



A stochastic model of interacting species on islands

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Resumen

We propose a general Lotka-Volterra type model with stochastic migrations to represent the dynamics of a pool of J species over an archipelago composed by I islands. This stochastic model includes two dynamic scales: a fast one, which refers to the interactions between species within each island, and a slow one, referring to migrations following a Poisson scheme. We show that we can study the long-term behavior of some species on some islands via Lyapunov exponents. Specifically, we show that a group of the species pool go to extinction over a group of islands within the archipelago whenever the corresponding Lyapunov exponent is negative; otherwise, it is equal to zero. Additionally, we show numerically that the model can depict migration/competition tradeoffs, in which species in competence can coexist or reverse the advantage due to the migration effect.

1. Approach of the model

Consider an archipelago compound by J species and I islands. Let $X_{ij}(t)$ be the biomass of the species j living in island i at time $t \in \mathbb{R}_+$. We assume that each $X_{ij}(\cdot)$ follows:

$$\begin{aligned}
 X_{ij}(t) = & X_{ij}(0) + \int_0^t f_{ij}(X_{ij}(s))ds + \sum_{j'=1}^J \lambda_{jj'} \int_0^t X_{ij'}(s)X_{ij}(s)ds \\
 & + \sum_{i'=1}^I \varepsilon_{ii'} \int_0^t X_{i'j}(s-) \int_0^\infty 1_{\{z \leq b_j\}} N_{i'j}(dz, ds), \tag{1}
 \end{aligned}$$

where $f_{ij} : \mathbb{R} \rightarrow \mathbb{R}$ is the growth function of $X_{ij}(\cdot)$, the $\lambda_{jj'}$'s are fixed parameters representing, in general terms, the interaction among species. When, $\lambda_{jj'} > 0$ the biomass of species j increases in the presence of species j' either because species j' is a mutualist or a resource (e.g. prey) of j . On the other hand, when $\lambda_{jj'} < 0$ species j decreases in biomass when j' is present because it competes or is consumed by species j' ; and when $\lambda_{jj'} = 0$ species j does not interact with species j' . Intraspecific interaction are included in the growth function f_{ij} , and thus $\lambda_{jj} = 0$. The $\varepsilon_{ii'}$'s are constants representing the mean proportion of biomass

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moving or migrating among islands. When $i \neq i'$, $\varepsilon_{ii'}$ quantifies the mean proportion of biomass migrating from island i' towards island i (and then $\varepsilon_{ii'} \geq 0$), while ε_{ii} quantifies the mean proportion of biomass emigrating from island i towards some of the other islands in the archipelago (and then $\varepsilon_{ii} \leq 0$). For consistency, we must have that all the emigrating biomass of any species and from any island is equal or less (biomass losses can occur during the migration process) than the biomass immigrating into the other islands of the archipelago, that is $|\varepsilon_{i'i'}| \geq \sum_{i \neq i'} \varepsilon_{ii'}$ for all $i' = 1, \dots, I$. The $\varepsilon_{ii'}$'s can depend upon the distance between islands as well as the size of them, as traditionally considered in the theory of island biogeography (MacArthur & Wilson (1967); Hanski & Ovaskainen (2000)). Finally, $\{N_{ij}(dz, ds)\}_{j=1, \dots, J}^{i=1, \dots, I}$ is an independent and identically distributed (IID) sequence of Poisson measures, with intensity $dzds$, representing the stochastic migration regime of the species among islands. The migration of biomass will depend upon the species-dependent parameters b_j 's, so that for every $i = 1, \dots, I$ and $j = 1, \dots, J$, $\int_0^\infty 1_{\{z \leq b_j\}} N_{ij}(dz, \cdot) = N_{ij}([0, b_j], \cdot)$ is a Poisson process with instantaneous rate b_j .

This model describes the dynamics of J interacting species living in an archipelago composed of I islands under two different scales: a fast one, depicting growth, intra and interspecific dynamics between species, and a slow one, describing the stochastic migration regime of species within the archipelago. The model is general and can accommodate different scenarios, from assuming that all species and islands are equal, to making the parameters characterizing the growth functions $f_{ij}(\cdot)$'s, such as carrying capacities and intrinsic growth rates, to be dependent on island and species attributes such as body size, trophic status or island area. The interactions between the species are of Lotka-Volterra type. The stochasticity of the model is due to the migration regime, which opens the interactions occurring on a focal island to the fluctuations due to migration of biomass to and from other islands in the system. Notice that, although the whole system is stochastic, there is no biomass transfer from and to the outside of the archipelago.

In what follows we will show the well-posedness of this model and study its long-term behavior under standard assumptions.

Assumptions of the model:

(A.1) The $X_{ij}(0)$'s are independent random variables (RVs) with corresponding densities $\rho_{ij}(\cdot)$'s, all having compact support in \mathbb{R}_+ .

(A.2) For each $i = 1, \dots, I$ and $j = 1, \dots, J$, $f_{ij}(\cdot)$ is a $C^1(\mathbb{R})$ function.

Condition (A.1) allows us to describe a plausible initial starting point for our system, since the limitations associated to the area of the islands would only allow for a bounded amount of biomass, and (A.2) sets a typical condition of regularity.

In order to study the well-posedness of our model, we are going to write the whole dynamics of the system via matrices and vectors. Consider:

$$\mathbf{X} = \begin{pmatrix} X_{11} & \cdots & X_{1J} \\ \vdots & \ddots & \vdots \\ X_{I1} & \cdots & X_{IJ} \end{pmatrix},$$

$$\mathbf{N}(dz, dt) = \begin{pmatrix} N_{11}(dz, dt) & \cdots & N_{1J}(dz, dt) \\ \vdots & \ddots & \vdots \\ N_{I1}(dz, dt) & \cdots & N_{IJ}(dz, dt) \end{pmatrix},$$

$$\mathbf{X} = \text{vec}(\mathbf{X}) = (X_{11} \quad X_{12} \quad \cdots \quad X_{21} \quad \cdots \quad X_{I(J-1)} \quad X_{IJ})^T,$$

$$\mathbf{N}(dz, dt) = \text{vec}(\mathbf{N}(dz, dt))^T$$

$$= \left(N_{11}(dz, dt) \quad N_{21}(dz, dt) \quad \cdots \quad N_{12}(dz, dt) \quad \cdots \quad N_{(I-1)J}(dz, dt) \quad N_{IJ}(dz, dt) \right)^T,$$

$$F(\mathbf{X}) = \left(f_{11}(X_{11}) \quad f_{12}(X_{12}) \quad \cdots \quad f_{21}(X_{21}) \quad \cdots \quad f_{I(J-1)}(X_{I(J-1)}) \quad f_{IJ}(X_{IJ}) \right)^T,$$

$$\Lambda(\mathbf{X}) = \text{diag} \left(\sum_{j'=1}^J X_{1j'} \lambda_{1j'}, \sum_{j'=1}^J X_{1j'} \lambda_{2j'}, \cdots, \sum_{j'=1}^J X_{2j'} \lambda_{1j'}, \cdots, \sum_{j'=1}^J X_{Ij'} \lambda_{(J-1)j'}, \sum_{j'=1}^J X_{Ij'} \lambda_{Jj'} \right)$$

and

$$B(\mathbf{X}, z) =$$

$$\begin{pmatrix} \varepsilon_{11} X_{11} 1_{\{z \leq b_1\}} \cdots \varepsilon_{1I} X_{I1} 1_{\{z \leq b_1\}} & 0 & \cdots & 0 \\ 0 & \cdot & & \vdots \\ \vdots & & \cdot & 0 \\ 0 & \cdot & \cdots & 0 \quad \varepsilon_{I1} X_{1J} 1_{\{z \leq b_J\}} \cdots \varepsilon_{II} X_{IJ} 1_{\{z \leq b_J\}} \end{pmatrix},$$

where $\text{vec}(\cdot)$ denotes the vectorization operator, T denotes the matrix transposition operator and $\text{diag}(a_1; \cdots; a_n)$ denotes an $n \times n$ diagonal matrix whose elements therein are a_1, \dots, a_n , respectively.

Thus, we have that \mathbf{X} , $F(\mathbf{X})$ and $N(dz, dt)$ are $IJ \times 1$ vectors, and $\Lambda(\mathbf{X})$ and $B(\mathbf{X}, z)$ are $IJ \times IJ$ matrices. Under this writing, we have that the whole dynamics of the system is given by:

$$\begin{aligned} \mathbf{X}(t) &= \mathbf{X}(0) + \int_0^t F(\mathbf{X}(s)) ds + \int_0^t \Lambda(\mathbf{X}(s)) \mathbf{X}(s) ds \\ &\quad + \int_0^t \int_0^\infty B(\mathbf{X}(s-), z) \mathbf{N}(dz, ds) \end{aligned} \quad (2)$$

We have the following proposition.

Proposition 1

Under assumptions (A.1) and (A.2), the system (2) (and hence (1)) has a unique local solution.

This proposition ensures only the existence of a unique local solution, that is, a unique well-posed solution when the state space of the process is limited. This is so since there are cases for which our system can explode in a finite time. In our context, however, the system should not explode since biomass has an upper bound given by the finite area of the island system. Therefore, we must consider additional conditions in order to state a more appropriate well-posedness result for our model.

First, consider that $F(\mathbf{X})$ in (2) can be written as $F(\mathbf{X}) = \tilde{F}(\mathbf{X}) \mathbf{X}$, where $\tilde{F}(\mathbf{X})$ is a $IJ \times IJ$ diagonal matrix. Define $\Gamma(\mathbf{X}) = \tilde{F}(\mathbf{X}) + \Lambda(\mathbf{X})$. Our system (2) can be now written as:

$$\mathbf{X}(t) = \mathbf{X}(0) + \int_0^t \Gamma(\mathbf{X}(s)) \mathbf{X}(s) ds + \int_0^t \int_0^\infty B(\mathbf{X}(s-), z) \mathbf{N}(dz, ds). \quad (3)$$

Note that $\Gamma(\mathbf{X}) = \text{diag}(\eta_1(\mathbf{X}), \dots, \eta_I(\mathbf{X}))$, where each $\eta_i(\mathbf{X})$ is a $J \times J$ diagonal matrix. Finally, assume the following condition:

(A.3) There exists some $n \geq 0$ such that the diagonal matrix $\max_{i=1, \dots, I} \eta_i(\mathbf{X})$ is negative-definite if $\|\mathbf{X}\| > n$.

We can prove now the following proposition.

Proposition 2

Under assumptions (A.1), (A.2) and (A.3), the system (3) has a unique solution such that:

$$\sup_{t \in \mathbb{R}_+} \max_{i=1, \dots, I; j=1, \dots, J} X_{ij}(t) < \infty, \quad (4)$$

almost surely.

On the other hand, in the following lemma we will show that species extinction can only occur in the long-term, the same as in the classic (non stochastic) general Lotka-Volterra model (see Hofbauer & Sigmund (2002)).

Lemma 3

Under assumptions (A.1), (A.2) and (A.3), if $X_{ij}(0) > 0$ for some $i = 1, \dots, I$ and $j = 1, \dots, J$, then $X_{ij}(t) > 0$ for any finite $t > 0$.

Remark: Notice that the initial condition can be $X_{ij}(0) = 0$, and for some $t > 0$, $X_{ij}(t) > 0$ due to migration. The essential issue here is that once the dynamics of $X_{ij}(\cdot)$ starts (i.e., with positive biomass), then the process can subsequently reach 0 only in the limit $t \rightarrow \infty$.

1.0.1. Example

Consider $f_{ij}(x) = r_j(1 - x/K_{ij})x$ in (1), where r_j is the intrinsic growth rate of species j and K_{ij} is the carrying capacity of species j in island i . Here, the term $-r_j/K_{ij}$ describes the effect of intraspecific competition on the growth of species across island. In the whole system (3), the elements of the diagonal of $\Gamma(\mathbf{X})$ are given by $\text{diag}(\eta_i(\mathbf{X})) = (r_1[1 - X_{i1}/K_{i1}] + \sum_{j' \neq 1} \lambda_{1j'} X_{ij'}, \dots, r_J[1 - X_{iJ}/K_{iJ}] + \sum_{j' \neq J} \lambda_{Jj'} X_{ij'})$, $i = 1, \dots, I$. This example constitutes a generalized Lotka-Volterra system, where intrinsic growth is logistic, migration is presented as a stochastic regime, and which under (A.1)-(A.3) the whole biomass does not escape from a limited state-space.

2. Stability at equilibrium

We can notice that $\mathbf{0}$ is an equilibrium solution of our system (3). In Lemma 3 we saw that if $X_{ij}(t) \neq 0$ for some $t \in \mathbb{R}_+$, $i = 1, \dots, I$ and $j = 1, \dots, J$, the only possible way that $X_{ij}(\cdot)$ reaches 0 again (i.e., extinction of species j in island i) is in the limit $t \rightarrow \infty$. In this regard, we can study the long-term persistence of some species within some islands. One of the most popular methods to do this is through *Lyapunov exponents*. The aim is to know under which conditions extinction/persistence of some species within some islands will occur in the long-term.

We say that a process $\mathbf{Z}(\cdot)$ taking values in \mathbb{R}^d has a *Lyapunov exponent* ℓ if:

$$\ell = \limsup_{t \rightarrow \infty} \frac{1}{t} \log(\|\mathbf{Z}(t)\|) < \infty, \quad (5)$$

almost surely. If it exists, for a sufficiently large t we have that:

$$\|\mathbf{Z}(t)\| \leq \xi \exp\{\ell t\}, \quad (6)$$

almost surely, for a positive random variable ξ (see Applebaum (2009), Chapter 6, Section 6.8). Thus, as a way to distinguish the decay velocity, we will say that 0 is *almost surely exponentially stable* if $\ell < 0$.

For our practical purposes, we are going to study the long-term behavior of observables of the form $g(\mathbf{x}) = u_{IJ}^T \mathbf{x}$, where u_{IJ} is an $IJ \times 1$ vector containing 1's and 0's depending on which species, over the J possible ones, and on which islands among the I possible ones, we want to carry out our analysis.

Notice that our system (3) can be written as:

$$\mathbf{X}(t) = \mathbf{X}(0) + \int_0^t [\Gamma(\mathbf{X}(s))\mathbf{X}(s) + \mathbf{b}(\mathbf{X}(s))]ds + \int_0^t \int_0^\infty B(\mathbf{X}(s-), z)\mathbf{M}(dz, ds), \quad (7)$$

where $\mathbf{M}(dz, ds) = \mathbf{N}(dz, ds) - \mathbf{1}_{IJ}dzds$ is a martingale and $\mathbf{b}(\mathbf{x}) = \int_0^\infty B(\mathbf{x}, z)\mathbf{1}_{IJ}dz$, with $\mathbf{1}_{IJ}$ the $IJ \times 1$ vector of 1's. Our aim here is to determine which components of $\mathbf{X}(\cdot)$ will go to zero in the long-term using Lyapunov exponents. Thus, we are interested in processes like:

$$\langle u_{IJ}, \mathbf{X}(t) \rangle = \langle u_{IJ}, \mathbf{X}(0) \rangle + \int_0^t \langle u_{IJ}, \Gamma(\mathbf{X}(s))\mathbf{X}(s) + \mathbf{b}(\mathbf{X}(s)) \rangle ds + \int_0^t \int_0^\infty \langle u_{IJ}, B(\mathbf{X}(s-), z)\mathbf{M}(dz, ds) \rangle, \quad (8)$$

where u_{IJ} is an $IJ \times 1$ vector containing 1's and 0's and $\langle \cdot, \cdot \rangle$ is the scalar product. Define the operator $\mathcal{L}\langle u_{IJ}, \mathbf{x} \rangle := \langle u_{IJ}, \Gamma(\mathbf{x})\mathbf{x} + \mathbf{b}(\mathbf{x}) \rangle$. We have the following result.

Proposition 4

Under assumptions (A.1), (A.2) and (A.3), the process (8) has a Lyapunov exponent $\ell < \infty$. If additionally, there exists a constant $c > 0$ such that $\mathcal{L}\langle u_{IJ}, \mathbf{x} \rangle \leq -c\langle u_{IJ}, \mathbf{x} \rangle$, for all $\mathbf{x} \in \mathbf{R}$, then $\ell < 0$.

Remark: Actually the condition to obtain a negative Lyapunov exponent can be replaced by $\mathcal{L}\langle u_{IJ}, \mathbf{X}(t) \rangle \leq -c\langle u_{IJ}, \mathbf{X}(t) \rangle$ almost surely, for a sufficiently large t .

However, the previous result is actually stronger, in the sense that there is an equivalence between extinction and the negativeness of ℓ , as stated in the following lemma.

Lemma 5

Under assumptions (A.1), (A.2) and (A.3), extinction holds whenever $\ell < 0$.

Finally notice that, as a consequence of the boundedness of (3) (Proposition 2) and Lemma 5, we have that the case of non-extinction implies that the corresponding Lyapunov exponent results equal to zero.

3. Numerical example: A migration/competition based model

We developed a numerical example using the specific structure given in section 1.0.1 with $J = 2$ competing species within an archipelago compound by $I = 2$ islands, given by the equations:

$$\begin{aligned} X_{ij}(t) = X_{ij}(0) &+ \int_0^t r_j \left(1 - \frac{X_{ij}(s)}{K_{ij}}\right) X_{ij}(s) ds + \sum_{j'=1}^2 \lambda_{jj'} \int_0^t X_{ij'}(s) X_{ij}(s) ds \\ &+ \sum_{i'=1}^3 \varepsilon_{ii'} \int_0^t X_{i'j}(s-) \int_0^\infty 1_{\{z \leq b_j\}} N_{i'j}(dz, ds), \end{aligned} \quad (9)$$

for $i = 1, 2$, $j = 1, 2$, and where $\lambda_{12}, \lambda_{21} < 0$ and $\lambda_{jj} = 0$.

It can numerically be shown that this model can depict migration/competition tradeoffs, in which species in competence can coexist or reverse the advantage due to the migration effect.

4. Discussion

Recently, in Hening et al (2018) a stochastic population model in spatially heterogeneous environments is developed. The flow evolves in a patchy habitat according to a drift compound by density-dependent intrinsic growth function and an irreducible dispersal, and a diffusive Brownian term. Despite the explicit species diversity set in our model and the fact that our “patches” are not contiguous, we would also have considered a stochastic noisy component that affects in the same “fast” scale of the continuous growth as in Hening et al (2018) (or as in Mao et al (2002) or Mao et al (2003)). That is, we could have introduced in (1) a stochastic term of the form $\sigma \int_0^t X_{ij}(s) dW_{ij}(s)$, where $\sigma > 0$ is a diffusion parameter and the $W_{ij}(\cdot)$ ’s are IID Brownian motions. It can be showed that our results basically remains unchanged, except for the boundedness result (4) of Proposition 2. This is a mathematically technical subtlety since the resulting diffusive process will be almost sure finite within each finite time horizon, and the probability that the biomass escapes from a “large compact” is actually small. To avoid such a mathematical inconvenient if considering a continuum noise term, we could conceive “borders in the diffusion”, which would keep the boundedness property (see, e.g., Skorokhod (1961), Skorokhod (1962), Lions & Sznitman (1984), Tanaka (2002)). However, we leave this issue as a future perspective.

Another aspect that may be very relevant to include in modeling, especially in the current times, is the influence of abiotic factors or climate change that can greatly affect the growth functions, migration rates and the direction of migration (see, e.g., Tejo et al (2017) for an approach of patchy habitats).

One of the novel aspects of our stochastic model of species interaction in islands is associated with our use of a stochastic migration that follows a jump Poisson process, which was first introduced by Rebolledo et al (2019) in the context of stochastic open network models in ecology. Although novel and interesting from a technical perspective, it has been shown that a general birth death process can be written trajectoryally as driven by Poisson measures. For example, from MacArthur & Wilson (1963, 1967), under their Theory of Insular Biogeography, the probability of observing s species within a pool of K species is given by the following master equation:

$$\frac{dP_s(t)}{dt} = P_{s-1}(t)\lambda_{s-1} + P_{s+1}(t)\mu_{s+1} - P_s(t)[\lambda_s + \mu_s], \quad (10)$$

$s = 0, 1, \dots, K$, where λ_s is the rate of colonization that increases s to $s + 1$ and μ_s is the rate of extinction decreasing s to $s - 1$. We also have to set the boundary conditions $\lambda_K = \mu_0 = 0$ in order to get a well-established process. The trajectoryal representation of a process that follows (9), $S(\cdot)$, can be set in order to get explicitly the flows or the time series of the species richness process. This is convenient since the data obtained empirically refer to the number of species. From Bansaye & Méléard (2015), a process $S(\cdot)$ that follows (9) is trajectoryally represented by:

$$S(t) = S(0) + \int_0^t \int_0^\infty (1_{\{z \leq \lambda(S(u-))\}} - 1_{\{\lambda(S(u-)) < z \leq \lambda(S(u-)) + \mu(S(u-))\}}) N(dz, du), \quad (11)$$

where $S(0)$ is the initial number of species and $N(dz, du)$ is a Poisson random measure of intensity $dzdu$.

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