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## Effect of the landscape context on the density and persistence of a predator population in a protected area subject to environmental variability

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### ABSTRACT

Protected areas are the most important tool for the conservation of biodiversity. However, many species are area-demanding and their populations seldom meet their space requirements in reserves. In this context, the unprotected exterior becomes an important part of their home range, and variations in habitat quality of the surroundings of a protected area might affect the dynamics of populations. Using a spatially explicit simulation model, we studied the effect of the surrounding landscape of a protected area on the density and persistence of a predator population inhabiting inside the reserve in different conditions of environmental variability. We simulated individuals of a predator population, their herbivorous prey and a vegetative substrate in a landscape comprised of a square protected area and different types of habitat quality outside the reserve. We studied the combination of three substrate qualities of protected area (inside) with three of the landscape context and three levels of variability of productivity. Our results showed that there were strong effects of both the relative quality of the surrounding landscape and of the environmental variability on the density and persistence of the simulated population inside the protected area. More importantly, we showed that complex patterns emerge when spatial heterogeneity and temporal variability interact with population dynamics. Specifically, under high environmental variability, when the protected area had a high habitat quality, the highest population persistence was not attained when the exterior was also of high quality, but when the surroundings had an intermediate quality. The latter result suggests that, under the mentioned conditions, small enhancements in the quality of the matrix may have, for some species, better effects on increasing persistence in small reserves than large and costly enhancements.

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### 1. Introduction

The reduction of natural spaces in the world due to human expansion has caused protected areas to become a fundamental support for maintaining the stability of ecological services. However, in the last years a great amount of information has made evident the failure of current reserve systems in achieving the proposed conservation objectives (Buechner et al., 1992; Schonewald-Cox et al., 1992). The lack of planning in the design of protected areas (Deguise and Kerr, 2006) and their reduced sizes (Simonetti, 1995) are described in the literature as common factors that negatively affect the management of many important species and their conservation status in many reserves throughout the world. In this context, it is known that the success of conservation measures of many species and communities that inhabit protected

areas but constantly cross the administrative limits is highly influenced by the areas outside these protected spaces (Woodroffe and Ginsberg, 1998; Ogada et al., 2003; Baskett et al., 2007). Therefore, a conservation approach that explicitly considers the surrounding areas is needed.

Of particular importance in terrestrial protected areas is the case of large predators (Beschta and Ripple, 2009). For example, many large carnivores tend to move beyond the boundaries of protection, triggering conflicts between people and their populations (Gusset et al., 2009; Patterson et al., 2004). The latter is the major source of mortality for large carnivores (Woodroffe and Ginsberg, 1998; Woodroffe, 2000), causing, in many cases, the landscape surrounding protected areas to act as population sinks for these species, especially for those with a wide range in relation to the reserve size (Marker et al., 2008; Woodroffe and Ginsberg, 1998). Carnivore populations living outside protected areas may also be affected by habitat degradation (Cardillo et al., 2004) reductions in prey availability or due to an increase in hunting pressure. Therefore, population parameters of the carnivore species that inhabit a protected area may be very sensitive to the effect of the

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conditions outside protected spaces (Revilla et al., 2001; Schone-wald-Cox et al., 1991; Simonetti and Mella, 1997).

Environmental stochasticity modifies the population dynamics of species that are directly related to the primary production level (Georgiadis et al., 2007; Sæther, 1997; Saltz et al., 2006), also affecting the top levels of trophic webs (Holmgren et al., 2001; Trahan et al., 2007). Those changes in productivity also may influence individual behavior as a response to stress. For example, Patterson et al. (2004) showed that hunting events of livestock by carnivore populations outside Tsavo East Park in Kenya are correlated to precipitation events. If predators leave a protected area as a response to temporal changes in habitat quality (in addition to normal natal dispersal), the characteristics of the surrounding landscape and the environmental variability may influence the behavior and dynamics of these populations and therefore their viability. We developed a spatially explicit individual-based simulation model in order to determine the effect of the habitat outside a protected area on the density and persistence of a “generic” predator population that inhabits the interior of a reserve that it is subjected to different degrees of environmental disturbances.

Understanding how the heterogeneity and environmental variability of a landscape interact and affect population and community dynamics, is an important area in applied ecology, and it has implications for successful conservation management in the long term. However, the design of animal conservation plans on a large scale is often limited by the lack of relevant biological information regarding the species (Kramer-Schadt et al., 2004; Schadt et al., 2002; Wiegand et al., 2004), in particular empirical information on how species respond to landscape structure. In this regard, our work offers new insights for the management of mobile populations in a context of environmental variability.

## 2. Method

### 2.1. The model

The description of the model follows the protocol created by Grimm et al. (2006) to explain Individual Based Models (IBMs) within an ecological framework. Following the description of the model, we explain the experiments conducted in detail.

#### 2.1.1. Purpose of the model

The objective of this model is to quantitatively evaluate the effect of the habitat in the exterior of a protected area on the dynamics and persistence of a population of predators inside the latter, and subject to environmental variability.

#### 2.1.2. State variables and scale

We created a  $200 \times 200$ -cell matrix with an interior patch, measuring  $100 \times 100$ , representing the protected area. Each cell maintained a level of vegetation  $V$  between 0 and a carrying capacity  $K$  (Fig. 1).

Spread out throughout the landscape were individuals of the prey and carnivore populations (Fig. 1). Each predator individual had a weight  $W$  between  $[W_{\min} = 11, W_{\max} = 16]$  that represented the body condition of the animal. We defined the habitat quality  $Q$  as the intrinsic conditions that determined the potential of vegetative growth from year to year for the interior and exterior of a protected area ( $Q_{\text{in}}$  and  $Q_{\text{out}}$  respectively). The environmental variability was entered into the system in the form of a factor (i.e. rainfall) that varied among years and which affected the amount of vegetative substrate in each cell (Vegetative substrate =  $f$  (intrinsic habitat quality  $Q$ , rainfall)) (Fig. 1), therefore affecting the carnivore population in a undirected way.

### 2.1.3. Process overview and scheduling

The routines that dictated the reproduction of both the prey and the predator were activated annually, predator mortality was activated monthly, and feeding and movement were initiated daily. Each year  $T$  contained 6 “months” and each month contained 30 days  $t$ .

### 2.1.4. Design concepts

**2.1.4.1. Emergence.** The dynamics of the predator population emerged from the interaction of the individuals with their nearest environment, that is, with the prey. The prey were the connection between the predator population and the environmental variability (expressed by changes of the vegetation levels). The individuals that survived from one period to another were tallied at the end of the season and the total number of individuals was the population size.

**2.1.4.2. Sensing.** Each individual predator knew its own weight (sensation of hunger) and, by function of this, modified its future actions such as movement, feeding, reproduction, and death.

**2.1.4.3. Stochasticity.** The movement and feeding of a prey depended on the substrate conditions of the cell in which it was found each day, and these actions were governed by probability functions. In the case of the predator, hunting attempts and movement were also a result of stochastic processes. The number of cells traversed by an individual in a day was a probabilistic process depending on the weight of the individual (sensing).

**2.1.4.4. Observation.** The model annually recorded the population density within the protected area.

### 2.1.5. Initialization

Two thousand prey and 100 predator individuals were “sown” in the landscape in a random manner, maintaining a scale relationship between the number of prey and predators (Carbone and Gittleman, 2002). The quantity of the initial vegetative substrate of each cell was a random value with normal distribution where the mean depended on the habitat quality assigned to the area.

### 2.1.6. Input

Each landscape cell had an annual substrate input that varied in relation to the location of the cell in the landscape (e.g. inside vs. outside the protected area). The environmental factor subjected to inter-annual variability (rainfall) was entered into the system at the same rate for the entire landscape.

### 2.1.7. Sub-models

**2.1.7.1. Vegetative substrate.** In each cell, a level of vegetative substrate  $V$  was calculated. The value of the substrate at a point in time  $T + 1$ , without taking into account the effects of herbivory, was:

$$V_{(ij)}^{T+1} = V_{(ij)}^T + \text{Rain}_{(T)} * Q_{(ij)}; \in [0 - K], \quad (1)$$

where  $V_{(ij)}^T$  was the level of substrate of the cell  $(ij)$  in the year  $T$ ,  $\text{Rain}_{(T)} \sim N(1, \sigma)$  the annual rainfall,  $Q_{(ij)}$  the quality of the habitat within the cell  $(ij)$ , and  $K$  the carrying capacity. It is important to point out that  $\text{Rain}_{(T)}$  was a sequence that affected all space equally and without temporal correlation.

**2.1.7.2. Feeding of prey (herbivory).** Each individual prey had a probability  $p_f$  between 0 and 1 of foraging.

$$P_f = V_{(ij)}^t / K; \in [0 - 1], \quad (2)$$

where  $V_{(ij)}^t$  was the value of the substrate on a given day  $t$  in the cells  $(ij)$  and  $K$  the carrying capacity. That is, there was a positive

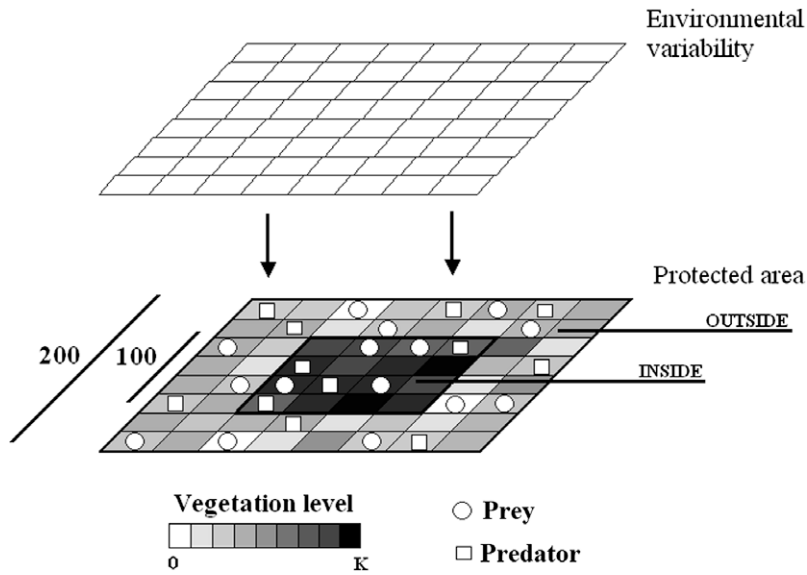


Fig. 1. Interior and exterior of a simulated protected area and the prey and predator populations. The environmental variability affects the entire landscape.

relation between the level of vegetation and the possibility that the prey would feed that day  $t$  on the cell in which it was. After the prey was effectively nourished, a constant vegetation rate  $C$  was eliminated from the cell. This structure affected the dynamics of the vegetation in such a way that the level of vegetation  $V$  might decrease daily. Therefore, the effective level of vegetation in a given year  $T + 1$  was:

$$V_{(ij)}^{T+1} = V_{(ij)}^T + \text{Rain}_{(T)} * Q_{(ij)} - \text{NF}_{(ij)}^T * C; \quad \in [0 - K], \quad (3)$$

where  $\text{NF}_{(ij)}^T$  was the number of times in a year  $T$  that preys were effectively nourished off the vegetation of the cell, and  $C$  the rate of consumption of each prey.

2.1.7.3. Prey movement. Prey moved one cell per day with probability

$$p_m = 1 - V_{(ij)}^t / K = 1 - p_r. \quad (4)$$

The latter means that the greater the quantity of vegetation, the greater the chances of eating and the lower the probability of movement for the prey.

2.1.7.4. Feeding of predators. Hunting depended on both the weight  $W$  of the individual predator (hunger) and chance. When  $W < W_{\max}$ , and prey were present in the cell, the individual engaged in hunting with a probability of success of less than one and with a maximal capture rate of three prey per time step. On the contrary, when  $W \geq W_{\max}$ , the individual did not attempt to hunt. For each prey that was successfully hunted, the predator increased its weight by a constant amount  $\omega$  ( $W^{t+1} = W^t + \omega$ ).

2.1.7.5. Predator reproduction and mortality. For the sake of simplicity, our model simulated asexual organisms and the reproduction of the predator depended solely on the weight of the individuals at the end of a year  $T$ . If, at the moment of reproduction, the weight  $W$  of an individual was higher than a threshold reproduction weight  $W_{\text{rep}}$ , the “mother” gave birth to a juvenile (with a probability of 0.8). When the reproduction occurred, the “mother” individual lost a constant amount of weight. In addition, every day each predator lost a constant amount of weight as an excretion process. If at the end of a month  $W < W_{\min}$ , then the individual died with probability =1.

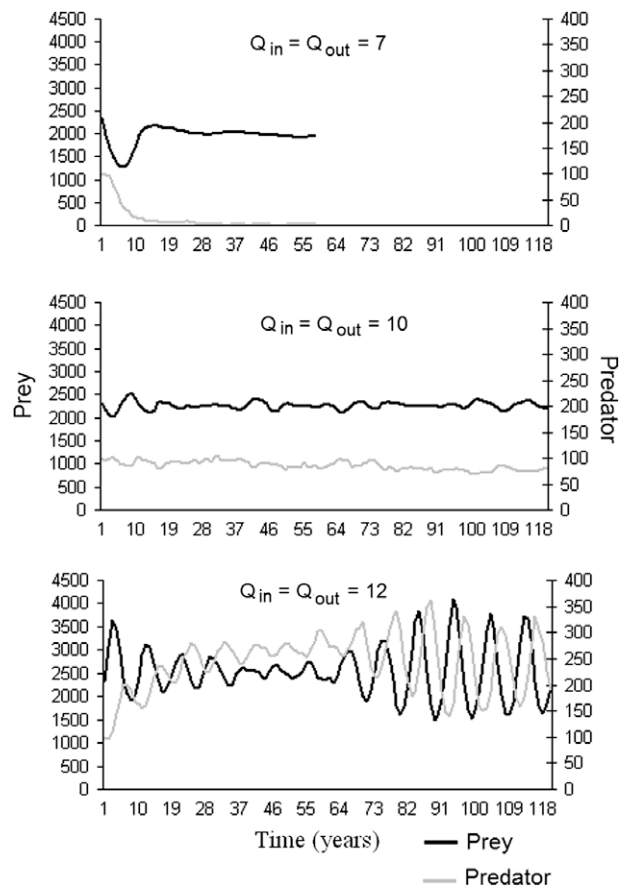


Fig. 2. Dynamics of prey (dark line) and predator (gray line) populations in the entire landscape as a function of three different levels of habitat quality in the entire landscape ( $Q_{in} = Q_{out}$ ). When  $Q_{in} = Q_{out} = 7$ , the predator population goes extinct and the system stops.

2.1.7.6. Prey reproduction and mortality. Each year prey reproduced, and the number of offspring per individual varied between 0 and 5, depending on the average level of substrate of the eight closest neighboring cells and the presence of at least one adult prey in the

central cell. The mortality occurred after reproduction (the “mother” died) and when a carnivore hunting intent was successful.

**2.1.7.7. Predator movement.** When the weight of individual predators was close to the minimal weight  $W_{min}$  they had the chance to move long distances, but when  $W$  was close to  $W_{max}$ , individuals moved short distances. This mechanism was important because it related the weight of the individuals to the search of food (behavior), increasing the foraging area and the chance to explore outside the reserve in periods of scarcity.

We defined  $Mx$  and  $My$  as the number of pixels that an individual covers per day, with  $x$  and  $y$  the coordinates of the lattice. Both were random integers with uniform distribution in the interval  $[-D(W), D(W)]$ , with

$$D(W) = 1 - (1.45 - W/W_{min}) * 11; \quad \in [1, 6] \text{ for } W_{min} \leq W \leq W_{max}, \quad (5)$$

where  $W$  is the weight of the carnivore before movement, and  $W_{min}$  is the minimal weight.

$D$  is a linear function defining the potential maximum distance that an individual can reach. The actual number of sites walked by an individual, and its direction, were related to the random integers

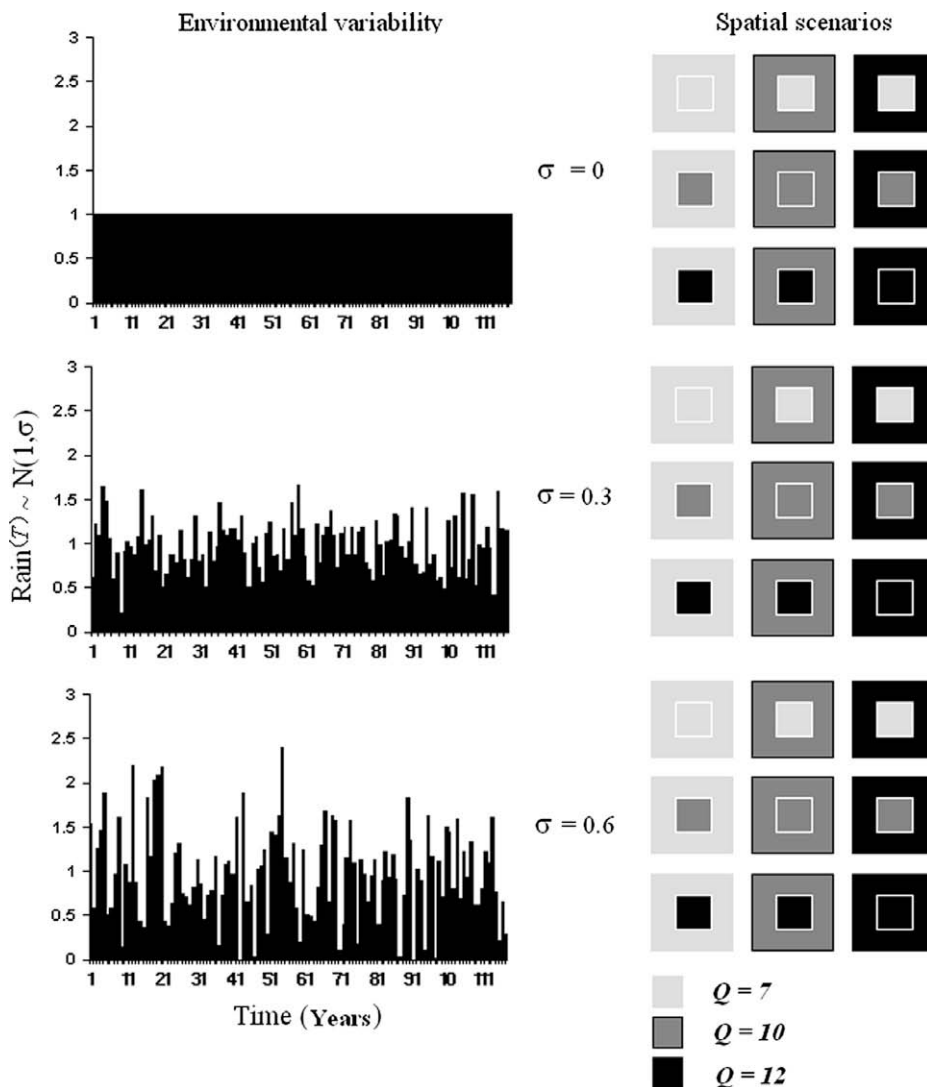
$$Mx = \text{round} [(2 * D) * \text{rand}_1 - D], \text{ and} \\ My = \text{round} [(2 * D) * \text{rand}_2 - D].$$

This means that even though the individual had the chance to move longer distance due to its body mass ( $D(W)$ ), the final distance and its direction were randomly assigned ( $Mx$  and  $My$ ).

**2.2. Experiments**

We defined three different habitat qualities  $Q$ : poor, average and, good quality ( $Q = 7, 10$  and  $12$  respectively, Fig. 2). With the latter, we created nine spatial scenarios by combining the three different levels of habitat quality in the interior ( $Q_{in}$ ) and the exterior ( $Q_{out}$ ) of the protected area ( $3 \times 3 = 9$ ).

Additionally, we simulated three different degrees of environmental variability. In the first case, the rainfall index was entered into the system with no inter-annual variation ( $\text{mean} = 1; \sigma = 0$ ). In the second and third cases, the rainfall was entered as a sequence of normally distributed values ( $\text{mean} = 1; \sigma = 0.3, \sigma = 0.6$ , respectively). In the last case, the value of 0.6 corresponded to the standard deviation of a normalized rainfall series for La Serena ( $29^{\circ}54'S, 71^{\circ}15'W$ , Chile), an area subjected to important El Niño and La Niña events (Holmgren et al., 2001). The combination of



**Fig. 3.** The twenty-seven scenarios. Each one is a combination of habitat quality inside and outside of the protected area (nine combinations) and one environmental regime (three more combinations).

all three factors and levels produced a total of 27 simulation scenarios ( $9 \times 3 = 27$ ; Fig. 3).

We ran simulations over a 120-year period, but only analyzed the last 100 years in order to eliminate the effect of the initial conditions (*Initialization*).

We conducted 20 replicates for each scenario, and the proportion of replicates in which the predator population became extinct determined the percentage of extinctions per scenario.

### 3. Results

#### 3.1. Population density

The greatest population levels inside the reserve were obtained in the scenarios that had a good quality exterior and a low degree of environmental variability ( $Q_{out} = 12$ ;  $\sigma = 0$ ; Fig. 4). Density decreased considerably in the scenarios with negative habitat quality in the exterior ( $Q_{out} = 7$ ), independently of the level of noise. The greatest oscillations occurred mainly when the conditions were positive both within and outside of the protected area ( $Q_{in} = Q_{out} = 12$ ) and when the variability was high ( $\sigma = 0.6$ ; Fig. 4).

#### 3.2. Persistence

There were marked differences in extinction likelihood in the entire landscape, particularly for scenarios with different environmental variability. The greatest number of extinctions was observed in the scenarios with poor quality, both inside and outside ( $Q_{in} = Q_{out} = 7$ ; Fig. 5). For the scenarios without environmental variability ( $\sigma = 0$ ), extinctions were only seen in the scenarios with poor quality conditions both in the interior and the exterior

( $Q_{in} = Q_{out} = 7$ ). In the scenario with negative conditions outside the reserve and positive conditions inside ( $Q_{in} = 12$ ;  $Q_{out} = 7$ ), there were no extinctions (Fig. 5).

For the scenarios with intermediate environmental variability ( $\sigma = 0.3$ ), the findings were very similar to the scenarios without variability, but the experiment in which the conditions were poor in the exterior and good in the interior ( $Q_{in} = 12$ ;  $Q_{out} = 7$ ) had 5% chance of extinction (Fig. 5).

In the experiments with the greatest environmental variability ( $\sigma = 0.6$ ), the results showed a high percentage of extinctions in the scenario with negative conditions in both the interior and exterior, just as in the scenario with positive conditions in both the interior and exterior ( $Q_{in} = Q_{out} = 12$ ).

Surprisingly, in an environment of high variability ( $\sigma = 0.6$ ), the scenario that showed the least percentage of extinctions was that with good conditions in the interior and average habitat quality in the exterior ( $Q_{in} = 12$ ,  $Q_{out} = 10$ ). As a result of this, we decided to increase the number of replicates from  $n = 20$  to  $n = 60$  in the nine scenarios with maximum variability ( $\sigma = 0.6$ ), with the aim of elucidating whether the observed trend was significant. In fact, in the scenario with the best habitat quality in the interior and with a surrounding area with conditions of average quality, the results showed a significant decrease of extinctions (40%) compared to the scenario with good quality inside and outside (60%; chi square,  $p < 0.025$ ; Fig. 5).

### 4. Discussion

Our results showed that the landscape context of a protected area may have a significant effect on the density and persistence of a population of a virtual predator inhabiting the reserve. First,

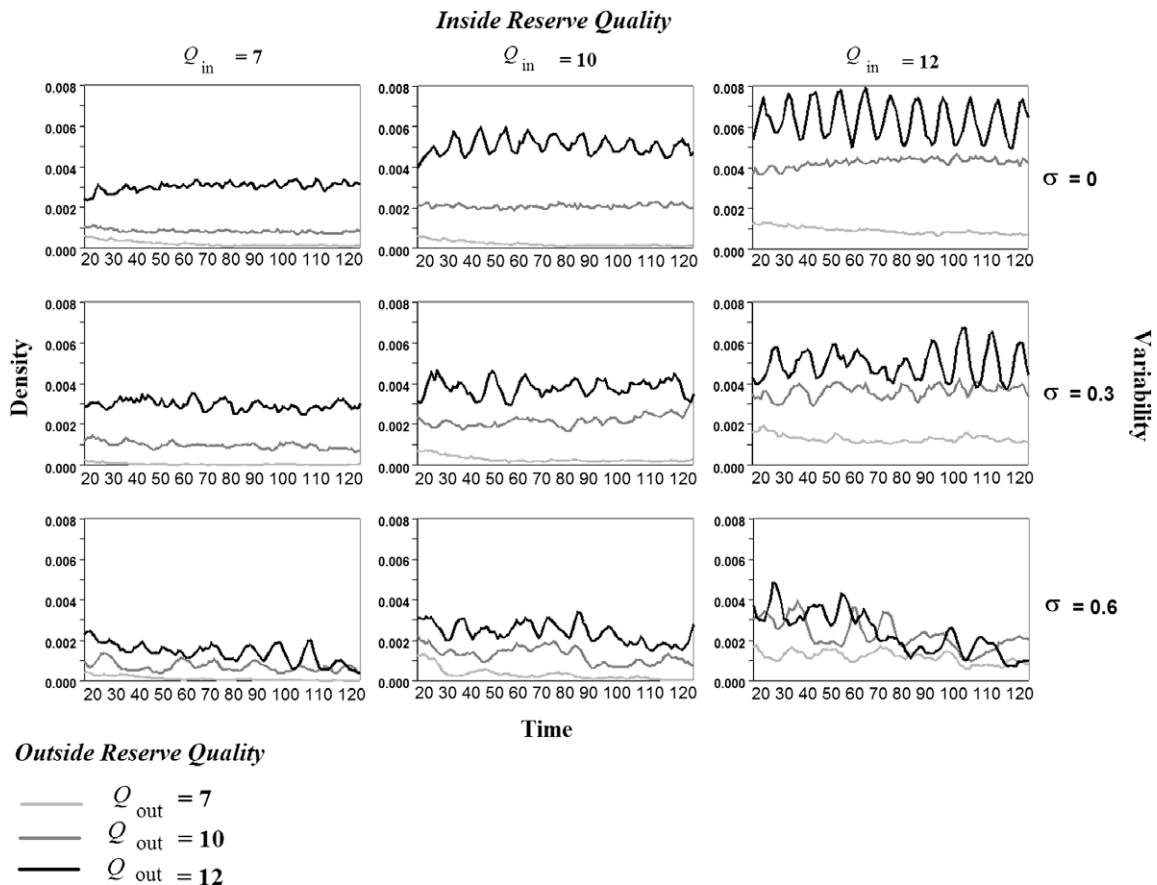
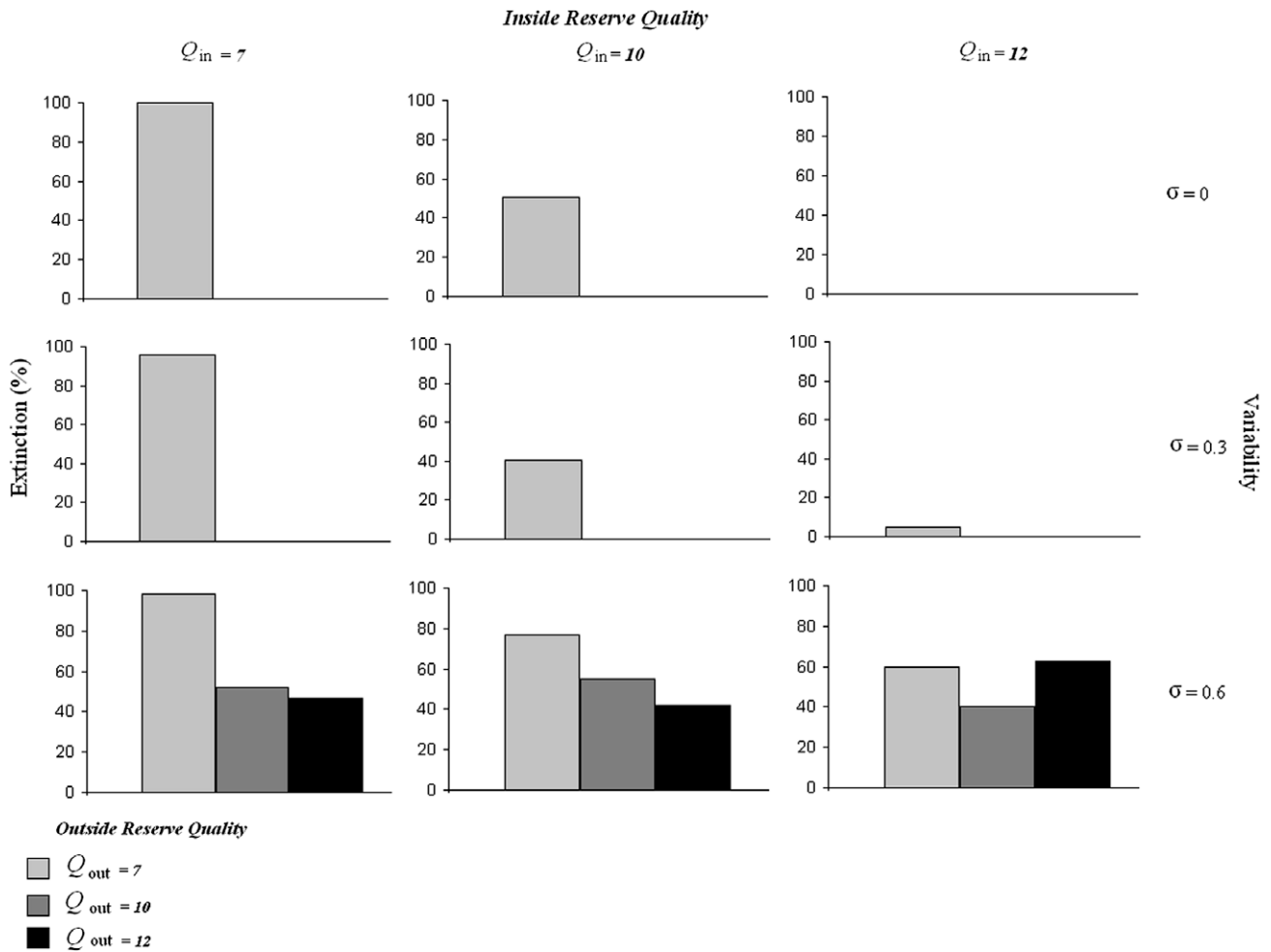


Fig. 4. Average predator population density ( $n = 20$ ) inside the protected area in a one hundred year simulation. Each graph contains three scenarios with the same  $Q_{in}$ , three different  $Q_{out}$  and one environmental regime ( $\sigma$ ).



**Fig. 5.** Extinction probability of predator population under each of the simulated scenarios ( $n = 20$ ). Each graph contains three scenarios with equal  $Q_{in}$ , three different  $Q_{out}$ , and one environmental variability regime ( $\sigma$ ). Percentages in scenarios with  $\sigma = 0.6$  were calculated for  $n = 60$ .

the average predator population size increased notoriously when the quality of the exterior of the reserve also increased. Secondly, the oscillations of population density in time tended to be positively associated with the habitat quality in the surrounding landscape, in accordance with evidence that such sub optimal habitats can have a buffer effect on population dynamics (Foppen et al., 2000; Grimm et al., 2005; Revilla et al., 2001).

One of the problems of populations in small protected areas is that, due to a change in ecosystem scales, predator-prey cycles can be exacerbated by environmental variability, thus threatening their persistence (Bode and Possingham, 2007). An interesting result of our model was the non-linear relationship between the persistence of the population and the ratio of habitat qualities inside and outside the reserve under high environmental variability. The fact that in a highly variable environment greater persistence was obtained in conditions of intermediate quality of the surrounding landscape highlights the importance of the interplay of temporal and spatial variation of the landscape and population dynamics (Long et al., 2007).

There are several mechanisms by which the surrounding landscape may influence the ecology of protected areas (Hansen and DeFries, 2007). Our model included behavior of the simulated populations, community interactions, landscape configuration and environmental variability, all in a dynamic context. This complexity made the mechanisms behind this observed pattern difficult to pinpoint. However, we believe that part of the explanation is related to the predator movement behavior (Hosseini, 2006); the hungry-

movement algorithm. Inside the reserve, density-regulated mechanisms and the source-sink structure of the landscape (inside vs. outside) cause a decrease in the oscillations of population size. When the system experienced high environmental variability, the movement algorithm provoked that during dry years, predators tended to move more between outside and inside the reserve, causing an over-compensatory density regulation (Münkemüller and Johst, 2006) inside the reserve. The movement of individuals due to poor conditions also increased the number of predators outside the reserve. This pattern is analogous to the source-sink inflationary effect described by Gonzalez and Holt (2002). According to these authors, a sink population may be present in great abundance if the exclusion rate is weak and the immigration rate is high. In our model, the combination of a reserve with high habitat quality, a landscape context with intermediate quality ( $Q_{in} = 12$ ,  $Q_{out} = 10$ ), and the high mobility in poor environments created the conditions of the above-mentioned inflationary effect. The theory predicts that in an open population, auto-correlated fluctuation in habitat quality can increase average population size, even if such fluctuations increase extinction risk in closed populations (Gonzalez and Holt, 2002). Our results are in concordance with these predictions, as fewer extinctions were observed in the scenario with inflationary effect conditions.

This pattern has been observed in other studies. For example, Bode and Possingham (2007), using a simulation model, showed that under high environmental variability, culling a population might indeed increase its chances of persisting in a small protected area. The reduction in population growth produced by culling the

population is analogous to the reduction in growth induced by a sub optimal surrounding landscape in our model. Additionally, Ruxton et al. (1997) showed that higher mortality experienced by individuals during dispersal may also act as a stabilizing mechanism for fluctuating populations. The key message here is that given the interaction between landscape heterogeneity, temporal variability, and changes in behavior, complex patterns in population dynamics can emerge.

Generally, it is expected that the ecosystems outside nature reserves are more degraded than those inside the protected areas, although this trend varies geographically (Joppa et al., 2008). Thus, in most real-life cases, the landscapes surrounding nature reserves likely represent situations analogous to our low or intermediate quality landscapes ( $Q_{out} = 7-10$ ). If our results are qualitatively correct, an interesting management implication arises: under high environmental variability small enhancements in the quality of the matrix may have better effects for some species on increasing persistence probability inside a reserve than large enhancements (e.g. raising habitat quality to similar levels as the reserve).

Our model represented a protected area of a fixed size, and although we did not explore the effects that size itself could have on the observed patterns, it seems reasonable to suggest that the effects of the surrounding landscape could be more relevant for smaller reserves, or when the home range of the species is increased (Estades, 2001). In addition, the simple geometry (square) of our protected area may also influence part of the observed patterns (Ewers and Didham, 2007). Finally, the extent at which the influence of the landscape takes place also needs to be identified (DeFries et al., 2007), and the latter information may be used as an input in the design of buffer or transitions zones (UNESCO, 1974) around the reserve.

Clearly, extensive further research is needed in order to identify landscape configurations that may increase the population viability of particular species at the landscape scale, and in particular environments (e.g. nature reserves). This is a key point since the integration of conservation strategies at the landscape level is crucial, considering the changes that are being produced throughout the planet (e.g. land use change, climatic change, etc.). An adequate strategy for the conservation of landscapes would maximize the effectiveness of conservation efforts, and a configuration that increases the viability of populations without necessarily increasing the size of legally protected lands would lower the costs associated with management.

Most conservation problems dealing with large carnivores are related to the insufficient size of reserves and their inability to maintain carnivores within their protected interiors (Forbes and Theberge, 1996; Simonetti, 1995; Woodroffe and Ginsberg, 1998). This work confirmed that the success of conservation does depend on the reserve conditions, the surroundings in which it is found (Harcourt et al., 2001; Woodroffe and Ginsberg, 1998), and the uncertainty of the environment. It also suggests that the interaction between the spatial and temporal disturbances might be a key factor affecting vulnerability and persistence inside protected areas (Gaston et al., 2002), highlighting that the interplay between these factors is crucial for the conservation of the world's carnivores (Cardillo et al., 2004).

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