

Competitive release and area effects

F. Azevedo^a, R.A. Kraenkel^{a,*}, D.J. Pamplona da Silva^b

^aInstituto de Física Teórica, Universidade Estadual Paulista-UNESP, R. Dr. Bento Teobaldo Ferraz 271, 01140-070 São Paulo, Brazil

^bUniversidade Federal de Alfenas, Campus de Poços de Caldas, R. Corumbá 72, 37701-100 Poços de Caldas, Brazil

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ABSTRACT

A common situation observed in fragmented habitats is that species densities diminish within smaller fragments. Some species, however, do show an opposite tendency. We argue that release of competition between a strong competitor and a weak one is a plausible explanation for these different sensitivities to area reduction. We provide a quantitative model for competitive release caused by habitat limitation, solely based on the balance of diffusion and growth of the species. We show that in small habitat patches the stronger competitor has its density diminished, as opposite to the weaker competitor who, in a certain area range, has its density increased. We examine field data from an ecological experiment in Amazonia (BDFFP) which measured densities of two Amazonian rodents who showed opposite sensitivity to area reduction and we argue that our model explains the observations accurately. This implies that (i) area reduction is a strong factor determining densities of species in patches of habitat, regardless of considerations on degradation or edge effects and (ii) that species interactions have to be taken into account to explain sensitivity to size of the patches in ecological communities. We also discuss alternative explanations, such as predator release and effects due to imperfect isolation. Moreover, we stress the conceptual and mathematical simplicity of our model, which, nevertheless explains a phenomenon not yet well understood.

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1. Introduction

Exploitative competition between two or more species is an indirect interaction between competitors who seek to obtain resources that are limited (Park, 1962). Strong competitive ability may result in a competitor outcompeting a weaker one, drastically depleting the population of the latter, eventually leading to its local extinction. This situation is known as competitive exclusion (Gause, 1932).

The effects of competition can depend by many external factors, such as seasonality (Namba, 1984), stochasticity (Chesson and Warner, 1981), habitat fragmentation (Huxel and Hastings, 1998) or spatial heterogeneity (Tilman, 1994), which can promote coexistence in situations which would otherwise lead to exclusion. Different species may show different sensitivities to these factors. When the external effect on a pair of competitors is such that the stronger is more negatively affected than the weaker, the competitive pressure on the latter is milder and we say that competitive release occurs (Kareiva, 1982). This may result in benefits for the weak competitor, whose population can consequently be augmented, avoiding competitive exclusion. Competitive release is the result of a balance: it will be incremental for the

population of the weak competitor if the gain from smaller competitive pressure is larger than the damage due to the external effects that affect both competitors.

Release of competition should be explained by the effects of some causative factor on the system. Here we argue that area effects – that is, the fact that a habitat is finite – are one such factor. Moreover, we invoke only diffusion through the borders of a patch and the intrinsic growth of the population on that same patch as the mechanisms mediating area effects and leading to competitive release.

Let us recall the essence of area effects when a single theoretical population inhabits a patch of habitat, surrounded by a matrix, supposed to be completely inhospitable (Skellam, 1951). Two tendencies are in action: the intrinsic growth of the population and the diffusion – the population flux – through the boundaries. The first of these is proportional to the area of the fragment, the second to the perimeter. Therefore, the first dominates large areas and implies persistence of the population, the second is more important in small fragments and leads to local extinction. A critical area exists, separating both regimes. The theory can be formulated mathematically through the use of the Fisher–Kolmogorov equations on a finite domain (Ludwig et al., 1978; Kenkre and Kuperman, 2003). The critical area turns out to be $\pi^2 D/r$, where D is the diffusion constant associated to the species and r is its intrinsic *per capita* growth rate. The expression for the critical area makes it patent that its existence stems from the counter-

* Corresponding author. Tel.: +55 1133937821.

E-mail address: kraenkel@ift.unesp.br (R.A. Kraenkel).

acting effects of diffusion and growth. The factor D/r has units of area and defines the square of the typical diffusive length, L_D , and represents an intrinsic, species-specific, spatial scale. The case of the matrix being not completely inhospitable, theory has been developed indicating that a small remaining population may inhabit the fragment (Artiles et al., 2008). Ecological experiments (Ferraz et al., 2007), testing the sensibility to area effects in understory birds in the Amazonian forest provide one of the best indications in favor of this basic theory.

The above result is valid if species do not interact, or the interaction has no strong effects on an ecological scale. The conclusions do not hold, however, if interactions are important. Here we consider the competition between two species in a limited habitat and examine the status of the principle of competitive release in this case. We will do so by considering a competitive Lotka–Volterra equation with diffusion and with the restriction that the population is zero outside a square of area L^2 . In Cantrell et al. (1998) and Fagan et al. (1999) (see also Leung (1980)) this same problem has been considered and coexistence has been shown to be possible by means of a mutual invasibility condition. Here we take a step further and look for the values of the equilibrium densities, more specifically, the maximum of the equilibrium densities inside the habitat patch. These values are important because they can be connected with actual field observations. Besides, knowing how equilibrium densities depend on the patch's area gives a more quantitative understanding of coexistence, and allows to establish ranges of area values where coexistence is more likely to be observed. A similar problem has also been considered in Mimura et al. (1991), but with different boundary conditions and involving considerations on the shape of the domain. Other authors (Britton, 1989; Holmes et al., 1994), have also touched upon the interplay of diffusion and interactions, focusing however on other aspects than ours. Here we provide a simple model that shows a qualitative result that can be extended to more complex contexts, and at the same time, offering quantitative comparison to data, namely two rodent species in fragments of the Amazonian forest.

In order to assess equilibrium densities we cannot rely on a linear analysis as these densities depend on carrying capacities and interaction terms. Here we numerically integrate the differential equations on a long enough time scale and provide plots of the dependence of maximum densities on area values.

We proceed as follows: in Section 2 we define the model and obtain a pattern of competitive release as consequence of area limitation; in Section 3 we compare the model results with previously published results on rodents in fragments of the Amazonian forest; in Section 4 we discuss more general models; and in Section 5 we set out to discuss the results in a broader context.

2. The model

Let us begin with a general case of two species, labeled 1 and 2, whose dynamics obeys the competitive Lotka–Volterra model with diffusion (Pacala and Roughgarden, 1982), which reads in non-dimensional variables (see Appendix A for details):

$$\frac{\partial \theta_1}{\partial t} = \nabla^2 \theta_1 + \theta_1 [1 - \theta_1 - \gamma_1 \theta_2] \quad (1)$$

$$\frac{\partial \theta_2}{\partial t} = \kappa \nabla^2 \theta_2 + \alpha \theta_2 [1 - \theta_2 - \gamma_2 \theta_1] \quad (2)$$

Here, θ_1 and θ_2 are the populations of species 1 and 2 measured in terms of their carrying capacities; time is measured in terms of the inverse of the intrinsic growth rate of species 1 and space is measured in terms of the typical diffusive length of species 1. The constant α is the ratio of the intrinsic growth rate of species 2 to the intrinsic growth rate of species 1. Finally, κ is the ratio of the diffusivities of both species (D_2/D_1) and γ_1 and γ_2 are phenomenological competition coefficients. Henceforth we will take α and κ to be equal to one, so that the results that we obtain are representative of effects of area on competition. This is a kind of neutrality with respect to growth and diffusion rates.

As mentioned above, this system of equations has been subject of previous studies, notably in Cantrell et al. (1998). There, the possibility of competitive reversal and coexistence has been established by a linear analysis. Exclusion and coexistence patterns depend on the parameters that appear in the equation, as well as on the domain where the equation is being integrated. As our focus in this work is the effect of area reduction, we will take fixed values for the parameters in a first moment and study the sensibility of population levels to changes in area.

We have numerically integrated the above equations on a square domain with the additional supposition that populations go to zero on the border of the habitat (Dirichlet boundary conditions). It follows from the theory of partial differential equations that we cannot impose a zero population flux on the boundary in the same problem. Indeed the flux is non-zero, and represents flow of individuals into the matrix. Further, we took two very different values of γ_1 and γ_2 . With $\gamma_1 = 0.5$ and $\gamma_2 = 1.8$ we would have competitive exclusion of species 2 in favor of species 1 if the habitat were unbounded. The limited area of the habitat modifies densities in the habitat. In Fig. 1 we plot the spatial (local) maximum of the densities θ_1 and θ_2 in terms of the area of the fragment. As can be seen, both species respond to area reduction in a very different way. Although both go to zero for very small areas, species 2 shows a coexistence region with species 1. This means

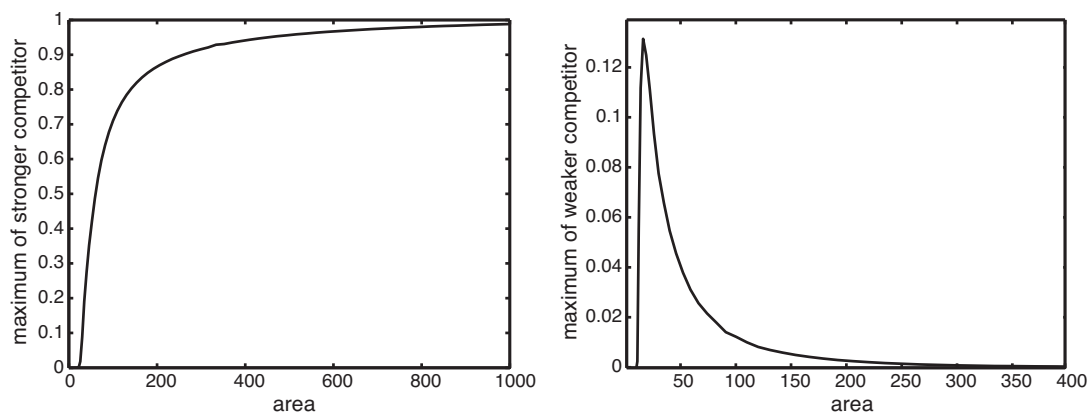


Fig. 1. The spatial maximum values of θ_1 (left) and θ_2 (right) in the equilibrium situation are plotted against the area of the domain. We used $\gamma_1 = 0.5$ and $\gamma_2 = 1.8$. For large areas, species 1 tends to outcompete species 2. For very small areas, both species go to zero, but in an intermediate range, coexistence is possible.

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