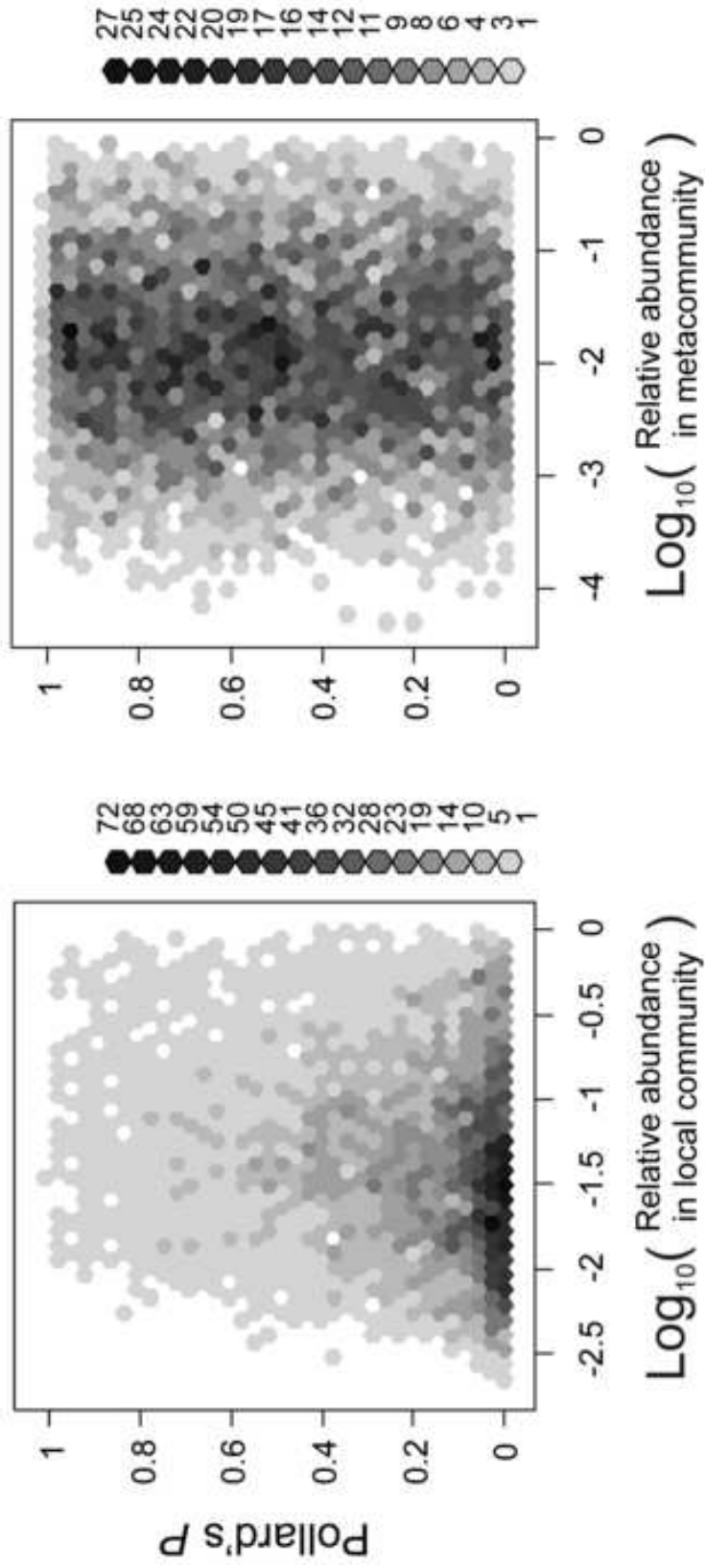
4. Figure



4. Figure







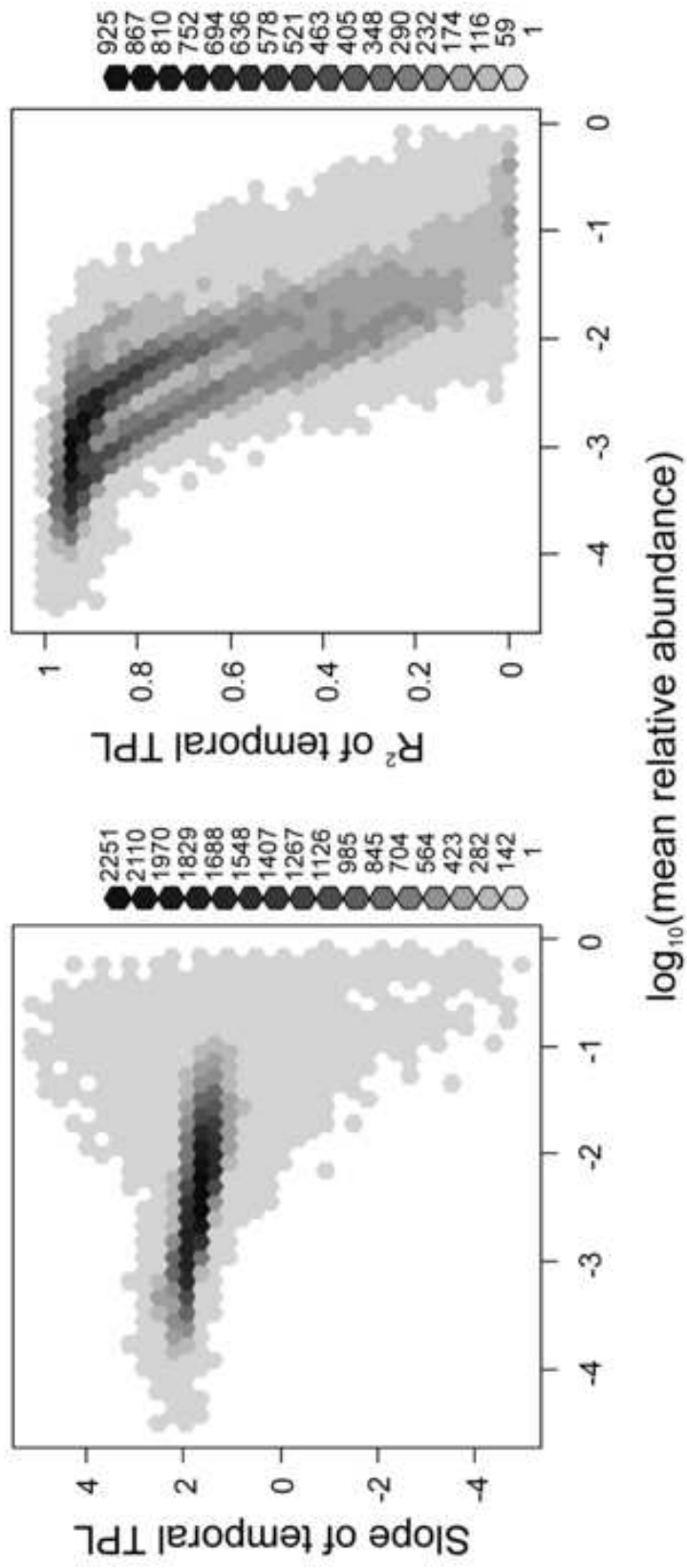


Table 1 An overview of the parameters and their levels used in our neutral model simulations. See material and methods for detailed description of the exact function of each parameter.

Parameter	Description	Levels used in simulations
Number of local communities	number of local communities that make up the metacommunity	100, 20
Size of each local community (J)	number of individuals in each local community	2000, 500
Mortality rate (d)	mortality rate of individuals per time step in the local community	0.6, 0.3
Migration rate (m)	proportion of vacant positions in the community replaced by migration from other local communities	0.1, 0.3
Speciation rate (s)	speciation rate per species per step	2×10^{-6} , 3×10^{-6}

Table 2 The strength of the effect of each parameter on the value of γ and the logit-transformed Pollard's P . Parameter γ describes the 'colour' of the spectra of a time series. Pollard's P is the probability of obtaining the data in case of density independence (random walk). The values of R^2 were estimated using a multiple ANOVA. Figures in bold show values higher than 0.001.

	Local communities			Metacommunities	
	R^2 (γ)	R^2 (logit of Pollard's P)	R^2 (γ)	R^2 (logit of Pollard's P)	R^2 (slope of TPL)
Mortality rate	0.045	0.078	<0.001	<0.001	0.019
Migration rate	0.11	0.19	<0.001	<0.001	0.0014
Speciation rate	<0.001	<0.001	<0.001	<0.001	<0.001
# of local communities	<0.001	0.014	<0.001	<0.001	0.048
Size of local community	<0.001	<0.001	<0.001	<0.001	0.0015