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Two examples of application of ecological modeling to agricultural production: Extensive livestock farming and overyielding in grassland mixtures

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ABSTRACT

Livestock production plays an important role in guaranteeing food security worldwide and has an important contribution to the economy of many countries. Precision livestock production (PLP), or the manipulation of livestock activity taking into account the different components of agroecosystems −pastures, cattle and pasture-cattle interactions−, has acquired growing importance in recent years to optimize productivity. Regarding the pasture component, multi-species pasture mixtures are commonly used worldwide to increase primary productivity and thereby secondary productivity.

Here we present two examples of how the combination of experimental research and quantitative modelling can help to the development of protocols for food production optimization. The first example is based on a model we are currently developing for the whole agroecosystem in terms of a predator-prey dynamical system. The second example focuses on the pasture component and is based on a generalized Lotka-Volterra model we recently proposed for describing the mixture of herbaceous species in the pasture. We discuss the usefulness of both models, whose parameters were estimated from experiments or field work, as quantitative predicting tools. Population dynamic models are the common thread in this paper.

1. Introduction

Livestock is the world's largest user of land resources. Grazing land and cropland dedicated to the production of feed represent almost 80% of all agricultural land and occupy about 25% of the terrestrial surface of the planet (Steinfeld et al., 2006). Livestock production plays an important role in guaranteeing food security worldwide and contributes to the livelihoods of over 800 million people (Steinfield et al., 2006).

From the 1950s several mathematical models where build for livestock systems (see for example the reviews on agricultural models and their classification as decision-making tools for farmers Janssen and van Ittersum (2007) and Dury et al. (2011)). In general these models are based on empirical rules and treat livestock systems as separate blocks.

However, livestock production agroecosystems based on direct forage harvesting by animals, like grassland farms can be considered as a complex system (Vayssières et al., 2011; Turner et al., 2013). Indeed it possesses the main properties that define complex systems: a) **nonlinearity**, *i.e.* the interaction between herbivores and grass is nonlinear, like the energy flow and the nutrient cycle (Pastor, 2008); b) **feedback**, *i.e.* animal performance (liveweight variations and reproductive results) is linked with grass consumption, which depends on forage availability, which in turn is affected by the grazing pressure from animals (Olson, 2005); c) **self-organization** *i.e.* some form of overall order arises from the interactions between the main parts of system, grass and animals (Ladyman et al., 2013). The resulting organization is typically robust and able to survive or self-repair substantial perturbation. Additionally, there are other further internal complications. For instance, meat production on grassland is highly dependent on voluntary forage intake (Allison, 1985). Many factors as forage availability and quality, dry matter (DM) content and chemical composition of the sward, species selection by cattle, stocking rate, among others are cited by Allison (1985) as drivers of animal grass intake. On top of this, an important external factor that contributes to the complexity of grassland livestock is climatic variability −e.g. hydric stress episodes− playing a main role in those

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systems (Bartaburu et al., 2009; Morales et al., 2012). According with Steiner et al. (2014) increasing the knowledge about these complex systems is crucial to enhance resilience of livestock farming and to help stakeholders for an adaptive management.

Precision livestock production (PLP) (Laca, 2009; Donald et al., 2010), i.e. the holistic manipulation of livestock activity by taking into account the different components of agroecosystems to optimize productivity, has acquired growing importance in recent years. In this sense, simulation with pertinent grassland farms models can provide important insights to enhance management of natural resources in a participative way with stakeholders (Vayssières et al., 2011; Gunderson and Holling, 2002; Norberg and Cumming, 2008). A recent attempt of modeling the pasture-cattle agroecosystem in the Uruguayan native grasslands is the MEGanE model (Dieguez et al., 2012). A limitation of MEGanE is that its solutions are not structurally stable i.e. small perturbations can have very dramatic effects (Murray, 2001).

Regarding the pasture component either natural native grasslands or artificially seeded prairies grasslands are commonly multispecies mixtures or polycultures. Benefits of multi-species mixtures include overyielding, i.e. production in mixtures that exceeds expectations based on monoculture (Trenbath 1974), stability, i.e. lower variability in production, and resilience, i.e. ability to recover after a perturbation such as drought. Perennial herbaceous polycultures are mixtures of perennial crop species grown for agricultural purposes (grain, forage or biomass production) that can increase diversity and productivity in agricultural landscapes while reducing soil erosion, especially in lands suitable for low-input systems (Cox et al., 2006; Jackson 2002). The solution of a wide variety of global problems that include malnutrition and hunger, worries about fossil fuel consumption, environmental degradation and loss of biodiversity (Lomborg, 2004) could be achieved through perennial polyculture farming (Dewar, 2007).

Identifying the optimal combinations of species in perennial crop mixtures in terms of richness and composition requires field experiments, which can quickly become too large in terms of treatments (species combinations), time, labor, and costs (Hector et al., 1999; Tilman et al., 1997, 2001). In addition to field experiments, the development of quantitative methods is required as tools to predict the performance of different polycultures as well as to provide a better evaluation of the effectiveness of management optimization practices. Examples are the Diversity-Interactions (DI) models (Kirwan et al., 2007, 2009) which address many of the issues. Nevertheless, applications of mechanistic models in terms of inter-specific interactions to practical agricultural situations are few. Moreover, despite the accepted importance of inter-specific interaction, analytical methods have rarely been capable of identifying the contribution of particular interactions as opposed to measuring the net effect of all interactions (Kirwan et al., 2007; Hector et al., 2009). Among these few models based on pairwise inter-specific interactions applied to grasslands is the generalized DI model of Connolly et al. (2013).

In this paper we present two examples of how the combination of experimental research and quantitative modelling can help to the development of protocols for food production optimization. The first example is based on the *predator-prey grassland-livestock* (PPGL) model (Dieguez and Fort, 2017). This model, which is an extension of the classical Lotka-Volterra predator-prey equations (Lotka, 1920, 1925; Volterra, 1926), involves two variables, the grass height and the individual (mean) live weight of animals, as well as the nonlinear interaction between them. That is, animal performance (liveweight variations and reproduction) is linked with grass consumption, which depends on forage availability, which in turn is affected by the grazing pressure. The main goal is to provide a quantitative management tool for PLP. The second example focuses on the pasture component and is based on a *generalized* Lotka-Volterra (GLV) model (Hofbauer and Sigmund, 1998) we recently proposed (Halty et al., 2017) for describing data from experiments involving seven perennial crop species carried out from 2006 to 2008 in Iowa (Picasso et al., 2008, 2011). We discuss the usefulness of both models, whose parameters were estimated from experiments or field work, as quantitative descriptive and prediction tools.

Our ultimate goal is contributing to the application of mathematical population dynamics to develop quantitative methods for agriculture science. This, asides from its scientific value, we believe will help the stakeholders to make decisions, set priorities and choose strategies from a more informed position. In addition, we hope this new approach will improve the interdisciplinary communication and eventually help to attract scientists from other disciplines (e.g. physicists, applied mathematicians and ecologists) to contribute to a scientifically based management of agroecosystems.

2. First application, PPGL: a parsimonious model for grass –LIVESTOCK

2.1. Materials and methods

2.1.1. The Model

The PPGL model was designed following a parsimonious approach and should be regarded as a minimal non-trivial description of the whole agroecosystem in terms of two main components, the grass (prey) and the animal (predator). This model involves two major approximations:

1. *Coarse grained approximation* (aggregate variables): The grass is considered as a single representative or ‘average’ native grass species describing the mixture of many coexisting species in natural pastures; and we also consider an ‘average’ animal i.e. homogeneity of breed, age, sex, etc.
2. *Mean field approximation*: That means that we work with mean values (over space) of the aggregate variables and parameters which are spatially independent.

Therefore the system is described in terms of two aggregate and average variables: For the grass we use, as a measure of the grass biomass, the average grass height x (in cm). For the cattle we use the mean live weight per animal y (kg animal^{-1}). The differential equations that control the dynamics of these components are based on the Lotka-Volterra predator-prey model with nonlinear Holling type III response function (Murray 2001; Pastor 2008). Therefore, the differential equation for the grass dynamics reads:

$$\frac{dx}{dt} = rx\{1 - \frac{x}{K(t)}\} - c\frac{x^2}{H^2 + x^2}y^{3/4}S, \tag{1}$$

where the first term on the right hand side is a logistic growth term for the grass that involves two parameters: the maximum growth rate for the grass r (measured in units of day^{-1}) and its carrying capacity $K(t)$ (cm) –which depends on the time (see below). The second term is a Holling type III consumption, which models the grazing by the animals. It involves three parameters: c (cm.kg^{-1}day^{-1}head^{-1}ha; Pastor, 2008) is the maximal intake rate per animal metabolic weight (Kleiber, 1932) law states that an animal's metabolic rate scales to the ¾ power of the animal's mass, this is why the animal's weight y appears to the ¾ power), H (cm; Pastor, 2008) is the half-saturation constant or the value of x for which the intake rate is equal to $c/2$ and S (head ha^{-1}) is the stocking rate, i.e. the number of animals per hectare.