Neutral Dynamics with Environmental Noise

David Kessler & Nadav Shnerb
Bar-Ilan Univ.

Samir Suweis & Marco Formentin
Univ. of Padova

Posted on arxiv
Stephen Hubbell in 2001 introduced a simple model for the interaction of species in an ecocommunity: The Neutral Model

All individuals compete with each other independent of what species they belong to in a zero-sum game.

From this model, Hubbell and collaborators calculated the species abundance distribution: how many rare species there are vs. how many populous species.

The data from tropical rain forests fits this predicted distribution very well.

Other predictions of the model are contradictory to observation: Species Lifetime Statistics and Age-Size Relationship.

In Hubbell’s model, all fluctuations are demographic, scaling as the square-root of the abundance, but the data shows much larger fluctuations.

We will try to solve the above two problems via this last observation - introducing environmental noise.
Neutral Model: The Basics

In Hubbell’s model, the only effect of competition is to ensure that each species has a zero average growth rate - each individual has on average exactly one descendant.

Otherwise, each individual’s descendants are independent of all others. We get a pure Galton-Watson branching process, with a common probability distribution $P_n^{(1)}$ of having $n$ offspring, $\sum nP_n^{(1)} = 1$.

Strength of demographic fluctuations controlled by $\sigma^2 = \sum n(n-1)P_n^{(1)}$.

$P_n^{(g)} = \text{Prob. of having } n \text{ descendants after } g \text{ generations.}$

The generating function $G^{(g)}(x) = \sum x^n P_n^{(g)}$ satisfies $G^{(g)}(x) = G^{(1)}(G^{(g-1)}(x))$.

The survival probability $1 - G^{(g)}(0) \approx 2/(\sigma^2 g)$, so that $P_E(g) \approx 2/(\sigma^2 g^2)$.

Since the mean number of descendants of an individual is 1 indept. of $g$, the mean size of a family that survives $g$ generations from its founder is large, $N_{\text{surv}}(g) \approx \sigma^2 g/2$, i.e. size proportional to age.
Environmental Noise

We want to model the effect of environmental noise, assuming the noise has a differential impact on different species.

So, we assume that the distribution of the number of descendants of an individual of a given species is species- and time-dependent.

We retain the assumption that "all species are created equal" in a time-averaged sense: The time-averaged distribution of descendants is species-independent.

A simple way to implement this is to let $P_n^{(1)}(t)$ depend on time only through a single parameter, $\gamma_t$.

Assume $\gamma_t$ is a zero-mean random variable with correlation time $T_e$. 
Environmental Noise

Two limiting cases come to mind:

- (case A - logarithmically balanced): $E[P_n^{(1)}(t)] = e^{\gamma t}$. A bad period wherein the population halves is followed by a good one wherein the population doubles.

- (case B - arithmetically balanced): $E[P_n^{(1)}(t)] = 1 + \gamma t$. A bad period wherein the population halves is followed by a good one wherein the population increases by a factor of $3/2$.

The two cases differ by a shift in the overall growth rate of order $\text{Var}[\gamma] \equiv 2D$, the strength of the environmental noise.

The truth is likely to be somewhere in-between.
Survival Probability

Denoting the survival probability of a species by \( \delta(t) \), where \( t \) is measured in generations, we have the equations

\[
\dot{\delta} = \gamma_t \delta(t) + D \delta(t) - \frac{\sigma^2}{2} \delta^2(t) \quad \text{case A}
\]
\[
\dot{\delta} = \gamma_t \delta(t) - \frac{\sigma^2}{2} \delta^2(t) \quad \text{case B}
\]

The net growth in case A increases the chance of survival.

Defining a rescaled time \( \tau = Dt \), a rescaled \( \bar{\delta} \equiv \sigma^2 \delta/(2D) \) and rescaling the noise variance to unit strength, one finds a \( D \)-independent equation, so that

\[
\delta(t) = \frac{\mathcal{F}(tD)}{t}; \quad \mathcal{F}(0) = 1
\]

Case A: \( \mathcal{F}(x) \sim \sqrt{x/\pi} \) for \( x \gg 1 \); Case B; \( \mathcal{F}(x) \sim e^{-x/4} \) for \( x \gg 1 \)
Survival Probability

\[ \delta(t) = \frac{\mathcal{F}(tD)}{t}; \quad \mathcal{F}(0) = 1 \]

Case A: \( \mathcal{F}(x) \sim \sqrt{x/\pi} \) for \( x \gg 1 \); Case B; \( \mathcal{F}(x) \sim e^{-x/4} \) for \( x \gg 1 \)

In Case A, ignoring the demographic noise population does an unbiased walk in \( \log(n) \). The qualitative effect of the demographic noise is to put an absorbing trap at \( \log(n) = 0 \). Thus, the survival probability decays as \( t^{-1/2} \) for long time.

In Case B, the good years do not compensate for the bad ones, so there is an additional drift to the left as compared to case A, and species quickly go extinct.
Simulate Wright-Fisher discrete time dynamics with an Ornstein-Uhlenbeck process for $\gamma_t$ of each species

Crossover Behavior

Data Collapse
Survival Probability: Case B

FIG. 2: A) A plot of $t$, the chance to survive at time $t$ for a certain levels of overall diffusion coefficient $D$. B) Plotting $\ln[t\delta(t)]$ versus time, showing an exponential decay with $t$. C) A plot of $\ln[t\delta(t)]$ in linear-log scale versus time.

FIG. 3: The survival probability of a species, $F$, versus time and will solve the problem with environmental stochasticity. The logarithm of $t\delta(t)$ is plotted against $Dt$ in case A (arithmetically balanced noise) and case B (logarithmically balanced noise). The logarithm of $t\delta(t)$ is plotted against $Dt$ for pure demographic noise, although the bottom line is similar.

In Appendix B-III we explain that the average result presented here and the typical result differ from each other due to differences between logarithmic and arithmetic means. When examined an empirical community one considers only the species that have not yet gone extinct, so the relevant quantity for the age-abundance relationships is the average age-abundance of the surviving species, instead of the typical age-abundance.

The failure of the UNTB to account for dynamic patterns of populations and communities is known for a long time and will solve the problem with environmental stochasticity. Regarding the statistics of the species lifetime, we will consider only the species that have not yet gone extinct, so the relevant quantity for the age-abundance relationships is the average age-abundance of the surviving species, instead of the typical age-abundance.

In Appendix B we define and calculate the mean age of a species at generation size $N$ and define the skewness of the distribution, so in the typical result divergence between logarithmic and arithmetic means of the skewness will be subexponential. The skew of $N$ is growing linearly, is growing exponentially, so the net result is again, the data collapse as predicted by Eq. (16). This case the data collapses as predicted by Eq. (16).

Thus the abundance of the surviving species, instead of the skewness of the distribution, all the possibilities considered here - scaling. Regarding the statistics of the species lifetime - have been suggested in the literature based on the analysis of fossil data, see [22].

Now let us turn to the dependence of abundance on the strength of the environmental noise, i.e., $D$. In this case the data collapses as predicted by Eq. (16). This case the data collapses as predicted by Eq. (16).

In Appendix B-IV we explain that the average result presented here and the typical result differ from each other due to differences between logarithmic and arithmetic means. When examined an empirical community one considers only the species that have not yet gone extinct, so the relevant quantity for the age-abundance relationships is the average age-abundance of the surviving species, instead of the typical age-abundance.

The failure of the UNTB to account for dynamic patterns of populations and communities is known for a long time and will solve the problem with environmental stochasticity. Regarding the statistics of the species lifetime, we will consider only the species that have not yet gone extinct, so the relevant quantity for the age-abundance relationships is the average age-abundance of the surviving species, instead of the typical age-abundance.

In Appendix B we define and calculate the mean age of a species at generation size $N$ and define the skewness of the distribution, so in the typical result divergence between logarithmic and arithmetic means of the skewness will be subexponential. The skew of $N$ is growing linearly, is growing exponentially, so the net result is again, the data collapse as predicted by Eq. (16). This case the data collapses as predicted by Eq. (16).

Thus the abundance of the surviving species, instead of the skewness of the distribution, all the possibilities considered here - scaling. Regarding the statistics of the species lifetime - have been suggested in the literature based on the analysis of fossil data, see [22].
Consider, $N_{\text{surv}}(t)$, the mean number of offspring after time $t$, conditioned on survival of the lineage.

For case A (log-balanced):

$$N_{\text{surv}} \approx \frac{2}{D \sqrt{t}} e^{Dt/2}$$

However, the typical size of a surviving lineage is smaller, $\sim e^{\sqrt{2Dt}}$.

For case B (arithmetically balanced):

$$N_{\text{surv}} \sim e^{Dt/4}$$

- Here, the average unconditioned size of a lineage is unity, but since the survival probability is exponentially small, the conditioned average is exponentially large.
**Case A or B?**

We consider a more realistic model: The species compete with time-dependent growth rates and the total pop. is under logistic control, with immigration of new species.

Case A is impossible, since there the avg. total population increases.

Case B also ruled out: can’t have exponentially abundant species.

We examined both the mean of \((N_{t+\Delta t} - N_t)/N_t\) and \(\ln(N_{t+\Delta t}/N_t)\):

![Graph showing mean log change and mean arithmetic change over different species abundances.](image)

The mean log change is negative, but the mean arithmetic change is positive: Between A & B!
Environmental Noise eliminates the very slow dynamics of the pure Neutral Model

In the independent species approach, it is not clear what the noise properties are: Log vs. arithmetically balanced?

The survival probability decays like $1/t^{1/2}$ in the log-balanced case, otherwise exponentially

In both models, the surviving species grow faster than polynomially with time

To progress further, have to go beyond the independent species approach