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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 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 distributions. Here we investigate the ability of a neutral model to predict phenomena 25 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

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49 Introduction

50

The neutral theory of biodiversity (NTB; Hubbell, 2001; Chave, 2004; Alonso et al., 51 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 McPeek, 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 long real-world time series from the perspective of NTB. They used the Bayesian 68 69 statistical framework and a neutral model of community dynamics (zero-sum

assumption relaxed) to show that sizes of natural communities fluctuate more than
expected under neutrality. However, Mutshinda et al. (2008) focused only on the
dynamics of local community size and they did not examine time series of individual
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 to obey some degree of stabilizing density dependence (Woiwod and Hanski, 1992; 77 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 size (s^2) called Taylor's Power Law (TPL) (Taylor et al., 1983; Tokeshi, 1995; 80 Ballantyne and Kerkhoff, 2007) which has the form $s^2 \propto m^b$. In natural populations, 81 the exponent b of TPL is usually observed to satisfy 1 < b < 2 (Kendal, 2004). Natural 82 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 density') S(f) is a function of the frequency f and often satisfies $S(f) \propto 1/f^{\gamma}$ 85 (Halley, 1996). The exponent y usually falls between 0 and 2 for natural time series 86 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 $\ln N_{t+1} = \ln N_t + e_t$ (1)

where *e_t* varies at random according to a given distribution with zero mean and
is independent on population size (Murdoch, 1994; Hanski et al., 1996). The model is
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 , (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 ($0 \le f \le f_{n/2}$; <i>n</i> is length of the time series). Values of <i>S</i> (<i>f</i>) 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 pr	ovided by Pable	Inchausti: see also	Inchausti and Hallev	. 2001.

196 2002).

197

198 Testing for density dependence

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

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

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:

(2)

(3)

212
$$\ln N_{t+1} = \ln N_t + r + \beta N_t + e_t$$

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

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

224

225 Taylor's power law

To test if populations in our model obey the Taylor's Power Law (TPL) we performed 226 50 simulations for each combination of parameters (Table 1). For each species in the 227 simulations we created a metapopulation matrix (MPM) of abundances in which rows 228 229 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 vales 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 sales is caused by more than just the
267	length of the sampled time series.

R

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 <i>P</i> 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

- 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

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 walk ($\gamma \approx 2$) in which there is little or no dependence on the abundances in other local 300 301 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	Ucorrelated noise in the form of census error also causes spurious detection of

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

There should also be real density dependence in our model. In an isolated community, the closer N_t gets to zero (extinction) or to J (monodominance) the lower 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 ($1 \le b \le 2$), 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

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

There is a general agreement that natural time series are not "brownian" (Fig. 1; Arino and Pimm, 1995; Inchausti and Halley, 2001, 2002) – they clearly fall into the whitened range of scaling exponents ($0 < \gamma < 2$; Fig. 2). Our simulations indicate that neutral models have the potential to explain part of this observed whitening, 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 $\boldsymbol{\gamma}$ 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

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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	G
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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., McPeek, 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.
- McGill, B.J. 2003. A test of the unified neutral theory of biodiversity. Nature 422,
 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., Woiwod, 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., Hubbbell, 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. 90, 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.

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5 million, D. 200 million diddooris, neutranty, and community structure. It stoenastic	541	Tilman, D.	2004.	Niche	tradeoffs,	neutrality.	, and	community	structure:	A stochastic
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- 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.
- Volkov, I., Banavar, J.R., Hubbell, S.P., Martian, A. 2003. Neutral theory and relative 548
- 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.
- 29. CCCC 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).

Figure 5 The slopes of temporal Taylor's power law (TPL) as produced by neutral
models with various levels of model parameters. Solid horizontal lines delimit the
range observed in natural populations. Shown as a box and whisker plot with median
and quartiles shown, outliers are not displayed.
Figure 6 Dependence of Pollard's P on relative abundance of species in local
communities and in metacommunities. Shades of grey represent density of points in
hexagonal bins.
Figure 7 Dependence of slope and coefficient of determination (R^2) of Taylor's
Power Law on mean relative abundance of species in local communities. Shades of
grey represent density of points in hexagonal bins.







METACOMMUNITIES 2.5 N > 1.5 1.0 1 ſ ſ ٦ 2 3 0.6 0.3 0.3 0.1 20 100 500 2000 # of local Mortality Migration Speciation Size of local communities community

LOCAL COMMUNITIES

logit (Pollard's P) N logit(0.5) 0 N 4 φ 0.6 0.3 0.3 0.1 2 3 20 100 500 2000 Mortality Migration Speciation # of local Size of local community communities METACOMMUNITIES φ. 4 logit (Pollard's P) N logit(0.5) 0 Ņ 4



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 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.

1	Levels used III
	simulations
number of local communities that make up	100, 20
the metacommunity	
number of individuals in each local	2000, 500
community	G
mortality rate of individuals per time step in	0.6, 0.3
the local community	
proportion of vacant positions in the	0.1, 0.3
community replaced by migration from other	
local communities	
speciation rate per species per step	2x10 ⁻⁶ , 3x10 ⁻⁶
	number of local communities that make up the metacommunity number of individuals in each local community mortality rate of individuals per time step in the local community proportion of vacant positions in the community replaced by migration from other local communities speciation rate per species per step

Accel

Table 2 The strength of the effect of each parameter on the value of γ and the logittransformed 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 R² were estimated using a multiple ANOVA. Figures in bold show values higher than 0.001.

	Local communities			ities		
	$R^2(\gamma)$ R^2 (logit of		$R^{2}(\gamma)$	R^2 (logit of	R^2 (slope of	
		Pollard's P)		Pollard's P)	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	< 0.001	0.014	<0.001	<0.001	0.048	
communities			\mathbf{D}			
Size of local	< 0.001	<0.001	<0.001	< 0.001	0.0015	
community		×C				
P	ccs	20				