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A general model linking environmental fluctuations and species richness is proposed. This model includes two important biological mechanisms. A first term describes the global negative effect of fluctuations on richness via stress and density-independent mortality; a second term represents the positive effect of perturbations on richness by competitive relaxation. Both effects are modeled as exponential functions. The model can be made richness-dependent putting the average competition coefficients as a function of the actual diversity. The system shows a non-trivial behavior since it has local maxima or minima in the richness function at intermediate values of environmental variability. The existence of these points depends on the ratio between stress sensitivity and competition coefficients. The discrete version of the model exhibits chaotic fluctuations when the initial richness is high.

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1   Introduction

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An old question in ecology is *how many species are there in a given place with a given level of fluctuations?* [14,15,17]. In fact, richness prediction is a fundamental problem both, in theoretical and applied ecology. Much of the variance in species richness of terrestrial organisms has been related to levels of available energy [10]; however, local patterns may be considered as depending on disturbance regimes.

Several models to describe the richness variation along a disturbance gradient have been proposed [11,13,15]; however, these models are either phenomenological [15] or very general [12], and they fail to predict, with the same mathematical and biological framework, a variety of data sets [1]. Models like those proposed by Dayton and Hessler [8], Connell [6], Huston [12] and Barradas [2] predict highest species richness under intermediate perturbations, but, in some cases [6,13], their predictions are qualitative; in the case of [2] the model only consider competitive interactions. There are no testable mathematical models considering simultaneously competition and stress. Moreover, the classical succession theory [5] states the existence of immature communities in fluctuating environments and mature or climacic communities in stable environments; on the light of this theory, the possibility of a low richness at intermediate disturbance regimes becomes plausible.

In this paper, we present and analyze a general model linking environmental fluctuations and the number of species (richness). The model includes two biological mechanisms: competition and physiological stress. We analyze the model's behavior under different values of the involved parameters and contrast the model's predictions against field data sets. Finally we describe and analyze some modifications of the initial model, including a discrete version.

2 Methods

The basic model makes the following assumptions:

1. Environmental fluctuations may have a negative effect on the number of species. This effect is due to physiological stress, which may even cause the extinction of some species.
2. Environmental variability may have a positive effect on richness because it relaxes interespecific competition.
3. Both effects are independent and additive.
4. Both effects, stress and competence, can be represented by average values in two different parameters, which may be considered as constants.

To analyze the model behavior under different scenarios we consider three cases. First, the competitive effect is bigger than the stress one; second, both effects have a similar magnitude; third, the effect of stress is the biggest:

- Environmental fluctuations may have a negative effect on the number of species. This effect is due to physiological stress, which may even cause the extinction of some species.
- Environmental variability may have a positive effect on richness because it relaxes interespecific competition.
- Both effects are independent and additive.
- Both effects, stress and competence, can be represented by average values in two different parameters, which may be considered as constants.

To contrast the model predictions against several sets of field data, we use richness values of benthic communities from Sousa Reis *et al.* [19], and earthworm richness data of forested soils [9]. We fit the model with each data set assuming a normal distribution of errors and minimizing the sum of square deviations [20].

In a second step, we derive three modifications of the model introducing different kinds of species-dependence in the competence parameter. For the last model, the discrete one, we analyze by means of simulation the effect of introducing exotic species in the system.

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3 Models and Results represent the negative effect of fluctuations (μ) on the species richness (S)

3.1 *The Basic Model represent the negative effect of fluctuations (μ) on the species richness (S)*

We represent the negative effect of fluctuations (μ) on the species richness (S) through an exponentially decreasing function:
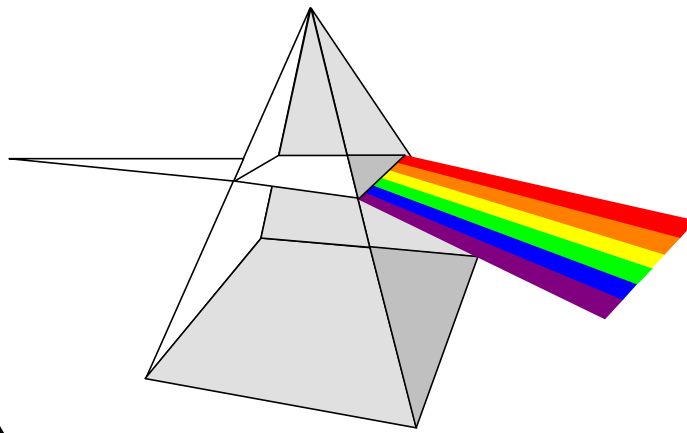
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Figure 1. This is a caption for figure one This is a caption for figure one This is a caption for figure one and one.

$$S_1 = S_0\, e^{-\alpha\mu} - A$$

where S_0 is the maximum number of species in a non-stress situation, μ is a measure of environmental fluctuation (or "noise"), α, called here "stress coefficient", is the parameter measuring the species sensitivity to fluctuations, and A is a correction term, necessary because of the existence of a fluctuation level above which the richness must be zero.

3.1.1 The Basic Model-I represent the negative effect of fluctuations (μ) on the species richness (S)

The positive effect of variability on the richness can be expressed as:

$$S_2 = S_m\,(1 - e^{-\beta\mu}) + B$$

where B is a minimum value of richness in a non-stress situation, and β is the average intensity of competitive interactions among species, called here "competitive coefficient". For intense fluctuations the richness function grows asymptotically up to $B + S_m$.

If we consider that both effects are additive, we may write the total richness (S_T) as:

- $S_T = S_1 + S_2$
- $S_T = S_0\, e^{-\alpha\mu} + S_m\,(1 - e^{-\beta\mu}) + C$

with $C = B - A$ constant.

To avoid the existence of correction terms, we can put the species number as a function of μ_∞, the minimum level of fluctuation above which there are no species; so, replacing in (3) has not correction terms. This formulation can be easily fitted in field studies because, under a gradient of fluctuation enough broad, μ_∞ may be estimated has not correction terms. This formulation can be easily fitted in field studies because, under a gradient of fluctuation enough broad, μ_∞ may be estimated.

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3.2   Model Behavior

The model was studied making the α/β ratio less, equal and greater than 1.

When the competitive effect is greater than the stress effect ($\alpha/\beta = 0.2$) we obtain a maximum of richness for intermediate perturbations (Fig. 1). If the weight of the two effects is the same ($\alpha/\beta = 1$) the richness lies down monotonically with the environmental fluctuation (Fig. 2) and the model is equivalent to the Mac Arthur's one [15]. When the stress coefficient is higher than the competitive coefficient ($\alpha/\beta = 5$) the species number has a minimum at intermediate levels of environmental fluctuation (Fig. 3).

Table 1 shows the response surface of the model.

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Table 1. Caption for Table.

Name	January	February	March
Mike Jones	20553.00	28036.00	35550.00
Pam Coburn	9177.00	9980.00	11000.00
Janis Kincaid	23788.00	998800.00	12300.00

3.3   Data Fitting

The data from Sousa Reis *et al.* [19] were fitted considering depth as an indicator of stability; so we assign the maximum noise to intertidal samples. In consequence, the fluctuation intensity μ was measured as

$$\mu = \text{Depth (in meters)} + 30$$

where we must remember that profundity is a negative value; so the noise is zero at 30 m below the littoral zone (0 m).

Figure 5 (a to f) shows the results of fitting the model to different group of data, corresponding to   benthic organisms   at different taxonomic levels (Crustacea, Amphipoda, Decapoda, Polychaeta, Mollusca and Gasteropoda). In all cases the fitting is very good.

In the case of earthworms [9], oligochaetes were collected from a soil in a field artificially forested with oak (*Quercus roburs*) and the noise indicator was computed as the coefficient of variation of the inter-tree distances, which is a good indicator of the variation of the soil exposure to the sun light. Results are shown in figure 6. The fitting is very good again.

4   Discussion

Our results are representative of different real ecological situations.

A maximum for the richness at intermediate levels of disturbance is predictable from models of competence [2], metapopulation models [4], general models of ecological succession [12,13] or models for populations interacting in heterogeneous environments

[6,7]. In all these cases, richness is maximized at intermediate levels of perturbations by effect of competence relaxing; this effect prevents competitive exclusion. When environmental fluctuations are high, all species are affected and the richness decays.

When both effects, competition and stress, are made equivalent, the richness diminishes monotonically following an exponential law. This result is similar to Mac Arthur's, who derived his model from a theorem of information theory and validated them with field data [15]. This is probably a common behavior at large scale, because competition and stress effects are roughly equivalent at the regional level. Undoubtly, understanding species diversity in local assemblages require knowledge of processes acting at larger spatial scales [3], but there are rules governing the assembly of local communities.

When the effect of competence is less important than the stress one, richness has a minimum at intermediate perturbations; this predictions are similar to the ones of the classical theories of succession [16] in which there exists a replacement of a mature community, with K-selection, which is characteristic of stable environments, by a community with species adapted to fluctuating environment (r-selection).
Our model integrates the three situations in a general framework showed in Figure 4.

The introduction of a sort of richness-dependence in β gives a new spectrum of behavior in the model because of the possibility of having several local maxima and minima. Moreover, the unstability when the initial richness is increased (figure 7) has important consequences for management options. We show that species introduction may produces a chaotic dynamic with a high probability of extinction or a hard loss of biodiversity.

5   Acknowledgements

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