



A forecast for extinction debt in the presence of speciation



Vasiliki Sgardeli^{a,*}, Yoh Iwasa^b, Harry Varvoglis^c, John M. Halley^a

^a Department of Biological Applications and Technology, University of Ioannina, 45110 Ioannina, Greece

^b Department of Biology, Kyushu University, 744 Motoooka Nishi-ku, Fukuoka 819-0395, Japan

^c Department of Physics, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece

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ABSTRACT

Predicting biodiversity relaxation following a disturbance is of great importance to conservation biology. Recently-developed models of stochastic community assembly allow us to predict the evolution of communities on the basis of mechanistic processes at the level of individuals. The neutral model of biodiversity, in particular, has provided closed-form solutions for the relaxation of biodiversity in isolated communities (no immigration or speciation). Here, we extend these results by deriving a relaxation curve for a neutral community in which new species are introduced through the mechanism of random fission speciation (RFS). The solution provides simple closed-form expressions for the equilibrium species richness, the relaxation time and the species-individual curve, which are good approximation to the more complicated formulas existing for the same model. The derivation of the relaxation curve is based on the assumption of a broken-stick species-abundance distribution (SAD) as an initial community configuration; yet for commonly observed SADs, the maximum deviation from the curve does not exceed 10%. Importantly, the solution confirms theoretical results and observations showing that the relaxation time increases with community size and thus habitat area. Such simple and analytically tractable models can help crystallize our ideas on the leading factors affecting biodiversity loss.

1. Introduction

Habitat loss and fragmentation are the main causes of biodiversity loss today. At the same time, the extinctions following such disturbances are not easy to predict because they do not all happen at once. A given disturbance can cause direct extinctions of species (imminent extinctions, e.g. spatially correlated disturbance on endemic species with a narrow geographic range (Kallimanis et al., 2005)), but it can also have long-lasting effects on the environmental conditions affecting the remaining species (e.g. area reduction, isolation, reduced populations, etc.). As a result, the community that is left after the disturbance is generally out of equilibrium and more species go extinct as the community relaxes to a new equilibrium (extinction debt, Jackson and Sax, 2009; Halley et al., 2014). This process is called relaxation. Because the extinctions that happen during the relaxation process are likely to be much more than imminent extinctions (Halley et al., 2014), predicting extinction debt is of great importance to conservation. To this end, a model of ecological community dynamics is necessary.

Early attempts to describe the relaxation process were based on the theory of island biogeography of MacArthur and Wilson (1967) (Diamond, 1972; Terborgh, 1974). Recently, the development of

stochastic models of community assembly gave the opportunity to describe the evolution of ecological communities on the basis of fundamental ecological processes like the births, deaths and immigration of individuals as well as speciation. The neutral model of biodiversity (Hubbell, 2001), in particular, has proven very successful in this respect as it provides closed-form solutions for the equilibrium as well as the dynamics of communities (e.g. McKane et al. 2000; Volkov et al., 2003; Azaele et al., 2006; Etienne and Alonso, 2007; Rosindell and Cornell, 2007; O'Dwyer and Green, 2010; Vanpeteghem and Haegeman, 2010; Chisholm, 2011). This has been used to model the relaxation process in isolated habitats. Gilbert et al. (2006) derived a closed-form solution for the variation of species richness with time in a completely isolated community (no immigration or speciation), which is applicable to short timescales. Halley and Iwasa (2011) gave a more complete solution to the problem by deriving a relaxation curve that also applies to long timescales. The relaxation curves of Gilbert et al. (2006) and Halley and Iwasa (2011) can predict the decline of species richness in isolated habitats such as islands that lie far away from the mainland. However, these might not give equally good estimates in habitats where species recruitment through immigration and/or speciation is high. Note that in the fully isolated model, the equilibrium

* Corresponding author.

E-mail addresses: wiki_sgardel@yahoo.gr (V. Sgardeli), yohiwasa@kyushu-u.org (Y. Iwasa), varvoglis@physics.auth.gr (H. Varvoglis), jhalley@cc.uoi.gr (J.M. Halley).

¹ Current address: HCMR, Elliniko, 16604, Agios Kosmas, Attiki, Greece.

state is fixation, i.e. eventually only one species is present in the community.

In this paper we extend previous results and derive a relaxation curve for a neutral community in which new species are recruited through speciation. To our knowledge this is the first closed-form solution to include species recruitment. The recruitment of new species balances species extinctions and results in a non-trivial number of species at equilibrium. To model speciation we use the mechanisms of random fission speciation (Haegeman and Etienne, 2010). This was introduced by Hubbell (2001) as an alternative to point mutation speciation to describe regional community dynamics. Where in point mutation new species are created by random mutations of individuals at birth, in random fission, new species are created by dividing the population of species into two fragments, with one of the fragments forming the population of the new species while the other remaining to the old species. Random fission speciation is considered a more realistic description of allopatric speciation than point mutation. This provides more realistic predictions for speciation rates, species longevities and the percentage of rare species (Etienne and Haegeman, 2011; Rosindell et al., 2011). Such a model is appropriate to describe the speciation process in groups of islands or fragments, which are often the type of habitats that result after habitat loss or fragmentation (e.g. see the model by Yamaguchi and Iwasa, 2013).

Here, we use the model of random fission speciation as described in Haegeman and Etienne (2010). This is an implicit-space model (i.e. the community is a mix of individuals with no geographic constraints) in which the only source of species number increase is random fission speciation (i.e. there is no immigration or emigration). We assume that the community has a fixed number of individuals through time (zero-sum rule) and that speciation events happen at a constant rate. The constant rate of speciation implies a constant per capita speciation rate (since the community size is fixed). So in the model, the speciation process is governed by individuals (individual-level random fission, Etienne and Haegeman, 2011). In an alternative (and more realistic) mode, the speciation rate is proportional to the number of species, but because the species number varies during the relaxation process this leads to significantly more complicated equations. Here we restrict ourselves to the individual-based model.

We solve the random-fission speciation model to derive a closed-form relaxation equation. The solution provides simple expressions for the equilibrium species richness, species-individual curves and relaxation times. In deriving the equation we assumed a fixed proportion of species with one individual throughout the relaxation process, corresponding to the broken-stick species-abundance distribution (SAD), and use simulations to investigate the range of parameters for which the equation lies close to the real solution (i.e. the one that takes into account the initial SAD). Finally, we discuss the potential for practical application of the equation and possible extensions towards a more realistic description of the relaxation process in the presence of speciation (or immigration).

2. Methods

2.1. The RFS model

The model of a neutral community subject to Random Fission Speciation (RFS) has been studied by Haegeman and Etienne (2010) and Etienne and Haegeman (2011). In this, the community evolves in time through birth-death events, which happen at a constant rate μ (community-level birth rate), and speciation events, which happen at a constant rate ν (community-level speciation rate). In a birth-death event a random individual is selected for death and is immediately replaced by the descendant of another random individual from the community. In a speciation event, a species is selected with probability proportional to its abundance to undergo speciation. The population of this species splits into two fragments, one corresponding to the newly

formed species and the other remaining to the old species. If the initial abundance of the old species is k , then, after the split, the old (or the new) species can have from 1 up to $k-1$ individuals, with all possible ways of splitting having the same probability. If a species with one individual is selected to speciate, the individual of this species is replaced by an individual of a new species. In this case, however, there is no net effect on the total species number. Note that both birth-death and speciation processes conserve the total number of individuals in the community, so that the community size is constant at all times.

2.2. Derivation of the relaxation curve

Starting from the master equation for the expected number of species having abundance n (equation 34 of Haegeman and Etienne, 2010), we derive a differential equation for the variation of the average species richness with time (see Appendix A. Supplementary material for the detailed derivation). This is:

$$\frac{dS}{dt} = \nu - \frac{\mu + \nu}{J} S_1, \quad (1)$$

where J is the community size (constant), ν and μ are the constant community-level speciation and birth rates and S_1 denotes the average number of species with one individual. Eq. (1) is not solvable at its current form because S_1 is a variable with unknown dependence on t or S . However, for a community at, or close to, equilibrium, S_1 is a given fraction of the total species richness, S , determined by the equilibrium species-abundance distribution (SAD). To express S_1 as a function of S , we assume that the fraction of species having one individual is fixed throughout the relaxation process, determined by the equilibrium SAD. For the random fission community, the equilibrium SAD is very close to the broken-stick distribution (see Etienne and Haegeman (2011) equation (74) of Appendix D), for which the expected number of species with one individual is $S_1 = [S(S-1)/J](1-1/J)^{S-2}$. For $J \gg S \gg 1$ this is well approximated by $S_1 \approx S^2/J$ (see Appendix B. Supplementary material). Upon substituting into Eq. (1) this results in a differential equation of the desired form:

$$\frac{dS}{dt} = \nu - \frac{\mu + \nu}{J^2} S^2. \quad (2)$$

Setting $dS/dt=0$ in Eq. (2) gives the equilibrium species richness:

$$S_{\text{eq}} = J \sqrt{\frac{\nu}{\nu + \mu}}. \quad (3)$$

Note that the same equilibrium relation has been derived empirically by Ricklefs (2003). In Eq. (3), the sum of the speciation and birth rates, $\nu + \mu$, is the total rate at which events happen in the community. Thus, the fraction $\nu/(\nu + \mu)$ represents the probability of speciation given that an event happens; that is the speciation probability in the discrete time model (see Hubbell, 2001). Eq. (3) simplifies to $S_{\text{eq}} = J\sqrt{\nu}$ and implies that the equilibrium number of species is proportional to the number of individuals, given a fixed per capita probability of speciation. This assumption is fair if we accept that the speciation process is driven by individuals (e.g. point mutation at birth), however in a more realistic situation (e.g. allopatric speciation) the probability of speciation will also depend on the number of existing species (Etienne, 2007, Etienne and Haegeman, 2011). That is, the per capita speciation rate is expected to vary with community size.

The differential Eq. (2) can be solved by separation of variables (see Appendix C. Supplementary material), which leads to our main result:

$$S = S_{\text{eq}} + \frac{2S_{\text{eq}}}{\frac{S_0 + S_{\text{eq}}}{S_0 - S_{\text{eq}}} e^{\gamma t} - 1}. \quad (4)$$

In Eq. (4) S_{eq} is the equilibrium species richness of Eq. (3), S_0 the species richness at time $t=0$ and $\gamma=2\nu/S_{\text{eq}}$ a constant determining the rate of increase or decrease of species richness, which we call the

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