

On-Line Supplementary Material for

“Do fitness-equalizing tradeoffs lead to neutral communities?”

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Citation for article:

Ostling (2011) Do fitness-equalizing tradeoffs lead to neutral communities? *Theoretical Ecology* ...

Appendix S1: Derivation of Eq. 12

Here I show in detail how to derive Eq. 12 from Eq. 11 in the main text by converting the sum over species k into an integral over types T' and using Eq. 10 in the main text:

$$\begin{aligned} p_T(t) &= \sum_{configs} \sum_k \rho(n_k, T_k, T) P(n_1, \dots, n_s, t) \\ &= \nu \sum_{configs} \sum_k f_{T_k}^{loss} \rho'(T_k, T) n_k P(\vec{n}, t) \\ &= \nu \sum_{configs} \sum_k \int dT' \delta(T_k - T') f_{T'}^{loss} \rho'(T', T) n_k P(\vec{n}, t) \\ &= \nu \int dT' f_{T'}^{loss} \rho'(T', T) \sum_k \delta(T_k - T') \sum_{configs} n_k P(\vec{n}, t) \\ &= \nu \int dT' f_{T'}^{loss} \rho'(T', T) \sum_k \delta(T_k - T') E[n_k(t)] \\ &= \nu \int dT' f_{T'}^{loss} \rho(T', T) N_{T'}(t), \end{aligned} \tag{1}$$

where $N_{T'}(t) = \sum_k \delta(T_k - T') E[n_k(t)]$.

Appendix S2: Derivation of Eq. 14 in main text

In the main text I began my treatment of the tradeoff community by writing down a differential equation for the joint distribution, $P(n_1, n_2, \dots, n_S, t)$, defined as the probability for the community to have the configuration $\{n_1, n_2, \dots, n_S\}$, where n_k is the abundance of species k , and the time t is the time since species 1 speciated. Implicit in the configuration of the community is the type of each species, $\{T_1, \dots, T_S\}$. The differential equation I wrote down was:

$$\begin{aligned} \frac{dP(n_1, \dots, n_S, t)}{dt} = & \sum_k l_{n_k+1}^k P(n_1, \dots, n_k + 1, \dots, t) \\ & + \sum_k g_{n_k-1}^k P(n_1, \dots, n_k - 1, \dots, t) \\ & - \sum_k (l_{n_k}^k + g_{n_k}^k) P(n_1, \dots, n_k, \dots, t) \\ & + \sum_k \rho(n_k + 1, \vec{T}_k, \vec{T}_S) \delta_{n_S, 1} P(n_1, \dots, n_k + 1, \dots, n_{S-1}, t) \\ & - \sum_k \sum_{\vec{T}_{S+1}} \rho(n_k, \vec{T}_k, \vec{T}_{S+1}) P(n_1, \dots, n_k, \dots, n_S, t). \end{aligned} \quad (2)$$

As mentioned in the text, the probability for a species of type T to have abundance n at time t , $P_T(n, t)$ is obtained from the distribution $P(n_1, n_2, \dots, n_S, t)$, by summing over the configurations of species other than species 1:

$$P_T(n, t) = \sum_{configs} P(n_1, \dots, n_S, t) \delta_{n_1, n}, \quad (3)$$

where the $\sum_{configs}$ is the sum over all possible configurations of the community, but with the implicit constraint that the type of species 1 is fixed at T (actually all of the species that were present at $t = 0$, when species 1 speciated are fixed in type in the sum over configurations). I then provided a differential equation for this partial distribution under a “non-interactive” approximation and using the speciation dynamics as modelled in the main text. This differential equation can be obtained carrying out this sum on both sides of the differential equation for the joint distribution. Here I provide the details of the derivation of the differential equation for the partial distribution (Eq. 12 in the main text).

Note that the $\sum_{configs}$ includes the sum over all possible values for the number of species in the community configuration, integration over the possible types (presuming T varies continuously) for all species that were not present when species 1 speciated ($t = 0$), and a sum over the possible abundances for all the

species. In other words:

$$\sum_{S=S_0}^N \left(\int_{T_{S_0+1}} dT_{S_0+1} \dots \int_{T_S} dT_S \right) \sum_{n_1=0}^N \dots \sum_{n_S=0}^N \quad (4)$$

where S_0 is the number of species that were present at time $t = 0$, including species 1. Applying this sum to both sides of Eq. 2 gives (note that I have already applied $\delta_{n_1,n}$)

$$\begin{aligned} \frac{dP_T(n, t)}{dt} = & \sum_{S=S_0}^N \left(\int_{T_{S_0+1}} dT_{S_0+1} \dots \int_{T_S} dT_S \right) \sum_{n_2=0}^N \dots \sum_{n_S=0}^N \\ & \{ l_{n+1}^1 P(n+1, \dots, n_S, t) + g_{n-1}^1 P(n-1, \dots, n_S, t) - (l_n^1 + g_n^1) P(n, \dots, n_S, t) \\ & + \rho(n+1, T, T_S) P(n+1, \dots, n_{S-1}, t) \delta_{n_S,1} - \sum_{T_{S+1}} \rho(n, T, T_{S+1}) P(n, \dots, n_S, t) \} \\ + & \sum_{S=S_0}^N \left(\int_{T_{S_0+1}} dT_{S_0+1} \dots \int_{T_S} dT_S \right) \sum_{n_2=0}^N \dots \sum_{n_S=0}^N \sum_{k=2}^S \\ & \{ l_{n_k+1}^k P(n, \dots, n_k+1, \dots, n_S, t) + g_{n_k-1}^k P(n, \dots, n_k-1, \dots, n_S, t) - (l_{n_k}^k + g_{n_k}^k) P(n, \dots, n_k, \dots, n_S, t) \\ & + \rho(n_k+1, T_k, T_S) P(n, \dots, n_k+1, \dots, n_{S-1}, t) \delta_{n_S,1} - \sum_{T_{S+1}} \rho(n_k, T_k, T_{S+1}) P(n, \dots, n_k, \dots, n_S, t) \} \quad (5) \end{aligned}$$

Regardless of whether one takes the non-interactive approximation or not, it turns that all of the terms $k > 1$ (i.e. the second of the two major terms in the above) cancel out. I'll focus on those terms now to show this. The sum over k is interchangeable with the integrals over types and sums over abundances, and we can bring the sum over n_k to the right to obtain

$$\begin{aligned} & \sum_{S=S_0}^N \sum_{k=2}^S \left(\int_{T_{S_0}} dT_{S_0} \dots \int_{T_S} dT_S \right) \sum_{\{n_i\}_{i \neq k}=0}^N \left\{ \sum_{n_k=0}^N l_{n_k+1}^k P(n, \dots, n_k+1, \dots, n_S, t) \right. \\ & \quad + \sum_{n_k=0}^N g_{n_k-1}^k P(n, \dots, n_k-1, \dots, n_S, t) \\ & \quad - \sum_{n_k=0}^N l_{n_k}^k P(n, \dots, n_k, \dots, n_S, t) \\ & \quad \left. - \sum_{n_k=0}^N g_{n_k}^k P(n, \dots, n_k, \dots, n_S, t) \right\} \\ + & \sum_{S=S_0}^N \sum_{k=2}^S \left(\int_{T_{S_0+1}} dT_{S_0+1} \dots \int_{T_S} dT_S \right) \sum_{\{n_i\}_{i \neq k}=0}^N \sum_{n_k=0}^N \rho(n_k+1, T_k, T_S) P(n, \dots, n_k+1, \dots, n_{S-1}, t) \delta_{n_S,1} \\ & - \sum_{S=S_0}^N \sum_{k=2}^S \left(\int_{T_{S_0+1}} dT_{S_0+1} \dots \int_{T_S} dT_S \right) \sum_{\{n_i\}_{i \neq k}=0}^N \sum_{n_k=0}^N \sum_{T_{S+1}} \rho(n_k, T_k, T_{S+1}) P(n, \dots, n_k, \dots, n_S, t) \quad (6) \end{aligned}$$

In the first grouping of terms, the first term (the l_{n_k+1} term) can be shown to cancel with the third term (the l_{n_k} term) by setting the summation variable in the first term to $n_{k'} = n_k + 1$, adjusting the limits of summation, and then noting that the $n_{k'} = N + 1$ term in the first term is zero and that the $n_k = 0$ term of the third term is also 0, and hence these two sums are actually identical in magnitude but opposite in sign. A similar trick can be used to show that the second and fourth terms cancel. The last two major terms also cancel, which can be seen by setting the species richness summation variable to $S' = S - 1$ and the abundance summation variable to $n_{k'} = n_k + 1$ in the second to last term, and then noting that any terms with $S' = S_0 - 1$ or $n_{k'} = N + 1$ are zero, and hence that the two terms are the same in magnitude but opposite in sign.

The $k = 1$ terms are essentially Eq. 12 from the main text. Under the non-interactive approximation is clear that the birth-death $k=1$ terms (i.e. all but the last two $k=1$ terms) simply become

$$l_{n+1}^1 P_T(n+1, t) + g_{n-1}^1 P_T(n-1, t) - (l_n^1 + g_n^1) P(n, t). \quad (7)$$

This is because under this approximation the transition rates $l_n^1 = g_n^1 \approx T_1 n$ depend only on the abundance of species 1, and hence they can be factored out of the sum over configurations, and that sum is just applied to the $P(n, n_2, \dots, n_s, t)$ leading to the partial distribution according to Eq. 3. A similar thing happens with the speciation $k = 1$ terms. Since as explained in the main text I assume $\rho(n, T, T_s) = f_T^{loss} \nu n \rho'(T, T_s)$, the first part of these transition rates also factors out of the sum over configurations, leaving:

$$f_T^{loss} \nu(n+1) \sum_{configs} \rho'(T, T_S) P(n+1, \dots, n_{S-1}, t) \delta_{n_S, 1} - f_T^{loss} \nu n \sum_{configs} \sum_{T_{S+1}} \rho'(T, T_{S+1}) P(n, \dots, n_S, t). \quad (8)$$

The sum over configurations in the first of these terms involves a sum_{T_S} . Since $\sum_{T_S} \rho'(T, T_S) = 1$ in the first term, and $sum_{T_{S+1}} \rho'(T, T_{S+1}) = 1$ in the second term, these terms become simply

$$f_T^{loss} \nu(n+1) P_T(n+1, t) - f_T^{loss} \nu n P_T(n, t). \quad (9)$$

Combining these with the birth death terms leads to Eq 12 from the main text.

Appendix S3: Derivation of Eq. 18 in main text

Then, from the differential equation for the partial distribution, I derived a differential equation for the species abundance distribution of each type, where analogous to in the neutral case, that species abundance distribution is related to the partial distribution by

$$S_T(n, t) \approx p_T \int_0^t dt' P_T(n, t - t') \quad (10)$$

Carrying out this integration on both sides of Eq. 12 from the main text leads to

$$p_T \int_0^t dt' \frac{dP_T(n, u)}{du} = w_{n+1}^T S(n+1, t) + g_{n-1}^T S(n-1, t) - (w_n^T + g_n^T) S(n, t) \quad (11)$$

where $u = t - t'$. Transforming variables using $dt' = -du$ the integral on the left becomes

$$-p_T \int_t^0 du \frac{dP_T(n, u)}{du} = -p_T (P_T(n, 0) - P_T(n, t)) = -p_T \delta_{n,1} + p_T P_T(n, t) = -p_T \delta_{n,1} + \frac{dS_T(n, t)}{dt} \quad (12)$$

where the last equality can be seen by using the Fundamental Theorem of Calculus ($f(x) = \frac{d}{dx} \int_0^x dy f(y)$) (Spivak, 1980):

$$\begin{aligned} \frac{dS_T(n, t)}{dt} &= p_T \frac{d}{dt} \int_0^t dt' P_T(n, t - t') \\ &= p_T \frac{d}{dt} \int_0^t du P_T(n, u) \\ &= p_T P_T(n, t) \end{aligned} \quad (13)$$

where the substitution $u = t - t'$ was used in the second line. Hence I arrive at the following set of differential equations for the SAD:

$$\frac{dS_T(n, t)}{dt} = w_{n+1}^T S_T(n+1, t) + g_{n-1}^T S_T(n-1, t) - (w_n^T + g_n^T) S_T(n, t) + \delta_{n,1} p_T \quad (14)$$

This is Eq. 16 in the main text. The equilibrium solution to this differential equation has the following properties:

$$\begin{aligned} w_{n+1}^T S_T(n+1) - g_n^T S_T(n) &= w_n^T S_T(n) - g_{n-1}^T S_T(n-1) \\ &= \dots \end{aligned}$$

$$\begin{aligned}
&= w_2^T S_T(2) - g_1^T S_T(1) \\
&= w_1^T S_T(1) - p_T = 0
\end{aligned}$$

The last equality arises because the total number of species of each type must be in equilibrium. That this is the correct equality can be seen in a way analogous to the neutral case above, i.e. by obtaining a differential equation for the total number of species of type T and setting it equal to 0. These equations imply the recursive relations:

$$\begin{aligned}
S_T(1) &= \frac{p_T}{w_1^T} \\
S_T(2) &= \frac{g_1^T}{w_2^T} S_T(1) \\
&\vdots \\
S_T(n) &= \frac{g_{n-1}^T}{w_n^T} S_T(n-1)
\end{aligned} \tag{15}$$

which imply that the equilibrium solution take the form:

$$S_T(n) = \frac{p_T g_{n-1}^T g_{n-2}^T \cdots g_1^T}{w_n^T w_{n-1}^T \cdots w_1^T} \tag{16}$$

which, with some further algebra yields Eq. 17 from the main text.

Appendix S4: Neutral community predictions

Here I derive the completely neutral community structure properties used to compare to the tradeoff case in the main text. In the completely neutral case, even under “zero-sum” dynamics, one can immediately write down a differential equation for the partial distribution $P(n, t)$, i.e. the probability for a species to have n individuals at time t after it arose through speciation. This is because the transition probabilities depend only on the abundance of the focal species. It takes the form

$$\frac{dP(n, t)}{dt} = l_{n+1}P(n+1, t) + g_{n-1}P(n-1, t) - (l_n + g_n)P(n, t) \tag{17}$$

with

$$l_n = dn \frac{N-n}{N} + \nu n \tag{18}$$

80

$$g_n = d(N - n) \frac{n}{N} \quad (19)$$

81 where N is the total number of individuals in the community and ν is the per-capita speciation rate, and
 82 the rate at which species speciate is taken to be proportional to their abundance (Alonso & McKane, 2004;
 83 Etienne et al., 2007). Note that Eqs. 18&19 as well as the transition probabilities for the tradeoff model
 84 in the main text assume that the new offspring replacing the dying individual can come from that dying
 85 individual. In contrast, Hubbell (2001) did not allow for such self-replacement, even though it seems to be
 86 more realistic and simplifies the algebra. The first term in Eq. 18 includes the rate at which individuals of
 87 the species die (dn) times the probability that the subsequent birth event comes from another species in the
 88 community ($\frac{N-n}{N}$). Eq. 19 can be understood similarly. Considering species abundances n much smaller
 89 than the community size N leads to the non-interactive approximation:

$$l_n \approx dn + \nu n \quad (20)$$

90

$$g_n \approx dn \quad (21)$$

91 Volkov et al. (2003) and Volkov et al. (2007) considered a non-interactive approximation like this, but did
 92 not explicitly model the effect of speciation on species' abundances and hence ignored the increased rate at
 93 which species lose individuals due to speciation. Instead they took $g_n = bn$ where b is a birth rate, and
 94 assumed $b < d$. Here, speciation causes each species to have a negative population growth rate (specifically
 95 $dE[n(t)]/dt = -\nu E[n(t)]$. Species must be on average declining in abundance to make room for the new
 96 species, otherwise the total community size will blow up over time.

97 One can use the differential equation for $P(n, t)$ to derive a differential equation for the species abundance
 98 distribution (SAD) $S(n, t)$ (i.e. the average number of species with n individuals), just as in the tradeoff
 99 case. I won't repeat the details of that again. The result is:

$$\frac{dS(n, t)}{dt} = l_{n+1}S(n+1, t) + g_{n-1}S(n-1, t) - (l_n + g_n)S(n, t) + \delta_{n,1}\nu N \quad (22)$$

100 Note that νN is the total rate at which species with one individual are arising in the community. At
 101 equilibrium we obtain the following:

$$l_{n+1}S(n+1) - g_nS(n) = l_nS(n) - g_{n-1}S(n-1)$$

$$\begin{aligned}
&= \dots \\
&= l_2 S(2) - g_1 S(1) \\
&= l_1 S(1) - \nu N = 0
\end{aligned}$$

102 The last equality is a necessity for having an equilibrium number of species—the extinction rate must balance
103 the speciation rate. These equations imply that the equilibrium solution satisfies the following recursive
104 relations:

$$\begin{aligned}
S(1) &= \frac{\nu N}{l_1} \\
S(2) &= \frac{g_1}{l_2} S(1) \\
&\vdots \\
S(n) &= \frac{g_{n-1}}{l_n} S(n-1)
\end{aligned} \tag{23}$$

105 which together imply that the equilibrium solution take the form:

$$S(n) = \frac{g_{n-1} g_{n-2} \dots g_1 \nu N}{l_n l_{n-1} \dots l_1} = \frac{\prod_{i=1}^{n-1} d i}{\prod_{i=1}^n (d + \nu) i} \nu N = \frac{\nu}{d} \langle N \rangle \frac{((1 + \nu/d)^{-1})^n}{n} \tag{24}$$

106 This is the log-series $S_n = \alpha \frac{x^n}{n}$ with $x = (1 + \nu/d)^{-1}$ and $\alpha = N\nu/d$.

107 Note that the SAD in the zero sum case is also the log series in the limit of large community size (Alonso
108 & McKane, 2004). As mentioned above, Etienne et al. (2007) have shown that the sampling probability,
109 i.e. the probability of sampling a given set of abundances across species when examining a fixed number of
110 individuals, are identical under the non-interactive approximation and the zero-sum approach. Ultimately
111 both the zero-sum approach and the non-interactive approximation are approximations to the dynamics of
112 real communities, where populations likely tend to in total remain near a community-level carrying capacity
113 through community-level density dependence. Haegeman & Etienne (2008) showed that there is structural
114 similarity for predictions of the likelihood of sampling a given vector of abundances across species (which
115 I'll call the “sampling probability”) between the zero-sum approach and an explicit community density
116 dependence approach, but it is as yet unclear exactly how far off the zero-sum approach is. In any case, we
117 use the zero-sum approach and non-interactive approximation as a good starting point for comparison with
118 a tradeoff model derived from a similar approach and approximation.

119 We can use Eq. 24 for the SAD to derive other properties of the community. The total species richness

120 is:

$$S = \sum_{n=1}^{\infty} S(n) = -\alpha \log(1-x) = \frac{\nu}{d} N \log\left(\frac{1+\nu/d}{\nu/d}\right) \quad (25)$$

121 where I used $1-x = \frac{\nu/d}{1+\nu/d}$. Note that the bigger the ν , the more species there will be in the same size
 122 community. The bigger the d , the faster the turnover rate of populations and hence the higher the extinction
 123 rate and the lower the species richness. We can also verify that the expected number of individuals in the
 124 community over time for equilibrium community configurations comes out to N :

$$N = \sum_{n=1}^{\infty} S_n \cdot n = \alpha \sum_{n=1}^{\infty} x^n = \alpha \frac{x}{1-x} = \frac{\nu}{d} N \frac{\frac{1}{1+\nu/d}}{\frac{\nu/d}{1+\nu/d}} = N \quad (26)$$

125 The mean abundance of extant species is:

$$\langle n \rangle = \frac{N}{S} = \frac{1}{\frac{\nu}{d} \log\left(\frac{1+\nu/d}{\nu/d}\right)} \quad (27)$$

126 Note that bigger ν and lower d lead to a higher number of species and hence a lower mean abundance of
 127 extant species.

128 **Appendix S5: Simulations of Case 2 to verify accuracy non-interactive approxi-** 129 **mation**

130 In the main text I used a “non-interactive” approximation to the zero-sum dynamics approach to derive an
 131 analytical prediction for the species abundance distribution of each type in the tradeoff model. To verify
 132 the accuracy of this approximation, I carried out simulations of zero-sum dynamics for one of the speciation
 133 dynamics scenarios. Specifically, I simulated Case 2 of Fig. 1 of the main text, but for a smaller community,
 134 total community size $N = 10,000$. In other words, I carried out simulations in which the rate at which
 135 a species speciates is independent of its life history type T , and the rate at which species of a given life
 136 history type arise is independent of their life history type T , i.e. f_T^{loss} and f_T^{gain} were both independent of
 137 T . Figures 1 and 2 below show that the non-interactive approximation agrees well with simulation results
 138 for this smaller tradeoff community.

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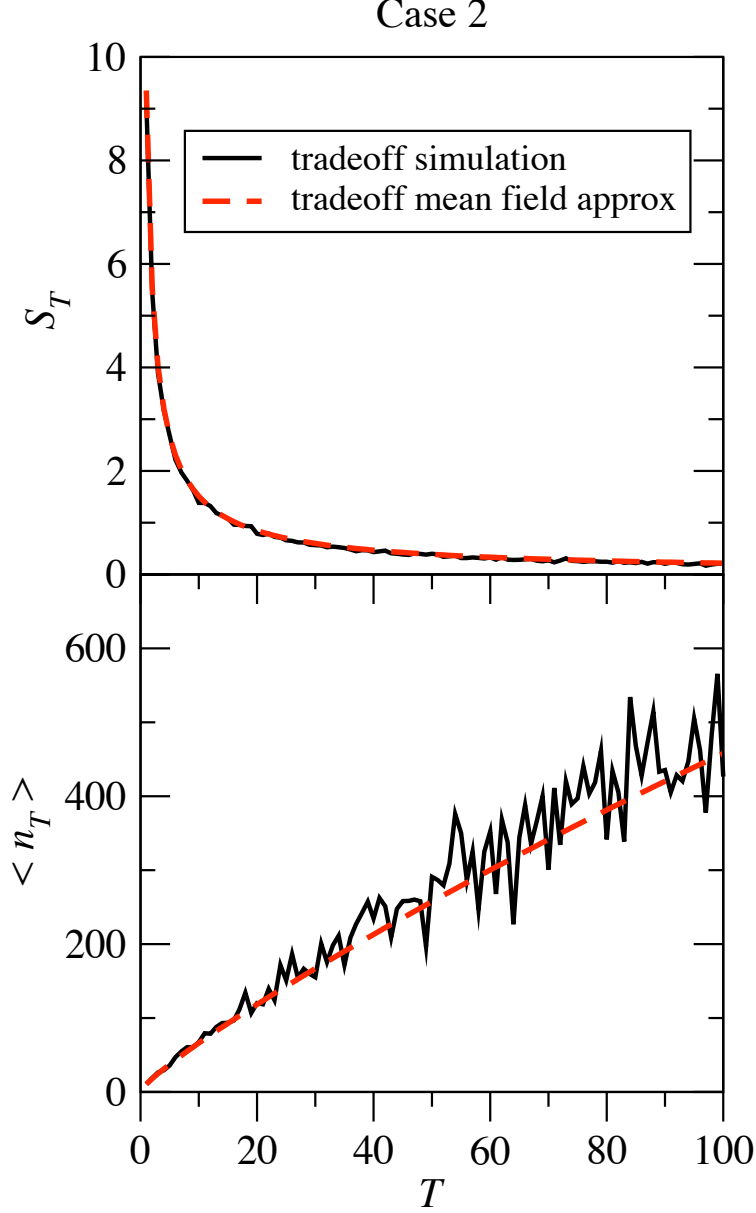


Figure 1: Simulation and “non-interactive” approximation results for Case 2 of Fig. 1 of the main text, but with a smaller community size of $N = 10,000$. Note that the life history type T is assumed to range over integer values from 1 to 100, and that the speciation rate per average death rate (ν) is 5×10^{-4} . Simulation results are an average over 1000 different equilibrium communities. Shown are the number of species of a given type, $S_T = \sum_n S_T(n)$ and the average abundance of a species present with a given life history type $\langle n_T \rangle = \sum_n S_T(n) \cdot n / S_T$. The “non-interactive” approximation is calculated using Eq. 20 of the main text. Although the total abundance of species of a given type T is not shown, since $N_T = S_T \cdot \langle n_T \rangle$, the “non-interactive” result should agree well with the simulation result for that property as well. For this case the expectation is that N_T is essentially independent of T .

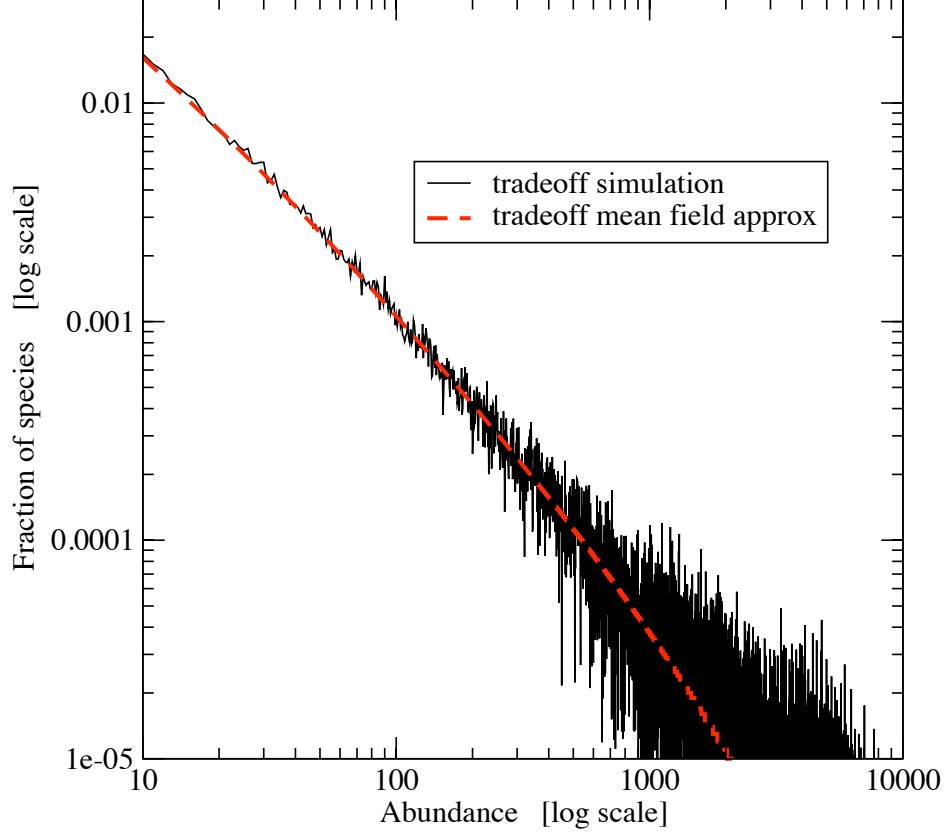


Figure 2: Simulation and “non-interactive” approximation results for Case 2 of Fig. 1 of the main text, but with a smaller community size of $N = 10,000$. Note that the life history type T is assumed to range over integer values from 1 to 100, and that the speciation rate per average death rate (ν) is 5×10^{-4} . Simulation results are an average over 1000 different equilibrium communities. Shown is the fraction of species with abundance n , $\frac{S(n)}{S} = \frac{\sum_T S_T(n)}{S}$. The “non-interactive” approximation is calculated using Eq. 19 of the main text. Although not shown on the graph, the total number of species in the community predicted by the non-interactive approximation ($S = 72.5$) also agrees well with the average simulation result ($S = 72.9$).