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Mathematical model of livestock and wildlife: Predation and competition under environmental disturbances

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ABSTRACT

Inspired by real scenarios in Northern Patagonia, we analyze a mathematical model of a simple trophic web with two herbivores and one predator. The studied situations represent a common practice in the steppes of Argentine Patagonia, where livestock are raised in a semi-wild state, either on the open range or enclosed, coexisting with competitors and predators. In the present work, the competing herbivores represent sheep and guanacos, while the predator is associated with the puma. The proposed model combines the concepts of metapopulations and patches dynamics, and includes an explicit hierarchical competition between species, which affects their prospect to colonize an empty patch when having to compete with other species. We perform numerical simulations of spatially extended metapopulations assemblages of the system, which allow us to incorporate the effects of habitat heterogeneity and destruction. The numerical results are compared with those obtained from mean field calculations. We find that the model provides a good theoretical framework in several situations, including the control of the wild populations that the ranchers exert to different extent. Furthermore, the present formulation incorporates new terms in previously analyzed models that help to reveal the important effects due to the heterogeneous nature of the system.

1. Introduction

The mathematical modeling of ecological interactions is an essential tool in predicting the behavior of complex systems across changing scenarios, such as those arising from climate change or environmental degradation. The literature abounds with examples of predator–prey models (Swihart et al., 2001; Bascompte and Solé, 1998; Kondoh, 2003), of intra- and inter-specific competition (Nee and May, 1992; Tilman et al., 1994; Hanski, 1983), of the relation between species richness and area size (Rosenzweig, 1995; Ovaskainen and Hanski, 2003) and of habitat fragmentation (Hanski and Ovaskainen, 2000, 2002; Ovaskainen et al., 2002). However, considerable effort still needs to be made in the integration of all these mechanisms together. Our intention is to advance toward the modeling of trophic web complexity in successive approximations. In this paper we take a first step in this direction: modeling a predator–prey-competition system in environments subjected to disturbances. We present as a case study the dynamics of a simple trophic web. As a paradigm of a more complex ecosystem, we analyze here the case of a single predator and two competing preys in the Patagonian steppe. Specifically, we focus on two native species: puma (*Puma concolor*, a carnivore) and guanaco (*Lama guanicoe*, a camelid), and on sheep (*Ovis aries*) as an introduced competitor to the native herbivore and further prey of the pumas. This system is the result of a long sequence of ecological and historical events that we briefly outline below.

The native mammalian fauna of Patagonia is composed of survivors of five main processes of extinction. One of the most relevant is known as the Great American Biotic Interchange (GABI) in which, upon the emergence of the Isthmus of Panama about 3 million years ago, the South American biota became connected with North America (Patterson and Costa, 2012). The last main event occurred during the Quaternary glaciations, when climate change was combined with the arrival of humans for the first time in the evolutionary history of the continent (Martin and Klein, 1984). This cast of species,

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resistant to these natural shocks, was afterwards not exempt from threats to their survival.

Pumas and guanacos, currently the two largest native mammals in Patagonia, coexisted with humans for at least 13,000 years with no evidence of shrinkage in their ranges of distribution until the twentieth century (Bastourre and Siciliano, 2012; Borrero and Martin, 1996; Nigris and Cata, 2005). There are records of a huge abundance of guanacos in sustainable coexistence with the different Native Patagonian hunter-gatherer populations, until shortly before the arrival of the European immigrants (Musters, 2007; Claraz, 1988).

In 1880–1890, as a consequence of what has been called the "Conquest of the Desert" or "Wingka Malon" in Argentina, the highly mobile native hunter-gatherers were overpowered and/or driven from their ancestral territories by the Argentine military army (Delrio, 2005). Large and continuous extensions of the Patagonian steppe were subdivided into private ranches by means of a gigantic grid of fences, and 95% of it was devoted to sheep farming (Marqués et al., 2011). The introduction of sheep significantly altered the ecological interactions of the Patagonian fauna and flora (Pearson, 1987). Ranchers, descendants of Europeans, built a new ecological niche where the puma, as a predator of sheep, and the guanaco, as competitor for forage, became part of the list of enemies of their productive interests and were therefore fought (Marqués et al., 2011).

1.1. The ecological context

Let us describe the current ecological scenario in which these three characteristic players interact. There is evidence of competition between sheep and guanacos (Nabte et al., 2013; Marqués et al., 2011), mainly for forage and water. From a diet of 80 species of plants, they share 76 (Baldi et al., 2004), so that sheep carrying capacity decreases when the number of guanacos increases. Besides, it has been observed in the field, and it is a well established knowledge from rural culture, that guanacos displace sheep from water sites (including artificial sources). However, human influence makes the density of guanacos decrease when the number of sheep increases. What needs to be understood is that there is no simple and direct competition between guanacos and sheep, but a competition between guanacos and "livestock," a term that includes sheep, herder dogs and humans with their guns. Without these "cultural bodyguards" of barks, bullets and fences, a herd of guanacos would displace a flock of sheep. As the fields deteriorate from overgrazing and desertification the guanaco increases its competitive superiority over the sheep, since it is superbly adapted to situations of environmental harshness, especially water scarcity (e.g., it may drink seawater in case of extreme necessity). Therefore, the guanaco density tends to increase naturally as field productivity decreases. However, this natural process is usually offset by an increase in hunting pressure on the guanaco as environmental conditions worsen, because ranchers want to maximize scarce resources for production. Drought periods catalyze these socio-environmental crises, as the lack of rain works somewhat like a destroyer of carrying capacity for both wildlife and livestock.

Predators (pumas and also foxes, *Lycalopex culpaeus* and *L. griseus*) are also subject to permanent removal, because their extermination reduces production costs (Marqués et al., 2011). The puma naturally hunted guanacos (Novaro et al., 2000), but since the introduction of sheep it has been dedicated almost completely to these last, as it is a prey that involves minimal exploration cost (i.e., the energy effort spent in searching for, pursuing and capturing prey) compared to the high energy cost of capturing the fast and elusive guanaco that co-evolved with them (Rau and Jiménez, 2002).

Of course, as hunting eradicates the predators, populations of herbivores have no natural demographic controls and can grow uncontrolably – exponentially at first until other limitations take over – as has happened in the case of some nature reserves. Subsequently the uncontrolled growth of guanaco increases the competition with sheep and, if guanaco populations are confined and cannot migrate, this may also result in an overconsumption of fodder, excessive destruction of the habitat, and subsequent population collapse by starvation. Such a case has recently been documented in the nature reserve of Cabo Dos Bahías in coastal Patagonia (Marqués et al., 2011).

This interaction between the guanaco, puma and sheep is heavily influenced by management decisions concerning the pastures. For ranchers, the fauna is a production cost, the tolerance of which can be characterized in three paradigmatic scenarios:

Low conflict scenario. If the cost of the presence of wildlife is financially compensated by the government or by ecotourism activities related to wildlife watching (Nabte et al., 2013), the ranchers tolerate the presence of wildlife in coexistence with a livestock density that is not harmful to the ecosystem. If the field changes from a productive use to a conservative use, the wildlife and the flora recover very fast (the San Pablo de Valdés Natural Reserve case, see Nabte, 2010).

Medium conflict scenario. In well-managed fields with adequate load, the carrying capacity is maintained in a healthy enough state to tolerate livestock and wildlife simultaneously. For this to happen, the field needs a large usable area. If the field changes from a productive to a conservative use, the wildlife recovers well, but not as fast as in the previous scenario, since growth is limited by the availability of resources (the Punta Buenos Aires, Península Valdés case (Nabte et al., 2009)). In those cases where the area is very large, the recovery is very good despite the partial deterioration, because the lower load per hectare is offset by the amount of surface (the Torres del Paine National Park case, Chile (Franklin and Fritz, 1991)).

High conflict scenario. When the farmer depends exclusively on sheep production, conflict is high because the wildlife goes against their economic interests. If these are not compensated, wildlife hunting increases and becomes much more intense as the field deteriorates. Wildlife is shifted to productively marginal sectors. The farmer prioritizes short-term income above sustaining long-term productivity of the field. This economic rationality creates a negative feedback loop: as productivity decreases, the farmer increases livestock density to try to sustain the same income; this leads to overgrazing and, in turn, to a further decline in productivity; the farmer then sets out to economically compensate this decline by loading the field even more. The result is a meltdown of the productive system and the abandonment of the field (Marqués et al., 2011). The populations of native herbivores (although they get a rest from the exterminated predators and the eradicated sheep) fail to recover viable population levels because there are not enough resources to sustain them, energetically and bio-geochemically (Flueck et al., 2011). As a consequence of this frequent scenario, the density of guanacos, rheas and other herbivores has decreased considerably in Patagonia (Marqués et al., 2011).

In this paper we study a mathematical model corresponding to a simplified instance of this ecosystem. Our purpose is to provide a theoretical framework in which different field observations and conceptual models can be formalized. The model has been kept intentionally simple at the present stage, in order to understand the basic behavior of the system in different scenarios, including the three just described. Subsequent mechanisms will be incorporated and reported elsewhere.

In the next section the metapopulation model is presented, followed by the analysis of the main results obtained with the spatially explicit stochastic simulations and the mean field model. Further discussion and future directions are discussed in the closing section.