# Characteristics of temporal changes in communities where dynamics differ between species

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## Abstract

Communities with different phenotypic variation among species can have identical species abundance distributions, although their temporal dynamics may be very different. By using stochastic species abundance models, both the lognormal and beta prime abundance distributions can be obtained with either homogeneous or heterogeneous dynamics among species. Assuming that anthropogenic activity disturb the communities such that species' carrying capacities are decreasing deterministically, the structure of the communities are studied using simulations. In order to construct homogeneous communities with reasonable variation in abundance, the parameter values describing the dynamics of the species can be unrealistic in terms of long return times to equilibrium. Species in heterogeneous communities can have stronger density regulation, while maintaining the same variation in abundance, by assuming heterogeneity in one of the dynamical parameters. The heterogeneity generates variation in carrying capacity among species, while reducing the temporal stochasticity. If carrying capacity decreases, changes in community structure occur at a much slower rate for the homogeneous

compared to the heterogeneous communities. Even over short time periods, the difference in response to deterministic changes in carrying capacity between homogeneous and heterogeneous community models can be substantial, making the heterogeneous model a recommended starting point for community analysis.

## 1. Introduction

In community ecology, biologists try to understand how species persists in concert with each other over time, in space or both. The initial studies of species communities were concerned with fitting probability distributions to abundances (counts) of butterflies (Fisher et al. 1943). Several different distributions have been applied to describe the composition of species communities in a wide variety of taxa, possibly where the data have been transformed to a log scale. The probability distributions fitted to abundance data are known as species abundance distributions in community ecology and can be used to compare the structure of communities at different spatio-temporal locations and assess the durability of communities based on the number of common and rare species present (McGill, 2011). Additionally, numerous indices have been constructed to describe the diversity and similarity of communities (Gotelli, 2011; Maurer, 2011). How communities may develop over time is a particularly important issue in conservation biology (Buckland et al., 2005; Magurran et al., 2010; McGill, 2011).

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While species abundance distributions can be fitted to data and compared at different points in time, the distributions themselves give no important information about how the community will develop in the future. It is, however, possible to describe a community of species assuming that each single species can be characterized by a dynamic population model and still obtain well-known abundance distributions. The population model used to describe single species dynamics contains the information needed to simulate each species' temporal fluctuations and can accordingly be used to study how the whole community progresses over time. Single species dynamics are determined by different biological attributes, for instance growth rate, carrying capacity and environmental stochasticity. Using single species dynamics to obtain species abundance distributions were introduced by Engen and Lande (1996a,b) and some of the main results are reiterated in the Methods section, but the focus in this article is on temporal dynamics of communities.

When characterizing communities using single species dynamics, a common simplifying assumption is that all the species have the same vital rates, i.e. the same growth rate and carrying capacity. However, it has been shown that dynamics of species can vary considerably among species within the same taxa (Engen et al., 2011). Such variation in dynamics among species will be described as heterogeneity in different vital rates in this article, while homogeneous communities have no variation in vital rates among species. The main topic of this article is to analyse how variation among species influence the structure of communities over time. Our comparison of communities is restricted to constructing species abundance distributions with different magnitudes of heterogeneity, starting with a homogeneous community, but

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identical abundance distributions.

Communities are often studied under the assumption that the environment of the different species are constant, meaning that vital rates and the magnitude of the variation in annual fluctuations are constant over the whole time frame considered. Anthropogenic activities, however, such as habitat destruction, over-exploitation, introduced species and pollution, are currently causing the sixth major mass extinction of species (Lande et al., 2003) and will generate changes in species community composition, structure and diversity (Kneitel and Pages, 2010). For instance, a reduction or fragmentation of habitat can reduce the carrying capacity of the species present in a community. Despite recent attempts by the international community to stop the reduction of biological diversity, the majority of indices measuring biodiversity show declining trends, while anthropogenic pressure on ecosystems have increased (Butchart et al., 2010). This study will emphasize on how anthropogenic activities can change species communities, by analyzing how communities with different degrees of heterogeneity in the dynamics will vary in their response to permanent changes in the environment, using simulations.

This article has the following structure: first, the main theory of Engen and Lande (1996a,b) on stochastic species abundance models and heterogeneous communities are described. Second, the simulation procedure used to study the temporal dynamics of the communities is explained, and the different community indices applied are presented. The first case study of community dynamics considered show species with a Gompertz type of density regulation. Communities with the same abundance distribution when observed at a single point of time, but with completely different temporal

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dynamics, are compared, both when the carrying capacities of the species'
are either constant or when the carrying capacities are gradually declining.
In the second case study we first consider species following a homogeneous
Beverton-Holt model of density regulation, meaning that all the species in
the community have the same vital rates. This Beverton-Holt dynamics are
compared to heterogeneous communities with logistic type of density regu-
lation, i.e. the vital rates vary between species in the community. Here also,
the different communities show different temporal dynamics, but maintain
the same instantaneous abundance distribution. Finally, the effect of a de-
clining trend in carrying capacity is studied for the second case. Considerable
differences between simulated homogeneous and heterogeneous communities
are illustrated, emphasizing the importance of allowing for variation in the
vital rates between species in a community.

## 2. Methods

### 2.1. General theory

The stochastic species abundance models introduced by Engen and Lande
(1996a,b) obtained the lognormal and gamma distribution, respectively, by
modelling the individual species' dynamics using multivariate diffusion pro-
cesses. The models assume that the temporal variation in population abun-
dance in a community is caused by environmental fluctuations in the growth
rate of each individual species independently. The dynamical approach by
Engen and Lande (1996a) generated abundances following an inhomoge-
neous Poisson process with rate $\lambda(x)$, where $x$ is the abundance, meaning
that the number of species with abundances in some region $\Omega$ is Poisson

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distributed with mean $\int_\Omega \lambda(x)dx$ at any time. The species abundance distribution is then the Poisson rate scaled as a proper distribution, that is, $f(x) = \lambda(x)/\int \lambda(u)du$, where the integration runs over all possible abundances. Such dynamical abundance models provide means to study the community dynamics over time, whereas the abundance distributions only provide snapshots of the community compositions at specified time points. Note that the abundance $x$ could be measured on a different scale, e.g. the log scale for a Gompertz model, without invalidating the theory described here.

Using the diffusion approximation for the single species dynamics with infinitesimal mean $\mu(x;\theta)$ and variance $\nu(x;\theta)$, Engen and Lande (1996a) derived a general expression for the Poisson rate of species abundances

$$\lambda(x;\theta) = \frac{2\beta}{\nu(x;\theta)} e^{2\int_a^x \mu(u;\theta)/\nu(u;\theta)du}, \tag{1}$$

where $a$ is the extinction barrier and $\beta$ the speciation rate. However, speciations are not included in the following analysis which deals with time intervals so small that speciations are unlikely. An advantage of the approach of Engen and Lande (1996a) is that it, in a simple way, allows for heterogeneity among species. Species entering the community are described by a set of parameters $\theta \in \Theta$, corresponding to abundance model $\lambda(x;\theta)$, thereby introducing heterogeneity by assuming that $\theta$ vary among species. If $\theta$ at speciation or colonization can be considered a realization of a stochastic variable with distribution $\pi(\theta)$, then the abundance model is given by the inhomogeneous Poisson rate (Engen and Lande, 1996a)

$$\lambda(x) = \int_{\theta \in \Theta} \lambda(x;\theta)\pi(\theta)d\theta. \tag{2}$$

This result shows the possibility of obtaining the same abundance model $\lambda(x)$

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from different combinations of its components $\lambda(x; \theta)$ and $\pi(\theta)$. An observation of a community at a given time will only give information about the rate $\lambda(x)$ and the corresponding species abundance distribution while containing no information about its components $\lambda(x; \theta)$ and $\pi(\theta)$. Knowledge of species heterogeneity is likely to be crucial when it comes to permanent environmental changes and management of ecosystems. Fluctuations in population abundance is assumed to be caused by environmental stochasticity, described by environmental variance in the infinitesimal variance of the diffusion process. Demographic stochasticity is only relevant in small populations and will not be considered in the following analysis. Although demographic variance increases the probability of extinction at small abundances, it will not change the general results presented here. Note also that the dynamics of the species within a community is assumed to be independent.

The non-uniqueness in temporal characteristics of abundance models with the same abundance distribution is the starting point of this analysis. Heterogeneity can be defined by considering variability among species in different parameters describing the population dynamics. If one parameter vary among species, one or more of the other population parameters have to be adjusted in order to obtain the same abundance distribution as in the homogeneous case. For example, when log abundances are described by a Gompertz type of density regulation, heterogeneity can be modelled with the stochastic growth rate $s$ being normally distributed with expectation $s_0$ and variance $\tau^2$. Equal abundance distributions can be obtained by adjusting the strength of density dependence as a function of $\tau^2$, $\gamma = g(\tau^2)$. The strength of density dependence is defined as $-Kr'(K)$ (May, 1981) where $r(N)$ is

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the deterministic (density-dependent) growth rate and $K$ is the carrying capacity, i.e. the population size where the growth rate is zero and $'$ is the derivative (see also text box). These communities with different values of $\tau^2$ and $\gamma$ will have the same log abundance distribution when observed at a single point in time, but the single species' dynamics over time will be different. Hence, these communities are likely to respond differently to environmental changes.

Species entering the heterogeneous community with population parameters sampled from $\pi(\theta)$ will go extinct at different rates depending on their value of $\theta$. Some values may be unfavourable, leading to short time to extinction of the species, while others may generate longer lifetimes. Species with favourable population parameters will therefore be more frequent in the community than given by their distribution at speciation. At a given time, extinctions will generate a distribution of parameters among species in the stationary community $\pi^*(\theta) \neq \pi(\theta)$. Engen (2007a) called $\pi^*(\theta)$ the sampling distribution of population parameters. The difference between the distributions $\pi(\theta)$ at invasion and $\pi^*(\theta)$ generated by extinctions can be substantial. In this analysis, all population parameters are generated from the sampling distribution $\pi^*(\theta)$.

Two different classes of species abundance distributions will be considered here: the lognormal and the beta prime distribution, also known as beta distribution of the second kind (Kempton, 1975). Heterogeneous dynamic models that have the same species abundance distribution are constructed in each case, and the communities' response to different environmental changes is investigated by simulations, recording the following different metrics: The

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total number of individuals, $N$, measures the abundance. The number of species, $S$, is a measure of richness. The Shannon diversity, $D_{Shannon} = -\sum p_i \ln p_i$, where $p_i = N_i/\sum N_i$, indicate whether there are a few species that make up a large part of the total abundance (small value) or if the species constitute a more uniform proportion of the total abundance (high $D_{Shannon}$). The modified Shannon diversity, proposed by Buckland et al. (2005), $D_{Mod-Shannon} = -\sum q_i \ln q_i$, where $q_i = N_i/\sum N_j$ and $N_j$ is the abundance of species $j$ at the first time point. The number of species that are above 10% of their initial abundance, $S_Q$, is used as a measure of quasi-extinctions in the community, and $S_{obs}$ is the number of species above a global threshold that for example could represent the *observable* species in the community, e.g. 10% of the species' mean abundance, $EN/ES$.

The simulations are implemented in the following manner: first, each species in the community is given a set of parameter values, sampled from $\pi^*(\theta)$. In the case of a homogeneous community, all the species have the same set of values. Second, the initial abundance of the species is sampled from their stationary distribution, which is different among the species of heterogeneous communities. Third, the species are simulated forward in time using their separate parameters values. When applying temporal changes to the parameters, the different community characteristics are computed for each time step. The R-code used to generate the data and figures are found in the supplementary materials.

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**Strength of density dependence:**

The deterministic version of logistic growth rate, can be written as $r(N) = r_0 - \delta N$ where $r_0$ is the growth rate and $\delta$ is a density dependence parameter. The carrying capacity $K$ is the population size where $r(K) = 0$, which is $K = r_0/\delta$. The strength of density dependence is defined as $-Kr'(K)$, which for the logistic model is $-K(-\delta) = (r_0/\delta)\delta = r_0$ (May, 1981).

For the deterministic Gompertz model $r(N) = r_1 - \gamma \ln N$ where $r_1$ is the deterministic growth rate at population size one, the log carrying capacity is $\ln K = r_1/\gamma$ and following the definition above, the strength of density dependence is $\gamma$.

**Other parameters:**

| | | |
|---|---|---|
| $s$ | : | stochastic growth rate, $s = r_1 - \sigma_e^2/2$ |
| $\pi(s)$ | : | distribution of $s$ at speciation, which is normal with mean $s_0$ and variance $\tau^2$ |
| $\sigma_e^2$ | : | environmental variance |
| $\eta$ | : | mean of the lognormal abundance distribution |
| $\rho^2$ | : | variance of the lognormal abundance distribution |
| $c$ | : | average number of offspring in the Beverton-Holt model if there is no density dependence |
| $b$ | : | density dependence parameter in the Beverton-Holt model |
| $p, q$ | : | shape parameters of the beta prime distribution where e.g. the mean is $p/(q-1)$ |
| $\pi(\delta)$ | : | distribution of $\delta$ at speciation, which is gamma with shape $k$ and scale $1/\alpha$ |

*2.2. Gompertz type of density regulation*

209 For a homogeneous community, where the individual species' dynamics

210 is described by a Gompertz type of density regulation, the log abundances

211 $x$ can be approximated by a linear diffusion process with mean $\mu(x; s, \gamma) =$

212 $s - \gamma x$, meaning that the density regulation is linear on the log scale, and

213 variance $\nu(x; \sigma_e^2) = \sigma_e^2$. The Poisson rate is found using Equation (1) with

214 $\theta = (s, \gamma, \sigma_e^2)$,

$$\lambda(x; \theta) = \frac{2\beta}{\sigma_e^2} e^{s^2/(\gamma\sigma_e^2)} e^{-(1/2)(x-s/\gamma)^2/\sigma_e^2/(2\gamma)}. \tag{3}$$

215 Since this Poisson rate is proportional to a Gaussian distribution, the log

216 abundances are normally distributed with mean $\ln K = s/\gamma$ and variance

217 $\sigma_e^2/(2\gamma)$, while the abundances have the corresponding lognormal distribu-

218 tion. Engen and Lande (1996a) used this model to define a heterogeneous

219 species abundance model with abundance distribution still being the lognor-

220 mal. By assuming that the stochastic growth rates were normally distributed

221 with mean $s_0$ and variance $\tau^2$ among species at invasion, the Poisson rate for

222 log abundances becomes

$$\lambda(x) = \frac{2\beta}{\sigma_e^2} e^{s_0^2/(\omega\sigma_e^2)} e^{-(x-\eta)^2/(2\rho^2)}, \tag{4}$$

223 where $\omega = (\gamma - 2\tau^2/\sigma_e^2)$. The log abundance distribution is then normal

224 with expectation $\eta = s_0/\omega$ and variance $\rho^2 = \sigma_e^2/(2\omega)$. Following Engen

225 (2007a), the distribution of $s$ in the stationary community $\pi^*(s)$ will be

226 normal with expectation $s_0\gamma/\omega$ and variance $\tau^2\gamma/\omega$. The variation in $s$ can

227 be interpreted as if the individual species' log carrying capacities $\ln K$ were

228 normally distributed among species with expectation $E[\ln K] = s_0/\omega$ and

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variance $\text{Var}[\ln K] = \tau^2/(\gamma\omega)$, while the temporal variance in log abundances $\sigma_e^2/(2\gamma)$ are the same for all species. The variation in log carrying capacity $\text{Var}[\ln K]$ expresses the heterogeneity in the community.

## 2.3. Lognormal abundance models with heterogeneity among species

Equal abundance distributions for communities with different individual variation in $s$ can be obtained by keeping the values of $\eta$ and $\rho^2$ fixed for different values of $\tau^2$ in Equation (4). The simplest solution is to change the strength of density dependence choosing $\gamma(\tau^2) = \gamma_0 + 2\tau^2/\sigma_e^2$ (Engen, 2007b), where $\gamma_0$ is the strength of density dependence for a homogeneous community. The linear function $\gamma(\tau^2)$ ensures that $\omega$, $\eta$ and $\rho^2$, are the same for any degree of heterogeneity described by $\tau^2$.

Figure 1 illustrates one homogeneous community and two heterogeneous communities with the same lognormal species abundance distribution. The variation in log carrying capacity $\ln K = s/\gamma$ among species is caused by the heterogeneity in stochastic growth rate sampled from $\pi^*(s)$. This variation in $\ln K$ reduces the species specific environmental variation, or temporal variance of log abundance $\sigma_e^2/(2\gamma)$, because the strength of density dependence increases with the heterogeneity (Fig 1, first row). The ratio between variation in carrying capacity and species specific environmental variation, depends on the amount of variation in the stochastic growth rate. The heterogeneity in the stochastic growth rate corresponds to a coefficient of variation in log carrying capacity among species, $\text{SD}(\ln K)/\text{E}(\ln K)$, of 0.395 and 0.362 for two communities, second and third column, respectively.

The time series plot (Fig 1, second row) illustrate the difference in the individual species dynamics over time due to the heterogeneity in $s$, which is

compensated for by stronger density regulation and reduced species specific environmental noise. The community in the second column has $\gamma = 0.2$, equivalent to a mean return time to equilibrium of $1/\gamma = 5$ time steps, and species specific environmental noise $\mathrm{Var}[x] = 0.1$, resulting in small perturbations from the individual species' carrying capacity. In the third column, with $\gamma = 0.0275$ and $\mathrm{Var}[x] = 0.727$, the perturbations are larger and return time longer. However, the snapshot of the species abundance distribution at a give time show no distinct difference between the communities (Fig 1, third row). This demonstrates that a fitted abundance distribution, i.e. estimating the mean $\eta$ and variance $\rho^2$ of the log abundances, contains little information about the temporal dynamics of individual species and the community, even when *all* individuals are sampled.

*2.4. Lognormal abundance models and gradual change in carrying capacity*

Anthropogenic activities may disturb the environment of species in a community in such a way that the parameters describing the species' dynamics change over time. A simple example of such a permanent change of the environment is to assume that the species' carrying capacity is reduced by multiplicative factor each time step. The change in log carrying capacity, $\ln K = s/\gamma$, is assumed to be caused by a linear change in $s$, i.e. $s(t) = s_0 + t\gamma \ln(\kappa)$, so that $\ln K(t) = s_0/\gamma + t \ln \kappa$. The proportional change in carrying capacity is the same for all species, both in homogeneous and heterogeneous communities. A gradual change in carrying capacity could for instance represent a reduction in the available area of the community. A gradual decline in carrying capacity of 2% each time step for three communities is illustrated in Figure 2a. The initial parameter values for the

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communities in Figure 2 are the same as those in Figure 1, i.e. the first is a homogeneous community (no variation in carrying capacity between species), while the communities in the second and third columns have a coefficient of variation in log carrying capacity of 0.395 and 0.362, respectively. For each of the three sets of parameter values, 200 communities are simulated and the metrics described in *General theory* are computed each time step in addition to the mean and 95% quartile range.

Species richness $S$ appears to change slowly the first 100 time steps as illustrated in Figure 2b, but the expected number of species going extinct in this time period is important, as illustrated in Figure 3. Five species are expected to go extinct in the heterogeneous community with the strongest density regulation in 50 time steps (Fig. 3), while the numbers are three and four for the homogeneous and the other heterogeneous community, respectively. Generally, the heterogeneous communities loose species at a much higher rate than the homogeneous community. On average, 25% of the species are extinct in 150 and 300 time steps for the heterogeneous and homogeneous communities, respectively (Fig. 2b). The number of species above 10% of their initial abundance $S_Q$ declines faster for the communities with the largest species' specific environmental variation (the homogeneous community in particular) the first 100 time steps. However, after 100 time steps, $S_Q$ drops rapidly for the heterogeneous communities, which is reasonable since the species have a shorter return time to equilibrium, fluctuating closely around the decreasing carrying capacity. The carrying capacity is reduced by almost 90% after 100 time steps. The number of species above a fixed *observable* threshold $S_{Obs}$ is roughly 75% of $S$ initially, when the threshold is set at 40 individuals,

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i.e. species with less than 40 individuals are considered unobservable. $S_{Obs}$ declines faster within the initial 100 time steps, than the other two species metrics. One third of the observable species are expected to be unobservable after 75 time steps in the heterogeneous community with the strongest density regulation (Fig 3).

The total abundance $N$ changes more dramatically by the decreasing carrying capacity, than the richness indices (Fig 2c). In particular, the heterogeneous communities have halved their total abundance by roughly 40 and 70 time steps, while the homogeneous community decreases much slower in addition to having a very large variation. The average value of the Shannon diversity $D_{Shannon}$ is fairly constant during the first 200 time steps, but can vary considerably among simulations. The Shannon diversity starts to decline after roughly 25% of the species are extinct and the total abundance is between $2 - 5\%$ of its initial value. The modified Shannon diversity $D_{Mod-Shannon}$ starts to decline immediately as carrying capacity decreases, and the shape of the curves resembles the total abundance closely. The considerable reduction in $N$ is captured by $D_{Mod-Shannon}$ since the relative abundances for this index is with respect to the initial population size. However, as $N$ has large variation among simulations, so does the modified Shannon index, especially for the homogeneous community.

*2.5. Beverton-Holt model and logistic density dependence*

Equal abundance distributions can be obtained using different kinds of population models. Now, consider the Beverton-Holt model with infinitesimal mean $\mu(n; b, c, s_a) = n[c/(1 + bn) + s_a - 1]$ and variance $\nu(n) = \sigma_e^2 n^2$, where $n$ is the abundance on the arithmetic scale. The factor $c/(1 + bn)$ is

the average number of individuals produced from one year to the next, while $s_a$ is the adult survival rate. Assuming species go extinct at $n = 1$, Equation (1) gives the abundance distribution for the Beverton-Holt model

$$f(n) = \frac{\Gamma(p+q)}{\Gamma(p)\Gamma(q)} \frac{b^p n^{p-1}}{(1+bn)^{p+q}}, \tag{5}$$

where $p = 2(c + s_a - \sigma_e^2/2 - 1)/\sigma_e^2$ and $q = 2(1 + \sigma_e^2/2 - s_a)/\sigma_e^2$. The distribution in (5) is a beta prime distribution, or beta distribution of the second kind (Stuart and Kendall, 1968), censored at $n = 1$, first proposed as a species abundance distribution by Kempton (1975).

For species in a community with dynamics described by a logistic type of density dependence, where $\mu(n; r_0, \delta) = r_0 n - \delta n^2$ and $\nu(n; \sigma_e^2) = \sigma_e^2 n^2$, the rate of the inhomogeneous Poisson process is proportional to a gamma distribution (Engen and Lande, 1996b)

$$\lambda(n; \beta, \delta, s, \sigma_e^2) = \frac{2\beta}{\sigma_e^2} e^{2\delta/\sigma_e^2} n^{2s/\sigma_e^2 - 1} e^{-(2\delta/\sigma_e^2)n} \tag{6}$$

where $s = r_0 - \sigma_e^2/2$. Assuming the heterogeneity in the community can be described by the density dependence $\delta$ being gamma distributed with shape $k$ and scale $1/\alpha$, the abundance distribution is equal to Equation (5) (Engen, 2007a), where $p = 2s/\sigma_e^2$, $q = k - 2s/\sigma_e^2$ and $b = 1/(\alpha \sigma_e^2/2 - 1)$. Furthermore, the distribution of $\delta$ due to parameter sampling $\pi^*(\delta)$ is gamma distributed with shape $q$ and scale $b\sigma_e^2/2$. The variation in $\delta$ generates variation in both the carrying capacity, $\mathrm{E}[n] = s/\delta$, and the environmental fluctuations $\mathrm{Var}[n] = s\sigma_e^2/(2\delta^2)$ among species, compared to heterogeneity in the lognormal distribution where the heterogeneity only generated variation among species in the carrying capacity.

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*2.6. Beta prime abundance models with heterogeneity among species*

351    Equal beta prime distributions can be obtained by keeping the param-

352 eters $p$, $q$ and $b$ fixed for different distributions of $\delta$. For instance, given a

353 Beverton-Holt model with a set of parameter values $\theta = (b, c, s_a, \sigma_e^2)$ results

354 in a beta prime distribution with values of $p$, $q$ and $b$. A logistic model with

355 heterogeneity in the density dependence $\delta$, which is sampled from $\pi^*(\delta)$, can

356 have the same abundance distribution if $k = q + p$, while for instance, a given

357 $\sigma_e^2$ determines the other parameter values through $\alpha = 2(1 + 1/b)/\sigma_e^2$ and

358 $s = p\sigma_e^2/2$. Figure 4 illustrates one homogeneous Beverton-Holt model and

359 two heterogeneous logistic models, all with the same abundance distribution.

360 In the homogeneous community, all species have the same carrying capacity

361 (first row, first column), while the heterogeneous communities have the same

362 distribution for carrying capacity, $K = s/\delta$. The environmental variance is

363 the same in the homogeneous and the first heterogeneous community (first

364 row, first and second column), while the last community (third column) have

365 only 10% of the same $\sigma_e^2$. The difference in both E[$n$] and Var[$n$] due to het-

366 erogeneity in $\delta$, i.e. small $\delta$ gives larger mean and variance, is very noticeable

367 from the individual species' stationary distributions (first row, second and

368 third column).

369    Even with the same environmental variance, the difference in temporal

370 fluctuations of individual species between communities is significant (second

371 row). In the homogeneous community, species can fluctuate over the en-

372 tire range of the abundance distribution (first column), while in the hetero-

373 geneous community (second column), each individual population fluctuates

374 rapidly within the range its own stationary distribution. In the second het-

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erogeneous community (third column), the species fluctuate within similar stationary distributions as the first heterogeneous community, but the density dependence is much weaker and the perturbations away from carrying capacity last longer. The abundance distribution at a fixed time point (third row) for all three examples are similar and do not reveal the difference in temporal dynamics between the communities.

*2.7. Beta prime abundance models and gradual change in carrying capacity*

A permanent change in the environment resulting in a gradual change in carrying capacity, i.e. $(c + s_a - 1 - \sigma_e^2/2)/[b(1 - s_a)]$ for the Beverton-Holt model and $s/\delta$ in the logistic model, can be modelled by replacing $b$ with $b(1/\kappa)^t$ and $\delta$ with $(s + \sigma_e^2)/(K'\kappa^t)$, respectively, where $K'$ is the carrying capacity in the deterministic model. If $\kappa < 1$, the density dependence increases and the carrying capacity decreases for all species in the community.

Figure 5 illustrates the gradual decline in carrying capacity due to increasing density dependence, for three different communities (Fig 5a). These communities have the same initial parameter values as those introduced in Figure 4, with one homogeneous Beverton-Holt model (first column) and two heterogeneous logistic models with the same environmental variance as the Beverton-Holt model (second column) or 10% of the environmental variance (third column). Some characteristics from the previous examples are also present here: species in the Beverton-Holt model have large fluctuations due to large environmental variance and weak density dependence, while the species of the heterogeneous communities trace their individual carrying capacities. For all communities the species specific environmental variation decreases as a result of the increasing density dependence.

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The number of species $S$ only declines for the heterogeneous community with large environmental variance (Fig 5b and 6), while the number is constant for almost 200 time steps in the other two communities. Then there is a rapid decline in the number of species, where the entire community goes extinct within roughly 100 time steps. The number of species above 10% of their initial abundance (Fig 5b, second column) has a pattern similar to the one obtained for the lognormal abundance models. The homogeneous model declines first, due to large environmental fluctuations and weak density dependence, while the heterogeneous communities declines faster when the carrying capacity has been reduced by 90%, which the species in the heterogeneous communities trace closely. The threshold for the observable species is in fact so low that all species are included initially, but looking closer at the first 100 time steps reveals considerable differences between the communities (Fig 6). The heterogeneous community with the highest environmental variance is expected to have the most unobservable species. On the other hand, the homogeneous community is expected to loose slightly more observable species the first 75 time steps than the heterogeneous community with small environmental variance.

The total abundance, $N$, again has the fastest response to the decreasing carrying capacity, the homogeneous community being the slowest due to a few species that overshoot due to weak density dependence and large environmental variance (Figure 5c). In roughly 50 time steps $N$ has been halved, the heterogeneous community with large environmental variance declining the fastest. In contrast to the lognormal model, the Shannon diversity, $D_{Shannon}$, is not equal for the three communities very long and the

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homogeneous community declines faster than the heterogeneous community with small environmental variance, similar to the changes in $S$. The modified Shannon diversity, $D_{Mod-Shannon}$, respond again faster than most of the other indices and heterogeneous models change most rapidly. Overall, there are smaller differences between the homogeneous and heterogeneous communities in the examples of beta prime abundance distributions compared to the lognormal, but the patterns are similar for communities with the same environmental variance, i.e. the heterogeneous communities respond faster to changes.

## 3. Discussion

While some abundance models which assume homogeneity among species can fit the shape of observed abundance distributions and describe the dynamics of certain communities, such as the neutral model for e.g. tropical trees (Hubbell, 2001), models with environmental noise, and in particular heterogeneous models, provide a more flexible framework for describing temporal fluctuations in very different taxa. For communities consisting of species from the same taxon, heterogeneity among species have been demonstrated in e.g. butterflies, birds and aquatic insects and the estimated heterogeneity accounts for $60 - 80\%$ of the variance in the lognormal species abundance distribution (Engen et al., 2002; Lande et al., 2003; Sæther et al., 2005; Engen et al., 2011). The examples from the lognormal abundance distribution (Figure 1) show that in order to obtain an abundance distribution with a reasonable variance, the homogeneous model must either have a large environmental variance or a weak density regulation. In order to make the

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dynamics as comparable as possible, the environmental variance in the lognormal models (Figure 1 and 2) was the same for both the homogeneous and heterogeneous models. With equal environmental variance, the strength of density regulation for the homogeneous community had to be 0.005 in order to obtain a variance in log abundance of 4. The strength of density regulation of the homogeneous community corresponds to a mean return time to equilibrium of 200 time steps (e.g. years). Compared to the first heterogeneous community (Fig 1, second column), the same variance in log abundance was obtained with a strength of density dependence equal to 0.2 or a mean return time to equilibrium of 5 time steps. The difference in temporal dynamics between the homogeneous and heterogeneous lognormal model is huge, but the abundance distribution cannot separate between the two. When analysing the consequence of a permanent change of the environment that reduces the carrying capacity of the species in the community, the time frame of the species' responses could differ by hundreds of years (Figure 2), depending on the assumption of homogeneity or heterogeneity (Solbu et al., 2013).

With available species community data collected over time, the amount of heterogeneity in the community can readily be estimated for the lognormal abundance model and has been shown to be the major component of the variance in the lognormal species abundance distribution (Engen et al., 2002, 2011). A good starting point for studying communities is therefore to assume that species are heterogeneous and infer from the estimated variation between species whether this effect is significant, instead of not considering heterogeneity at all.

The time frames considered in the simulations of gradual change in carry-

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ing capacity for the lognormal and beta prime abundance distribution (Figure 2 and 5), suggest that it may take a long time before changes in species composition are detected. However, the expected loss of species the first 100 time steps (Figure 3 and 6) reveals considerable differences between the homogeneous and heterogeneous community models even at these 'early' stages. The loss of even a few species can be critical to a community. For instance, two species are extinct in the homogeneous lognormal distribution after 50 time steps compared to five species in the heterogeneous community with strong density regulation (Fig. 3). After 100 time steps their expected losses are five and 15 species, respectively, while the expected number of unobservable species is much larger. Although the boundary defined for species being observable is usually unknown, it can give an indication of how much the number of observed species could change, while the true species number serves as a lower bound. Applying species abundance models which provide realistic rates of extinction is essential when studying consequences of anthropogenic activity, from a conservation biology point of view.

The reduction in total abundance is an immediate response to the change in species' carrying capacity, especially for communities with strong density dependence. While total abundance is an important factor for ecosystem services, such as pollen grain deposits (Winfree et al., 2015), it contains no information about change in community structure. The modified Shannon diversity is designed to change with both abundance and community structure (Buckland et al., 2005). The rapid decline in $D_{Mod-Shannon}$ is caused by the reduction in total abundance compared to the initial abundance. If the relative abundance of species is calculated within each year, as the Shan-

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non diversity, little change in relative abundance is expected until a large proportion of the species are extinct. Recent estimation techniques for relative abundance (Chao et al., 2015) could improve estimates of $D_{Mod-Shannon}$, making it a desirable metric to monitor community changes.

Demographic variance is not included in the analysis, and while it would reduce the time to extinction, it would not change the main results regarding differences between homogeneous and heterogeneous communities. The dynamical species abundance models used here assume that the dynamics of each species is independent of other species, but variation in abundance due to interspecific interactions have been found to be small in communities of different taxa (Mutshinda et al., 2009). Changes in the community could have been described by stochastic variation common to all species, in addition to the species specific environmental variation (Sæther et al., 2013). Long term data sets of communities are necessary to study changes, both by natural and anthropogenic causes (Magurran et al., 2010), as snapshots of species abundance distributions provide no information about the temporal dynamics. Changes in community structure due to habitat changes have been found in long term data sets of bird communities, and their response to changes are diverse (Tingley and Beissinger, 2013). The current analysis show that community models assuming heterogeneity can explain the potential large variation in species abundances while maintaining reasonable individual dynamics. Heterogeneous models can also provide realistic responses to changes on a temporal scale, comparable to the dramatic changes of species richness observed in modern history.

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## Acknowledgments

Buckland, S., Magurran, A., Green, R., Fewster, R., 2005. Monitoring change in biodiversity through composite indices. Philosophical Transactions of the Royal Society B: Biological Sciences 360 (1454), 243–254.

Butchart, S. H., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P., Almond, R. E., Baillie, J. E., Bomhard, B., Brown, C., Bruno, J., et al., 2010. Global biodiversity: indicators of recent declines. Science 328 (5982), 1164–1168.

Chao, A., Hsieh, T., Chazdon, R. L., Colwell, R. K., Gotelli, N. J., 2015. Unveiling the species-rank abundance distribution by generalizing the goodturing sample coverage theory. Ecology 96 (5), 1189–1201.

Engen, S., 2007a. Heterogeneity in dynamic species abundance models: the selective effect of extinction processes. Mathematical Biosciences 210 (2), 490–507.

Engen, S., 2007b. Heterogeneous communities with lognormal species abundance distribution: species–area curves and sustainability. Journal of Theoretical Biology 249 (4), 791–803.

Engen, S., Aagaard, K., Bongard, T., 2011. Disentangling the effects of heterogeneity, stochastic dynamics and sampling in a community of aquatic insects. Ecological Modelling 222 (8), 1387–1393.

Engen, S., Lande, R., 1996a. Population dynamic models generating the lognormal species abundance distribution. Mathematical Biosciences 132 (2), 169–183.

551 Engen, S., Lande, R., 1996b. Population dynamic models generating species
552     abundance distributions of the gamma type. Journal of Theoretical Biology
553     178 (3), 325–331.

554 Engen, S., Lande, R., Walla, T., DeVries, P. J., 2002. Analyzing spatial struc-
555     ture of communities using the two-dimensional poisson lognormal species
556     abundance model. The American Naturalist 160 (1), 60–73.

557 Fisher, R. A., Corbet, A. S., Williams, C. B., 1943. The relation between the
558     number of species and the number of individuals in a random sample of
559     an animal population. The Journal of Animal Ecology, 42–58.

560 Gotelli, N. J., Colwell, R. J., 2011. Estimating species richness. In: Magurran,
561     A. E., McGill, B. J. (Eds.), Biological Diversity: Frontiers in measurement
562     and assessment. Oxford University Press, Oxford, Ch. 4.

563 Hubbell, S. P., 2001. The unified neutral theory of biodiversity and biogeog-
564     raphy. Vol. 32. Princeton University Press.

565 Kempton, R., 1975. A generalized form of fisher's logarithmic series.
566     Biometrika 62 (1), 29–38.

567 Kneitel, J., Pages, C., 2010. Successional changes in communities. Nature
568     Education Knowledge 1 (8), 36.

569 Lande, R., Engen, S., Saether, B.-E., 2003. Stochastic population dynamics
570     in ecology and conservation. Oxford University Press Oxford.

571 Magurran, A. E., Baillie, S. R., Buckland, S. T., Dick, J. M., Elston, D. A.,
572     Scott, E. M., Smith, R. I., Somerfield, P. J., Watt, A. D., 2010. Long-

term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends in Ecology & Evolution 25 (10), 574–582.

Maurer, B. A., McGill B. J., 2011. Measurement of species diversity. In: Magurran, A. E., McGill, B. J. (Eds.), Biological Diversity: Frontiers in measurement and assessment. Oxford University Press, Oxford, Ch. 5.

May, R. M., 1981. Theoretical Ecology. 2nd ed., Blackwell Scientific Publications.

McGill, B. J., 2011. Species abundance distributions. In: Magurran, A. E., McGill, B. J. (Eds.), Biological Diversity: Frontiers in measurement and assessment. Oxford University Press, Oxford, Ch. 9.

Mutshinda, C. M., O'Hara, R. B., Woiwod, I. P., 2009. What drives community dynamics? Proceedings of the Royal Society of London B: Biological Sciences 276 (1669), 2923–2929.

Preston, F. W., 1948. The commonness, and rarity, of species. Ecology 29 (3), 254–283.

Sæther, B.-E., Engen, S., Møller, A. P., Visser, M. E., Matthysen, E., Fiedler, W., Lambrechts, M. M., Becker, P. H., Brommer, J. E., Dickinson, J., et al., 2005. Time to extinction of bird populations. Ecology 86 (3), 693–700.

Sæther, B.-E., Engen, S., Grøtan, V., 2013. Species diversity and community similarity in fluctuating environments: parametric approaches using

species abundance distributions. Journal of Animal Ecology 82 (4), 721–738.

Solbu, E. B., Engen, S., Diserud, O. H., 2013. Changing environments causing time delays in population dynamics. Mathematical Biosciences 244 (2), 213–223.

Stuart, A., Kendall, M. G., 1968. The advanced theory of statistics. Hafner Publishing Company.

Tingley, M. W., Beissinger, S. R., 2013. Cryptic loss of montane avian richness and high community turnover over 100 years. Ecology 94 (3), 598–609.

Winfree, R., W Fox, J., Williams, N. M., Reilly, J. R., Cariveau, D. P., 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecology letters.

608  FIGURE 1. Heterogeneity in the stochastic growth rate. **First row:** The
609  species' stationary distribution (solid lines) and the distribution of log carry-
610  ing capacities (dashed lines). The first column is a homogeneous Gompertz
611  model with parameters $s = 0.025$ and $\gamma = 0.005$. The second column is a
612  heterogeneous Gompertz model where $s$, after parameter sampling, is nor-
613  mally distributed with mean 1 and variance 0.156 and $\gamma = 0.2$. In the third
614  column $s$ has mean 0.137 and variance 0.00247 and $\gamma = 0.0275$. For all com-
615  munities $\sigma_e^2 = 0.04$. Five single species' stationary distributions are selected,
616  although for the homogeneous community these are all equal. **Second row:**
617  All the species' fluctuations over time. The total number of species in each
618  community is 200. **Third row:** The log abundance at the time point indi-
619  cated by the vertical red lines for the three communities in addition to the
620  theoretical distribution, which is normal with expectation $\eta = 10$ and vari-
621  ance $\rho^2 = 5$. The dots indicate the highlighted species from the time series
622  plot and distributions in the first row.

623  FIGURE 2. Permanent change in environment of lognormal abundance dis-
624  tributions.

625  (A) The species' fluctuations over time for a each community. The initial
626  parameter values for the three different communities are the same as those
627  described in Figure 1. The carrying capacity for each species is reduced by
628  a multiplicative factor $\kappa = 0.98$.

629  (B) The lines are mean values from 200 simulated communities, where solid
630  lines are the homogeneous Gompertz model, and dashed and dotted lines
631  are heterogeneous Gompertz models with $\gamma = 0.2$ and 0.0275, respectively.

632 The shaded area around the lines is the 95% quartile range of the simu-

633 lated communities. The indices are: total number of species $(S)$, number of

634 species above 10% of their initial abundance $(S_Q)$, number of species above

635 an observable threshold $(S_{Obs})$.

636 (C) Same as in (B), but indices are total abundance $(N)$, Shannon diversity

637 $(D_{Shannon})$ and the modified Shannon diversity $(D_{Mod-Shannon})$.

638 FIGURE 3. The solid lines are the homogeneous models, while the dashed

639 and dotted lines are heterogeneous models as described in Figure 2. **Left:**

640 Expected number of species extinct within the first 100 time steps for the

641 lognormal abundance distributions when the carrying capacity is reduced by

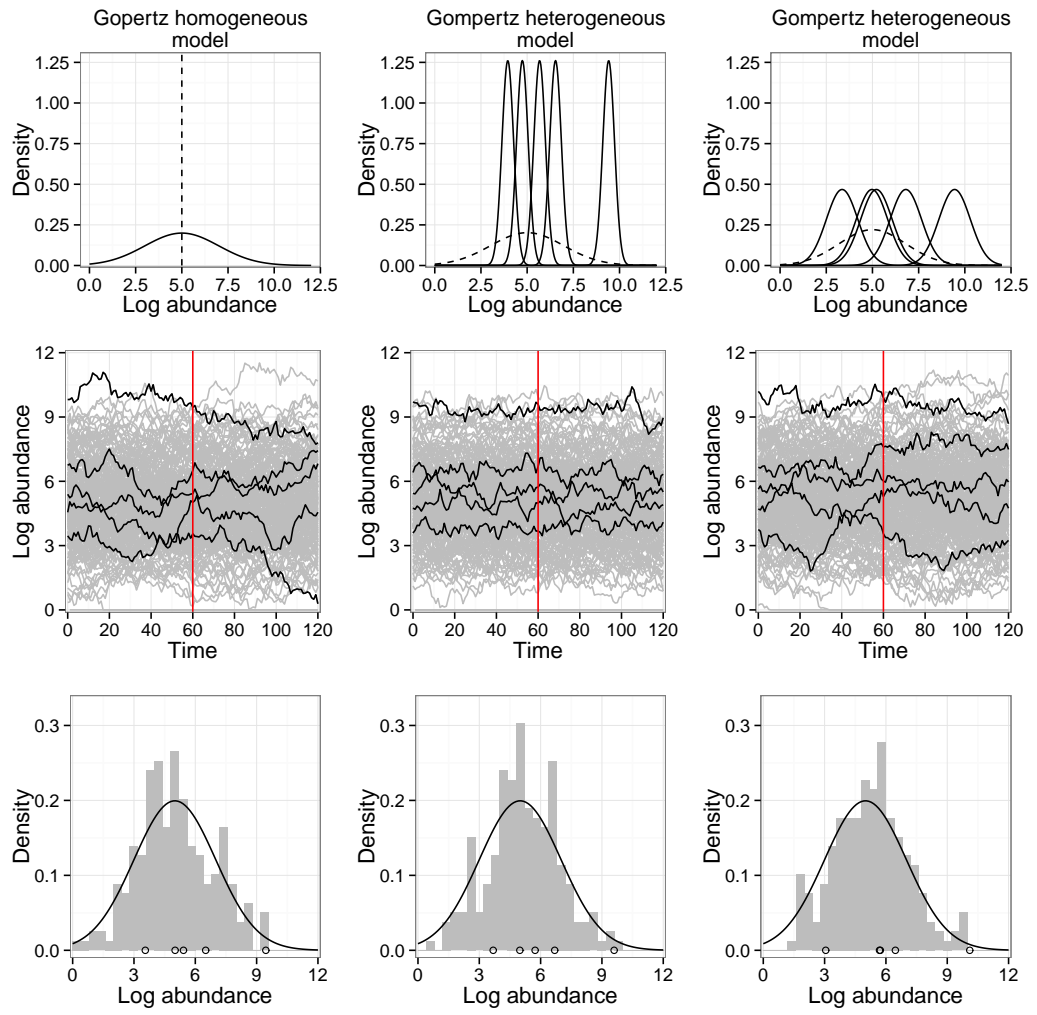642 2% each time step. **Right:** Expected number of unobserved species.

643 FIGURE 4. Heterogeneity in the density regulation. **First row:** The species'

644 stationary distributions (solid lines) and the distribution of carrying capaci-

645 ties (dashed lines). The first column is a homogeneous Beverton-Holt model

646 with parameter values $a_s = 0.95$, $b = 0.1$, $c = 1$, and $\sigma_e^2 = 0.04$. The second

647 column is a heterogeneous logistic model where $\delta$ is gamma distributed with

648 shape $q = 3.5$ and scale $1/(\alpha - 2/\sigma_e^2) = 0.002$, so that $\mathrm{E}[\delta] = 0.007$, while

649 the other parameters are $s = 0.93$ and $\sigma_e^2 = 0.04$. In the third column $\delta$ has

650 scale 0.0002, so that $\mathrm{E}[\delta] = 0.0007$, while the other parameters are $s = 0.093$

651 and $\sigma_e^2 = 0.004$. Five species' stationary distributions are selected, although

652 for the homogeneous community these are all equal. **Second row:** The

653 species' fluctuations over time. The total number of species in each com-

654 munity is 200. **Third row:** The abundance at the time point indicated by

655 the vertical red line for the three communities in addition to the theoretical

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distribution, which is beta prime with expectation $E[n] = 186$ and variance $Var[n] = 23064$. The dots indicate the highlighted species from the time series plot and distributions in the first row.

FIGURE 5. Permanent change in environment of beta prime abundance distributions.

(A) The species' fluctuations over time for each community. The initial parameter values for the three communities are the same as those described in Figure 4. The carrying capacity for each species is reduced by a multiplicative factor $\kappa = 0.98$.

(B) The lines are mean values from 200 simulated communities, where solid lines are the homogeneous Beverton-Holt model, and dashed and dotted lines are heterogeneous logistic models with $E[\delta] = 0.007$ and $0.0007$, respectively. The shaded area around the lines are the $95\%$ quartile range of the simulated communities. The indices are: total number of species ($S$), number of species above $10\%$ of their initial abundance ($S_Q$), number of species above an observable threshold ($S_{Obs}$).

(C) Same as in (B), but indices are total abundance ($N$), Shannon diversity ($D_{Shannon}$) and the modified Shannon diversity ($D_{Mod-Shannon}$).

FIGURE 6. The solid lines are the homogeneous models, while the dashed and dotted lines are heterogeneous models as described in Figure 5. **Left:** Expected number of species extinct within the first 100 time steps for the beta prime abundance distributions when the carrying capacity is reduced by $2\%$ each time step. **Right:** Expected number of unobserved species.
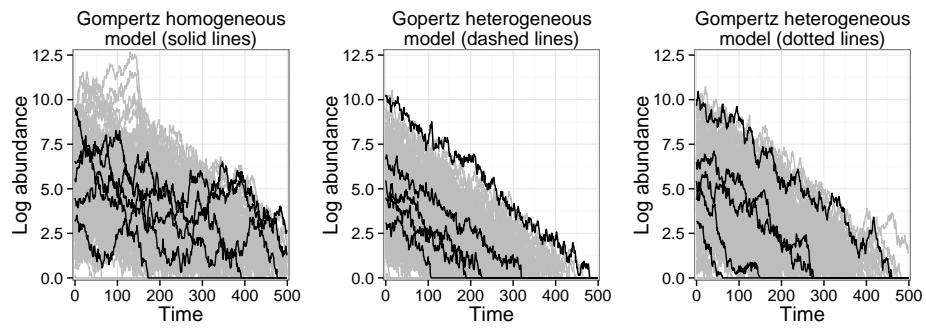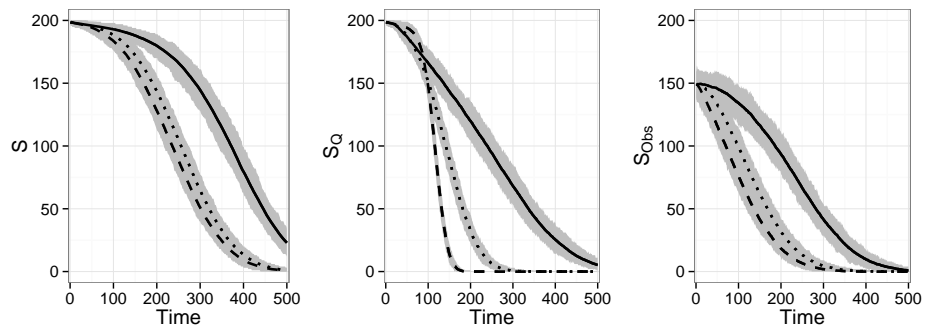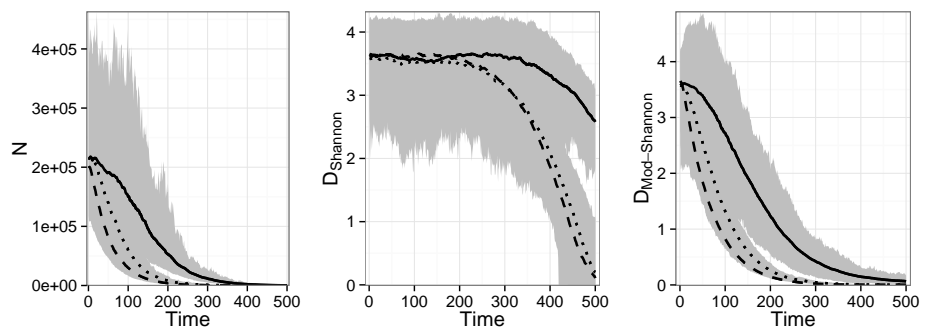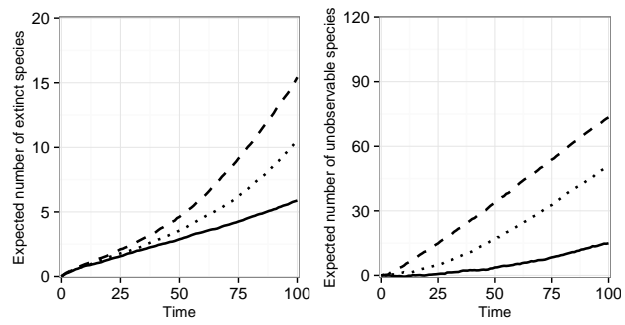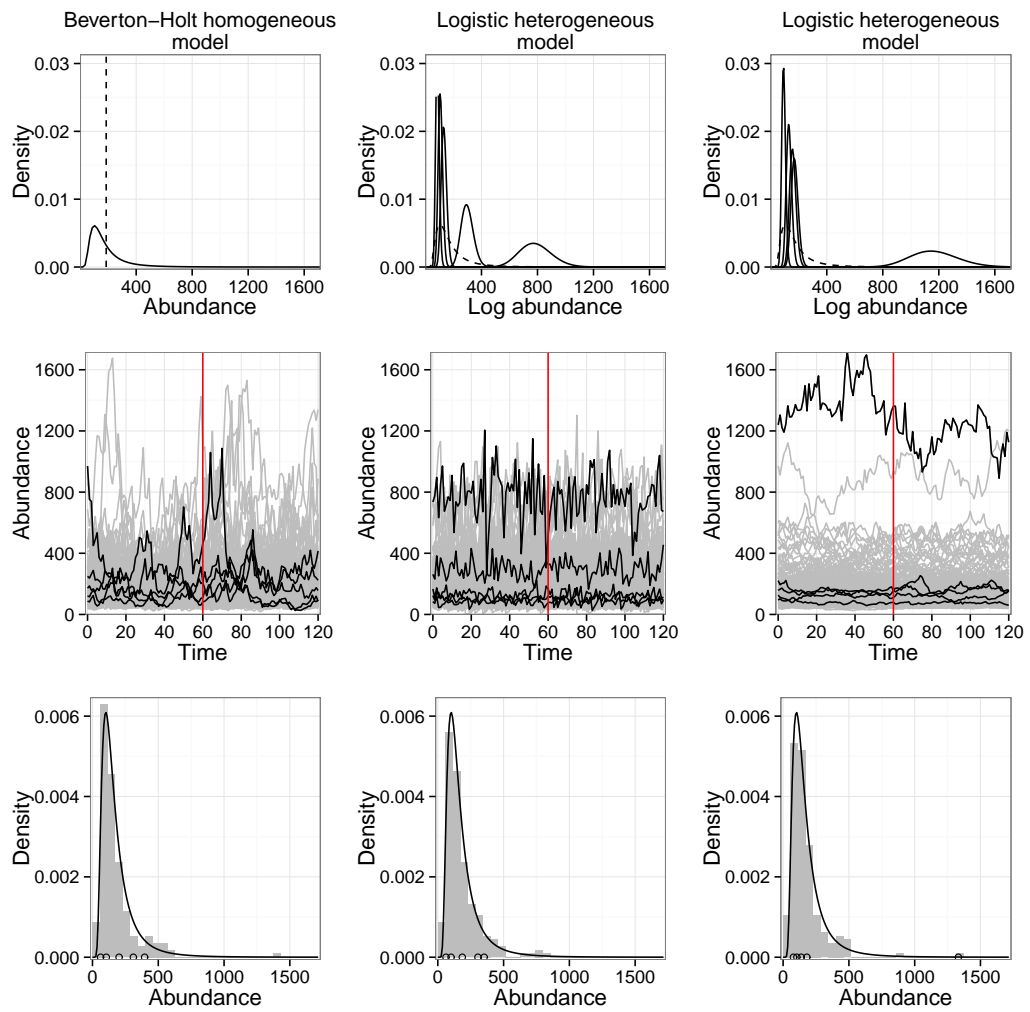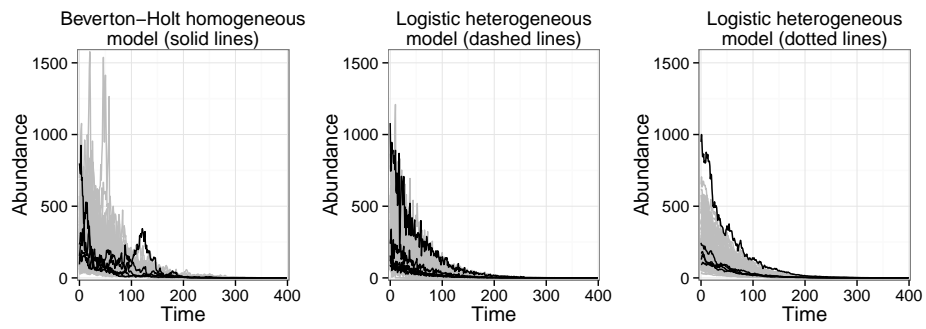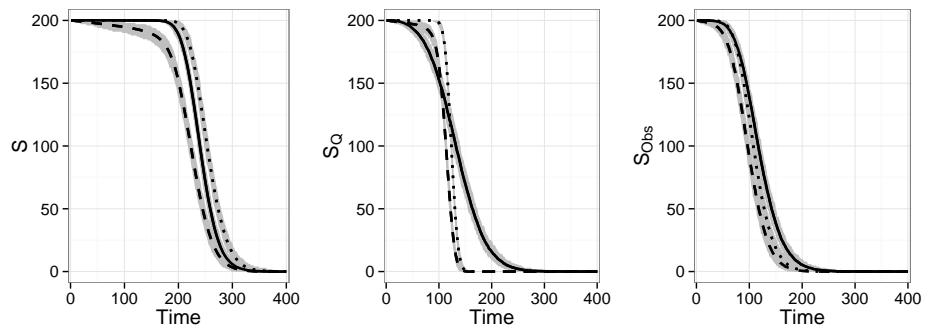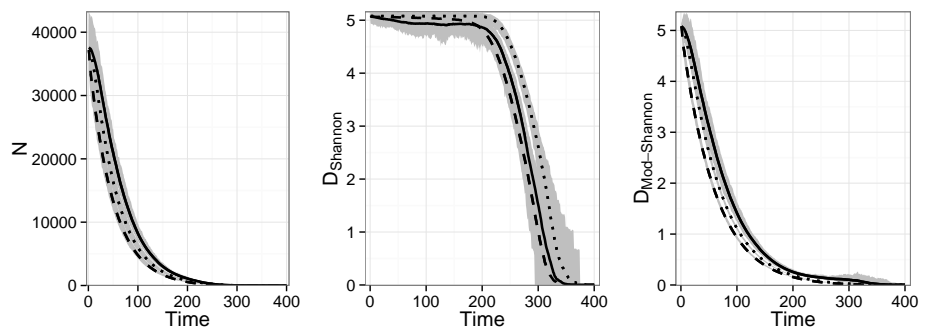
Figure 1

(a)



(b)



(c)

Figure 2

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Figure 3

Figure 4

Figure 5

Figure 6