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# A Simple Stability Analysis for a Mathematical Model of Migration Due to Noise and Resources

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**Abstract:** This research studies a metapopulation model where each patch is considered a form of fragmentation of the environment produced by the spatio-temporal variability of anthropogenic noise. A deterministic mathematical model is proposed that describes two processes of migration between patches. The first process consists of migration due to chronic critical noise produced by an anthropogenic and biological source (self-generated acoustic signals of higher intensity, due to the Lombard effect). The second process consists of migration due to a higher level of stain occupancy. A simple and classical analysis of the local stability of the model is performed. The results indicate that no subpopulation goes extinct; in fact, a necessary condition for long-term stabilization of the size of the subpopulations is that the noise attenuation rate is higher. Moreover, as long as the noise is of low intensity the differences in the carrying capacity of each patch do not produce substantial, long-term differences in the sizes of the subpopulations. However, as the noise intensity increases, the difference in carrying capacities produce noticeable, long-term differences between subpopulation sizes. Finally, the results are corroborated by numerical simulations.



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**MSC:** 34D20; 92B05; 92D25; 92D40

## 1. Introduction

Biologists have explored a variety of population models that incorporate spatial characteristics. One such model is called a metapopulation model. This term was proposed in 1969 by the mathematical ecologist R. Levins when he observed that the effectiveness of any insect pest control program is inevitably complicated by environmental heterogeneity [1]. This produces a fragmentation of the environment into a group of subpopulations, linked and distributed in a set of spatially discrete habitats or patches, called a metapopulation [2,3]. Currently, several researchers use the metapopulation approach to study, for example, the persistence of local populations [4–7].

In a metapopulation, the subpopulation occupying different patches is linked through exchanges of individuals (migration) [8,9]. Migration is a consequence of different factors such as the season of the year, competition, or a lack of some resource relevant to survival [10–13].

Patches with different noise intensity levels can be seen as a form of fragmentation of the environment due to the spatio-temporal variability of noise. Thus, animals are exposed to a large number of different acoustic environments within which they must survive with the resources of each environment [14–16]. One of the effects, little studied, on animal behavior is migration to avoid noisier patches [17] because noise acts as a sound that masks biologically relevant acoustic signals of animals, negatively affecting communication, distribution, mate searching, foraging and even survival [18–26]. For

example, in birds, anthropogenic noise affects migration rates to wintering grounds as some species avoid noisier stopover sites [27,28], and it has been observed that chronic traffic noise affects embryo growth and mortality rates in zebra finches [29]. In marine animals, such as whales, migration is diverted in response to the avoidance of noise sources [30]. Ship noise negatively affects the survival of beaked whales, damselfish, and marine invertebrates, thereby increasing their mortality rates [31–34]. In amphibians, traffic noise causes physiological stress and impairs breeding migratory behavior in frogs.

In response to noise, animals tend to increase the intensity of acoustic signals (a phenomenon known as “Lombard effect”) [35–37] so that acoustic signals relevant to the survival of the population are not masked by noise and are recognized by their target receptors [38–41]. However, when anthropogenic noise is chronic and critical (i.e., because of its long duration and high intensity, it positively affects the mortality rate), increasing the intensity of acoustic signals favors both the negative effects of anthropogenic noise and the energetic [42–48], behavioral [49,50], and predation costs [51–54]. Therefore, sounds generated by the use of higher intensity acoustic signals as a consequence of the Lombard effect together with chronic and critical anthropogenic noise negatively affect population survival [55,56].

Another factor that may increase migration rates is the transient availability and changing location of resources [57]. Since higher occupancy levels (which is the proportion between the size of the subpopulation and the carrying capacity of the patch) decrease resource availability, patch occupancy can play a crucial role in promoting migration. There are, however, few studies that have investigated migration as a process that depends on the level of occupation [58,59]. Nevertheless, there is evidence of an increase in the rate of migration with increasing occupancy level [60–62].

In this sense, this research studies, by means of a new deterministic mathematical model, the effects of noise and lack of resource on two processes of population migration, complementing the model proposed in Ramírez Carrasco et al. [56], where the effects of noise on population persistence are studied. The first is a unidirectional migration of the population towards the nearest patch with lower noise intensity level. The noise is fed from two sources: an anthropogenic source and the use of higher amplitude acoustic signals self-generated by the population and caused by the Lombard effect. The second is a random migration in search of the patch with the lowest occupancy level. The objective of this research is to obtain sufficient conditions on the model parameters to characterize the asymptotic values of the subpopulation sizes. Finally, the theoretical results are corroborated by numerical simulations.

## 2. Model Formulation

A single species population is considered where individuals are identical and distributed in  $n$  discrete patches in a noisy environment. The state variables of the model are non-negative functions of time  $N_i(t)$  and  $I_i(t)$ , which denote the population density and noise intensity in patch  $i$  at time  $t$ , respectively. Each patch is characterized by two dynamics, the internal one of birth-death, and the migratory one that links it to other patches and that is associated with a noise dynamic fed by an anthropogenic source and the use of higher intensity acoustic signals, due to the Lombard effect, by the population. Migration is the population response to the high noise and higher occupancy level in each patch, so that each patch may act as a source of individuals to, and can be colonized by individuals coming from, any other patches. A general model (Z) that describes this phenomenon in patch  $i, i \in \{1, 2, \dots, n\}$  is given by:

$$(Z) \begin{cases} N'_i(t) = f_i(N_i(t))N_i(t) - \sum_{\substack{j=1 \\ j \neq i}}^n \mathcal{M}_{ij}^- + \sum_{\substack{k=1 \\ k \neq i}}^n \mathcal{M}_{ki}^+, \\ I'_i(t) = \alpha_i F(t) + \beta(I_i(t))N_i(t) - \gamma I_i(t), \end{cases}$$

where  $f$  is the per capita growth rate in patch  $i$  in the absence of migration;  $\mathcal{M}_{ij}^- = (a_{ij}(I_i(t)) + b_{ij})N_i(t)$  is the emigration rate from patch  $i$  to patch  $j$  defined by per capita rates  $a_{ij}(I_i)$  and  $b_{ij}$  due to noise and occupancy level, respectively;  $\mathcal{M}_{ki}^+ = (a_{ki}(I_k(t)) + b_{ki})N_k(t)$  is the immigration rate towards patch  $i$  from patch  $k$ , given by per capita rates  $a_{ki}(I_k)$  and  $b_{ki}$ , due to noise and occupancy level respectively;  $F$  is a non-negative, continuous, bounded function denoting the noise emitted by an anthropogenic source;  $\alpha_i$  is the rate of anthropogenic noise in patch  $i$ ;  $\gamma$  is the rate of noise attenuation by various atmospheric factors such as variation in temperature, humidity and wind speed [63,64]; and  $\beta$  is a non-decreasing, non-negative, continuous, bounded function denoting the acoustic signals emitted by the population in response to anthropogenic noise, due to the Lombard effect.

The nature of the migration processes depends largely on the behavior of the individual and the quality of the habitat inhabited by the population. The model (Z), by appropriate choice of coefficients  $a_{ij}$  and  $b_{ij}$ , can accommodate a wide range of different migration processes. This research assumes that all patches are aligned, equally spaced, and distributed along a gradient in which noise decreases linearly. Furthermore, each subpopulation grows with logistic dynamics. Two migration processes between patches are considered, where individuals move only between adjacent patches:

- *Unidirectional dependent on noise level.* Individuals migrate towards patches with decreasing anthropogenic noise rate. For this, the migration rate is considered proportional to the noise as

$$a_{ij} = aI_i, \tag{1}$$

where, to simplify calculations, the value of  $a > 0$  is considered the same for all patches.

- *Random dependent on the difference between occupation levels.* Individuals migrate towards patch with lower occupancy level (independent of subpopulation sizes). For this, the migration rates is considered inversely proportional to the carrying capacity of each patch as

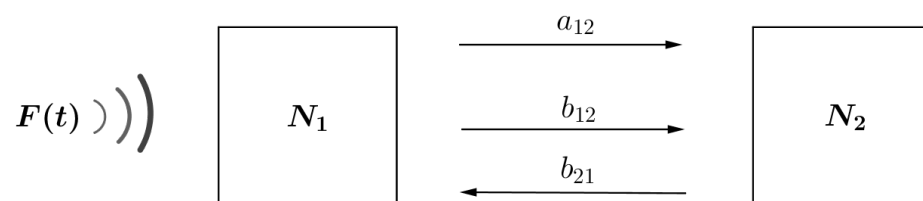
$$b_{ij} = \frac{b}{K_i}, \tag{2}$$

where  $b > 0$  is the marginal rate of migration, which for simplicity, in the calculations, is considered the same value for all patches.

Therefore, for  $n = 2$  (Figure 1), the following system of equations is obtained:

$$(\mathcal{M}) \begin{cases} N_1'(t) = r_1 \left(1 - \frac{N_1}{K_1}\right) N_1 + b \left(\frac{N_2}{K_2} - \frac{N_1}{K_1}\right) - aI_1 N_1 \\ N_2'(t) = r_2 \left(1 - \frac{N_2}{K_2}\right) N_2 - b \left(\frac{N_2}{K_2} - \frac{N_1}{K_1}\right) + aI_1 N_1 \\ I_i'(t) = \alpha_i F(t) + \beta(I_i(t))N_i(t) - \gamma I_i(t), \quad i = 1, 2, \end{cases}$$

where  $\alpha_1 > \alpha_2$ ;  $r_i > 0$  and  $K_i > 0$  are the intrinsic growth rate and carrying capacity of the population in patch  $i$ , respectively.



**Figure 1.** Diagram of two migration processes between patches. In order to avoid noise and occupied patches, individuals migrate by two processes: a unidirectional process where individuals migrate from patch 1 to patch 2 due to anthropogenic noise with migration rate  $a_{12} = aI_1$  and a random process where individuals migrate between patches 1 and 2 in search of the patch with the lowest occupancy level with migration rates  $b_{12} = b/K_1$  and  $b_{21} = b/K_2$ .

### 3. Model Analysis

To simplify the analysis of the  $(\mathcal{M})$  model, it is assumed that the level of noise intensity emitted by the anthropogenic source and the acoustic signals self-generated by the population are always constant. That is,  $F(t) = F_0 > 0$  and  $\beta(I) = \beta_0 > 0$ . In addition, the  $(\mathcal{M})$  model can be expressed in dimensionless quantities to reduce the number of parameters describing the system.

The following substitutions are used:

$$x_i = \frac{N_i}{K_i}, \quad I_i = y_i, \quad \delta_i = \frac{b}{rK_i}, \quad \rho = \frac{a}{r}, \quad k = \frac{K_1}{K_2}$$

$$\lambda_i = \frac{\alpha_i}{r}, \quad \eta_i = \frac{K_i}{r}, \quad \mu = \frac{\gamma}{r} \quad \tau = rt, \quad i = 1, 2.$$

Since only the noise dynamics in the patch closest to the source is of interest,  $y_1 = y$  is considered. The dimensionless quantities are substituted into the model  $(\mathcal{M})$  and the following system of equations is obtained:

$$(\mathcal{M}') \begin{cases} x_1'(t) = x_1(1 - x_1) + \delta_1(x_2 - x_1) - \rho y x_1 \\ x_2'(t) = x_2(1 - x_2) - \delta_2(x_2 - x_1) + k \rho y x_1 \\ y'(t) = \lambda F_0 + \eta \beta_0 x_1 - \mu y. \end{cases}$$

#### 3.1. The Existence of Equilibrium Points

The model  $(\mathcal{M}')$  is discussed, and it is observed that it has the following equilibrium points:

- $E_0 = (0, 0, \frac{\lambda F_0}{\mu})$ , which represents the extinction of the population in both patches.
- $E_1 = (x_1^*, x_2^*, \frac{\lambda F_0}{\mu} + \frac{\eta \beta_0 x_1^*}{\mu})$ , which represents the persistence of the population in both patches.

With

$$x_2^* = \frac{x_1^*}{\delta_1} \left[ \left( \frac{\rho \eta \beta_0}{\gamma} + 1 \right) x_1^* - \left( 1 - \delta_1 - \frac{\rho \lambda F_0}{\mu} \right) \right],$$

and  $x_1^*$  being a root of the following polynomial

$$-D_3 z^3 + D_2 z^2 + D_1 z + D_0 = 0,$$

where

$$D_3 = \left[ \frac{1}{\delta_1} \left( \frac{\rho \eta \beta_0}{\mu} + 1 \right) \right]^2,$$

$$D_2 = \left( \frac{2}{\delta_1^2} \right) \left( \frac{\rho \eta \beta_0}{\mu} + 1 \right) \left( 1 - \delta_1 - \frac{\rho \lambda F_0}{\mu} \right),$$

$$D_1 = \frac{1}{\delta_1} \left[ \frac{\rho \eta \beta_0}{\mu} + 1 - \delta_2 - \frac{1}{\delta_1} \left( 1 - \delta_1 - \frac{\rho \lambda F_0}{\mu} \right)^2 \right] \quad \text{and}$$

$$D_0 = \frac{1}{\delta_1} \left[ \delta_2 - \left( 1 - \delta_1 - \frac{\rho \lambda F_0}{\mu} \right) \right];$$

Since every polynomial of odd degree has at least one real root and by Descartes' sign criterion,  $x_1^*$  is the unique positive real root of the equation, provided that

$$0 < \left( 1 - \delta_1 - \frac{\rho \lambda F_0}{\mu} \right) < \delta_2 \quad \text{and}$$

$$\left( 1 - \delta_1 - \frac{\rho \lambda F_0}{\mu} \right) \left( \frac{\rho \eta \beta_0}{\mu} + 1 \right)^{-1} < x_1^*.$$

### 3.2. Local Stability Analysis

In this part, the local stability of the model ( $\mathcal{M}'$ ) is analyzed for each of the equilibrium points.

**Theorem 1.** *The equilibrium point  $E_0$  is unstable.*

**Proof.** The Jacobian matrix of the model ( $\mathcal{M}'$ ) at point  $E_0$  is calculated is obtained:

$$J(E_0) = \begin{pmatrix} 1 - \delta_1 - \frac{\rho\lambda F_0}{\mu} & \delta_1 & 0 \\ \delta_2 + \frac{k\rho\lambda F_0}{\mu} & 1 - \delta_2 & 0 \\ \eta\beta_0 & 0 & -\mu \end{pmatrix} \tag{3}$$

and the characteristic equation is given by

$$(\zeta^2 - A_1\zeta + A_0)(\zeta + \mu) = 0,$$

where

$$A_1 = 1 + \left(1 - \delta_1 - \frac{\rho\lambda F_0}{\mu} - \delta_2\right) \quad \text{and} \\ A_0 = \left(1 - \delta_1 - \frac{\rho\lambda F_0}{\mu} - \delta_2\right).$$

Using the Routh–Hurwitz criterion, the characteristic polynomial has roots with negative real parts if and only if  $A_1 < 0$  and  $A_0 > 0$ . However, if  $A_0 > 0$  then  $A_1 < 0$  is impossible. Therefore, the result is obtained.  $\square$

The above result indicates that, despite the noise, the subpopulations in each of the two patches never become extinct.

**Theorem 2.** *The equilibrium point  $E_1$  is stable if  $B_2 > 0, B_1 > 0, B_0 > 0$  and  $(B_2B_1 - B_0) > 0$ , where*

$$B_2 = \mu - [(1 - 2x_2^* - \delta_2) + (1 - 2x_1^* - \delta_1 - \rho y)] \\ B_1 = \eta\beta\rho x_1^* - \mu[(1 - 2x_2^* - \delta_2) + (1 - 2x_1^* - \delta_1 - \rho y)] + [(1 - 2x_2^* - \delta_2)(1 - 2x_1^* - \delta_1 - \rho y) \\ - \delta_1\delta_2 - \delta_1k\rho y] \\ B_0 = \mu[(1 - 2x_2^* - \delta_2)(1 - 2x_1^* - \delta_1 - \rho y) - \delta_1\delta_2 - \delta_1k\rho y] - \eta\beta\rho x_1^*[\delta_1k - 2x_2^* - \delta_2 - 1]$$

**Proof.** The Jacobian matrix of the model ( $\mathcal{M}'$ ) at point  $E_1$  is calculated and is obtained:

$$J(E_1) = \begin{pmatrix} 1 - 2x_1^* - \delta_1 - \rho y & \delta_1 & -\rho x_1^* \\ \delta_2 + k\rho y & 1 - 2x_2^* - \delta_2 & k\rho x_1^* \\ \eta\beta_0 & 0 & -\mu \end{pmatrix} \tag{4}$$

and the characteristic polynomial is given by

$$p(\zeta) = \zeta^3 + B_2\zeta^2 + B_1\zeta + B_0 = 0,$$

Using the Routh–Hurwitz criterion, the result is obtained.  $\square$

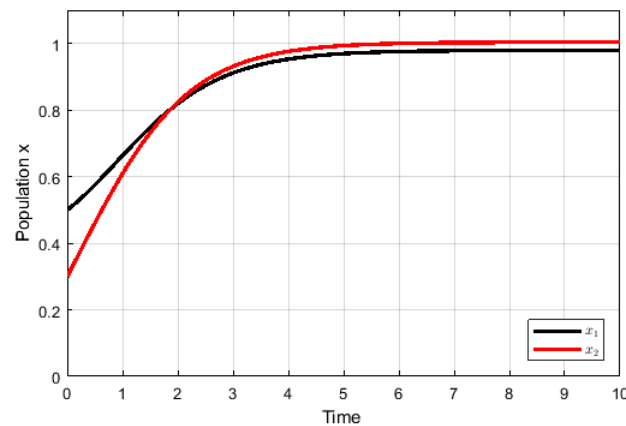
The previous result indicates that a necessary condition for the populations in both patches to stabilize is that  $B_2 > 0$ . That is, the noise attenuation rate must be high.

### 4. Numerical Simulations

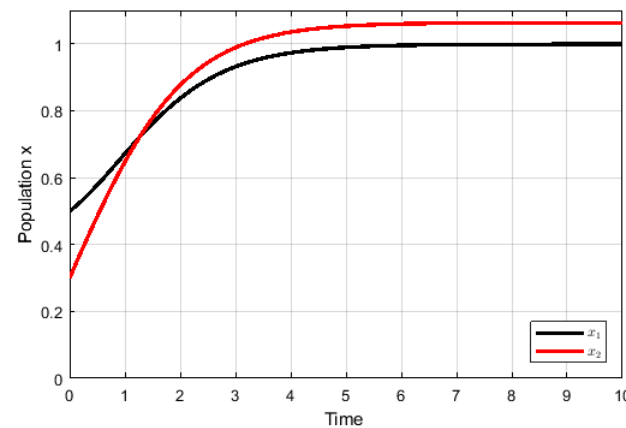
In this section, MATLAB software is used to numerically explore the dynamic behavior of the system ( $\mathcal{M}'$ ). To obtain the real values of the intrinsic growth rate ( $r_0$ ), the intraspecific competition coefficient ( $\lambda$ ), and the attenuation rates ( $\alpha, \gamma$ ), an empirical study is needed, with a concrete species and a controlled noisy environment. For the purposes of our research, we illustrate the results of our theoretical model using arbitrary selected values.

Let the values of the following parameters be  $\delta_1 = 0.5, \delta_2 = 0.5, \rho = 0.5, \lambda = 1, \eta = 1, \mu = 2$  and the initial conditions  $x_1(0) = 0.5, x_2(0) = 0.3, y(0) = 0.1, F_0 = \beta_0 = 0.1$ .

Note that Figures 2 and 3 show that as long as the noise is of low intensity, the differences in the carrying capacity of each patch do not produce substantial, long-term differences in the sizes of the subpopulations  $F_0 = \beta_0 = 1$ .

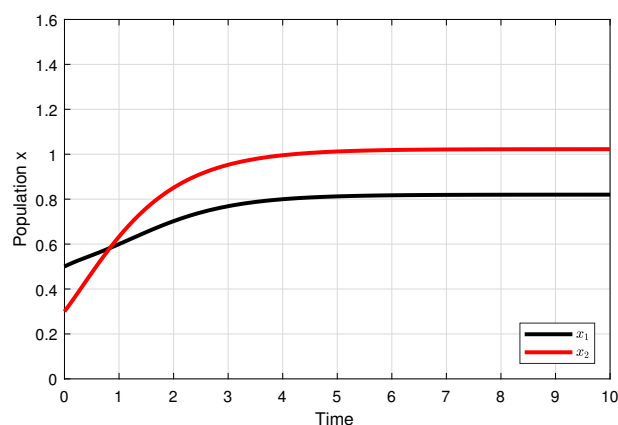


**Figure 2.** Evolution over time of the occupancy levels of two patches with different noise levels (more noise: black line; less noise: red line), when noise intensity is low. In this simulation,  $K = 0.5$ , i.e., the carrying capacity of the noisy patch ( $K_1$ ) is lower than that of the less noisy patch ( $K_2$ ).

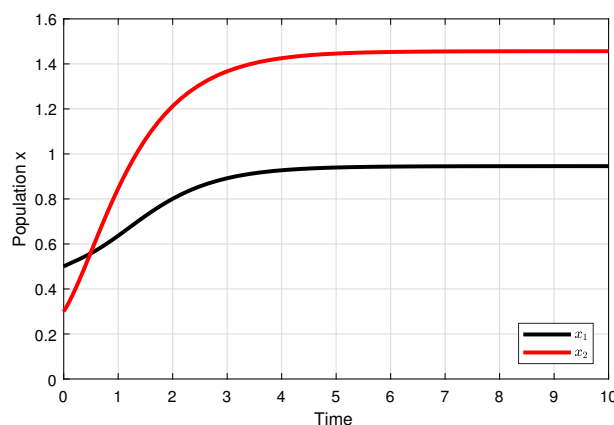


**Figure 3.** Evolution over time of the occupancy levels of two patches with different noise levels (more noise: black line; less noise: red line), when noise intensity is low. In this simulation,  $k = 3$ , i.e., the carrying capacity of the noisy patch ( $K_1$ ) is higher than that of the less noisy patch ( $K_2$ ).

Note that Figures 4 and 5 show that when noise intensity is high, the loading capacities of each patch are relevant produce more marked difference in the subpopulations. When  $K_1 < K_2$  (Figure 4), there is a relatively moderate difference in favor of the subpopulation in the second patch. When  $K_1 > K_2$  (Figure 5), the difference between the two subpopulations is more marked.



**Figure 4.** Evolution over time of the occupancy levels of two patches with different noise levels (more noise: black line; less noise: red line), when noise intensity is high. In this simulation,  $k = 0.5$ , i.e., the carrying capacity of the noisy patch ( $K_1$ ) is lower than that of the less noisy patch ( $K_2$ ).



**Figure 5.** Evolution over time of the occupancy levels of two patches with different noise levels (more noise: black line; less noise: red line), when noise intensity is high. In this simulation,  $k = 3$ , i.e., the carrying capacity of the noisy patch ( $K_1$ ) is higher than that of the less noisy patch ( $K_2$ ).

## 5. Discussion and Conclusions

There are stochastic [65–68] and deterministic [56] mathematical models that study noise as an important factor in the persistence of populations. However, to our knowledge there are no deterministic models that study noise as a cause of population migration. This research responds to this need in the literature and analyzes a metapopulation model using a system of equations that describes two migration processes between two patches. The first is a unidirectional migration of the population from the noisy patch to the less noisy patch. The noise is considered constant, chronic, and critical and originates from two sources, one anthropogenic and one biological (self-generated as a consequence of the Lombard effect). The second is a random migration in search of the patch with the lowest occupancy level.

The results are consistent with many empirical studies showing that in many terrestrial and aquatic animals, both anthropogenic noise and the occupancy level cause migration due to their potential detrimental effect on population survival [17,27–34,57–62]. These results indicate that, despite the noise, subpopulations in each patch never go extinct. This may be because the process of random migration in search of the patch with the lowest occupancy level constantly moves individuals towards the noisy patch (Theorem 1)). Furthermore, a sufficient condition for the long-term stabilization of the subpopulation sizes of both patches is that the noise attenuation rate is high (Theorem 2). When the noise intensity is low (Figures 2 and 3), the differences in the carrying capacity of each patch do not produce substantial long-term differences in the size of the subpopulations. However, when the

noise is high (Figures 4 and 5), the effects of difference in the loading capacities of each patch are relevant, thus producing a marked difference in subpopulation sizes. In both cases, the entire population increases until the asymptote, but the difference in size between the subpopulations in favor of the second population is more marked when  $K_1 > K_2$ .

In conclusion, the results of this research suggest that to conserve a high abundance of a species in noisy environments, proper management in reducing the level of anthropogenic noise intensity or otherwise increasing the rate of noise attenuation is necessary. For terrestrial species, such as birds, it may be useful to extend the surface of green spaces, which can be considered as vegetative noise screens [69–71], while for marine species avoiding or taxing high noise levels in naval sonars may be recommended [72,73].

Finally, it is noted that the literature with deterministic mathematical models describing this phenomenon is almost nonexistent. Therefore, this research opens a new line of study and confirms many empirical results on the detrimental potential of noise on species abundance.

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