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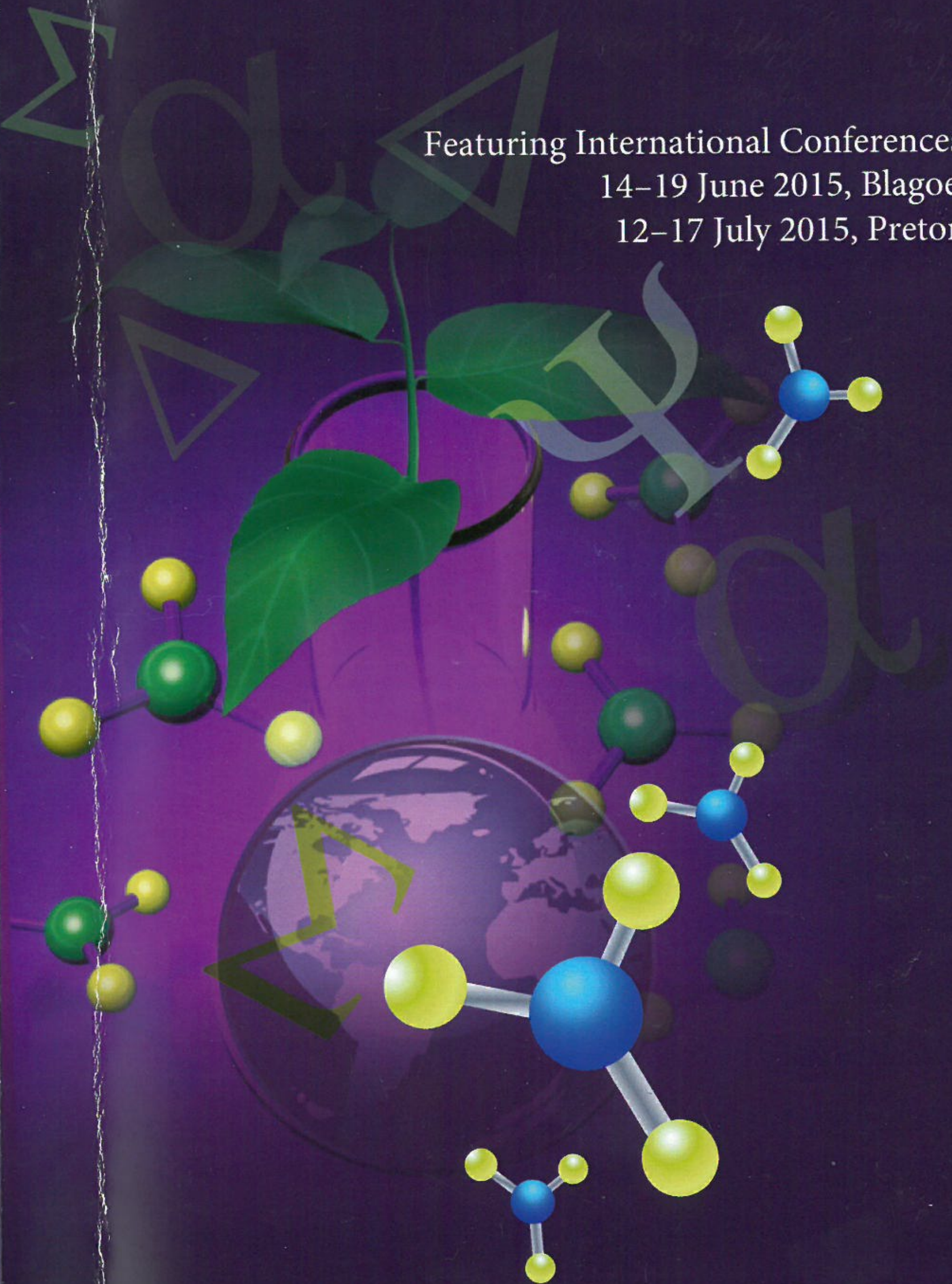

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Population Games

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The three main avenues of research in ecology focus on animal behavior, population dynamics, and evolution of traits. Historically, differences between these three research programs are the underlying time scales: fast changes in animal behavior, intermediate fast changes in animal numbers, and slow changes in traits. Following these time scales various mathematical methodologies were applied to develop corresponding mathematical models. While changes in population abundance are often described by differential/difference equations, models of animal behavior or evolution often rely on methods of optimization and evolutionary game theory. It is clear that an "ideal" mathematical model should integrate all these three time scales, but such models would be difficult if not impossible to analyze. Recently some new approaches integrating processes operating on different time scales have been developed. In my talk I will discuss the so called "population games" showing that the new insights they lead to are not only of mathematical interest, but are also important tools for better understanding mechanisms regulating biodiversity.

I will start with the classical Lotka–Volterra predator-prey model that describes changes in predator and prey numbers. This model assumes a homogeneous environment where predators and prey are well mixed. I will focus on an extension of this model to a heterogeneous environment consisting of two patches [11]. The resources in both patches (denoted as R_1 and R_2) do not disperse, but consumers (C) do. The topology of such a food web has been called the "apparent competition module" [9], because although the two resources do not directly compete, the competition is "apparent" through the shared predator. If one resource increases in abundance, predator population increases too and this exerts a negative effect on the other population and vice versa. Provided consumers form a monomorphic population with individual preference for the ith resource u_i ($u_1 + u_2 = 1$), a direct extension of the Lotka–Volterra model is described

by the following set of differential equations

$$\begin{aligned} \frac{dR_1}{dt} &= R_1(r_1 - u_1\lambda_1 C) \\ \frac{dR_2}{dt} &= R_2(r_2 - u_2\lambda_2 C) \\ \frac{dC}{dt} &= C(e_1u_1\lambda_1R_1 + e_2u_2\lambda_2R_2 - m) \end{aligned} \qquad (1)$$

where r_i is the per capita intrinsic prey population growth rate, λ_i is the consumer search rate for prey type i, e_i is the efficiency with which consumed resources are transformed to new consumers, and m is the consumer mortality rate. The classical models of population dynamics assume that interaction strength in food webs is fixed, which means that consumer preferences u_i ($i = 1, 2$) are fixed. For model (1) this leads to prediction that the resource with the lower ratio $r_i/(u_i\lambda_i)$ will be outcompeted from the food web. However, the assumption on the interaction strength given by fixed consumer preferences is not supported by observations that come from behavioral ecology. It has been observed many times that if the preferred resource is rare, generalist consumers are adaptive in the sense that they shift their preference to an alternative, more abundant, resource.

Several behavioral models under the general term "optimal foraging" were developed to describe animal feeding preferences [4, 5, 19]. These models assume that those individuals that maximize energy intake rate achieve higher fitness and their phenotype is promoted during evolution. Thus, food web models should consider not only changes in population numbers, but also changes in interaction strength. In fact, this leads to a complex feedback where changes in population numbers change consumer preferences which, in turn, influence population dynamics. For example, in the case of model (1) a proxy for consumer fitness can be defined as the per capita population growth rate, i.e.,

$$W(u) = e_1u_1\lambda_1R_1 + e_2u_2\lambda_2R_2,$$

where $u = (u_1, u_2)$, $u_1 + u_2 = 1$, $u_i \geq 0$, $i = 1, 2$. If $W_i = e_i\lambda_iR_i$ is the i–th patch payoff, consumer fitness W is the mean payoff an individual obtains when it spends a proportion u_i of its lifetime in patch i. To describe changes in consumer preferences we can use, e. g., the replicator dynamics of the game theory

$$\frac{du_i}{dt} = u_i(W_i - W(u)), \quad i = 1, 2. \qquad (2)$$

The replicator equation assumes that proportion of time spent in patch 1 increases, provided payoff in patch 1 is larger than payoff in patch 2 ($W_1 > W_2$), and decreases otherwise. There are other game dynamics (e.g., the best response dynamics) that can be more relevant than the replicator dynamics in some contexts [15]. This example shows that integration of population dynamics with behavioral/evolutionary dynamics increases complexity of the model because it increases the number of differential equations. This leads to difficulties when analyzing the resulting model. However, by separating the population and behavioral time scale, model (1) and (2) can be substantially simplified. Here I will assume that changes in consumer preferences occur on a much faster time scale than changes in demography. In fact, I will assume that consumers' diet choice instantaneously track current population densities. This assumption allows me to write consumer preferences P as a function of population densities, i.e.,

$$P(R_1, R_2) = \begin{cases} 1 & W_1 > W_2 \\ 0 & W_1 < W_2 \\ [0,1] & W_1 = W_2. \end{cases} \qquad (3)$$

Then behavioral dynamics (2) are replaced by algebraic inclusion

$$u_1 \in P(R_1, R_2).$$

Substituting this feedback in model (1) leads to a differential inclusion. This model predicts indefinite coexistence of all three species [11, 3]. A similar prediction holds also for more complex di- and tri-trophic food webs with many species [14]. From the ecological point of view, a new result here is that adaptive animal foraging promotes species biodiversity.

In many cases finding the "optimal" animal strategy at current population abundance may not be a straightforward optimization problem like the one mentioned above. In particular, this is the case where animal fitness is frequency dependent, i.e., when it depends on the animal strategy. In such cases it has been argued since the pioneering work of J. Maynard Smith and G. R. Price [18] that Darwinian evolution corresponds to evolutionarily stable strategies. The evolutionarily stable strategy is a strategy that resists invasions of individuals that use a different strategy. For example, let us consider a population that disperses between two habitat patches, each with a frequency dependent payoff $W_i(u_i)$ where $u = (u_1, u_2)$ is the distribution of the population between the two patches. If all individuals have the same preferences for patches measured by the proportion of their lifetime spent in either patch the population distribution coincides with individual strategies. Let us consider a mutant that differs from the residents

in its patch use described by $\tilde{u} = (\tilde{u}_1, \tilde{u}_2)$. Fitness of such a mutant in the resident population with distribution $u = (u_1, u_2)$ is defined as the mean payoff, i.e.,

$$W(\tilde{u}, u) = \tilde{u}_1 W_1(u_1) + \tilde{u}_2 W_2(u_2).$$

Provided patch payoffs W_i are negatively density dependent, i.e., patch payoffs are decreasing functions of population numbers, it was proved [6] that the interior strategy/distribution satisfying $W_1(u_1) = W_2(u_2)$ is an evolutionarily stable strategy. Such a population distribution is also called the Ideal Free Distribution (IFD) in ecology [8]. The single species distribution was extended to two species that compete for resources in both patches [16]. Here the problem is how to define a two-species IFD/ESS, because the original definition is for a single species only. Using a two-species extension of the ESS [15] coexistence of two competing species in a two-patch environment was studied in [1, 7]. In particular, it was shown there that conditions for evolutionarily stability of spatial distribution of the two populations are different from the conditions on population stability for the classic Lotka–Volterra competition model in two patches. In other words, it is possible that while population dynamics of the two populations converge to a stable equilibrium at each patch when neither species disperses, directional dispersal can destabilize these equilibria and lead to fluctuations in population densities.

These theoretical concepts have also been applied to real ecological problems, e.g., [2, 12, 13, 10, 17]. For example [12] shows that the lac operon is evolutionarily optimized. It is well know that in mixed substrates with glucose and an alternative carbon source (e.g., lactose) bacteria utilize glucose first and then switch to lactose. At the molecular level this switch is known as the lac operon. The question here is whether bacteria switch between the two resources at the time that maximizes their fitness? To answer this question a model of bacterial growth on two substrates that assumes adaptive bacterial switching that maximizes bacterial per capita population growth rate was constructed [12]. Using data from the literature, this model allows us to predict the time and the sugar concentrations at which bacteria should switch. These predicted times of switching fit very well with observed times for different substrates and different initial sugar concentrations. This strongly supports the idea that the molecular mechanism regulating resource switching is evolutionarily optimized.

It should be mentioned that the above modeling approach assumes that changes in animal behavior operate on a short time scale when compared to population dynamics. There is an alternative approach, called adaptive dynamics, that assumes that trait changes operate on much slower time scale when compared to population demography. This approach is relevant especially in cases where traits undergo slow evolutionary changes.

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