

Non-Linearity in population ecology

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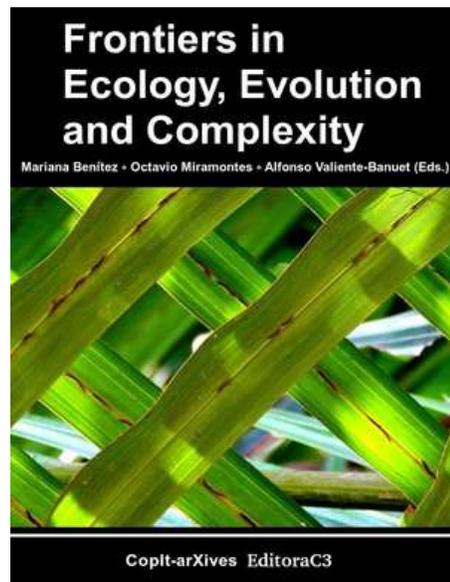
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Non-Linearity in population ecology

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1 Abstract

Non-linearity pervades population ecology at all levels, from the vital rates of individuals to multispecies interactions. Here, I exemplify some of such non-linear processes, and how the models that we use to describe them suggest that a wide variety of complex phenomena may arise, e.g., chaos, self-organization, or critical thresholds. In some cases I also point out how the usage of different non-linear functions determines the behavior of the models. Thus, it is important to know which functions describe real processes appropriately, parametrize them with actual data, and assess their effects on population dynamics that is modeled. This is critical to understand the causes of complexity in nature.

2 Resumen

Los procesos no lineales caracterizan a la ecología de poblaciones en diferentes niveles, desde las tasas vitales de los individuos que las componen hasta las interacciones con numerosas especies. Aquí se ejemplifican algunos de estos procesos no lineales, y cómo los modelos que empleamos para describirlos sugieren la existencia de una gran variedad de fenómenos complejos, e.g., el caos, la autoorganización o los umbrales críticos. En algunos casos se señala cómo el uso de diferentes funciones no lineales determina el comportamiento de los modelos. En consecuencia, es importante conocer cuáles de dichas funciones describen más adecuadamente los procesos reales, parametrizarlas con datos, y evaluar sus consecuencias sobre la dinámica poblacional modelada. Esto es fundamental para comprender cuáles son las causas de la complejidad en la naturaleza.

3 Non-Linearity in population ecology

Non-linearity permeates biology, and populations are no exception. In fact, populations have played a central role in the development of non-linear sciences. They have also ignited the interest of many scientists in complexity, self-organization, critical transitions,

and chaos, perhaps because non-linearity arises so naturally in population ecology. The causes for non-linearity in populations span different levels of organization, from the attributes of individuals to interactions with other species.

Demography integrates the vital rates (survival, growth, and fecundity) of individuals in order to understand and model population growth. These vital rates are intrinsically non-linear, frequently as a result of bounds on parameter values; for instance, survival probability is bounded at zero and one, and only non-negative fecundities are biologically feasible. Several models based on different assumptions have been proposed to describe the growth of individuals, but none of them is linear. Our everyday experience confirms that we animals do not grow indefinitely, but undergo a series of changes in growth rate and ultimately reach a maximum size that changes very little as we grow older. Perhaps because linearity in vital rates is so biologically absurd we know little about how demography would change if linearity were assumed. However, the specific form of non-linearity chosen when modeling vital rates has a significant impact on our inferences about population dynamics [1].

Intraspecific competition has received much attention from population ecologists. The earliest models for population dynamics, i.e., the changes in population numbers over time, already incorporated the effect of diminishing resource availability as population density increases. The well-known logistic curve dates from 1838. Subsequent development of the discipline has resulted in a true bestiary of functions that describe population growth, both in continuous and discrete time. These models are known by the names of their authors: Ricker, Gompertz, Hassell, Beverton-Holt, Maynard-Smith and so on. All of them are non-linear, as changes in competition over time modify the population growth rate, which eventually becomes zero (or shows a more or less complex dynamics). Each model is based on different mechanistic assumptions, and appears to describe accurately the dynamics of different taxa. For instance, the Ricker model

$$N_{(t+1)} = \lambda N_t e^{-\alpha N_t} \quad (1)$$

(where N_t is the size of the population at time t , λ is the intrinsic growth rate, and α is the per-capita competitive effect) has been used to model animal populations successfully [2], while the Hassell model

$$N_{(t+1)} = \frac{\lambda N_t}{(1 + \alpha N_t)^\beta} \quad (2)$$

almost universally provides the best fit to plant data. It must be noted that β frequently equals one, so the Hassell model becomes the Beverton-Holt model in most plant species [3].

Population growth models have played a prominent role in the development of the theory of complex systems. In a groundbreaking paper, Robert May (who at the time was studying population growth models with George Oster) popularized the notions of bifurcations and chaos by showing that, as the intrinsic population growth rate increases,

the population does not reach a fixed size but instead cycles between two points. Further increments in the intrinsic growth rate induce new doubling (or bifurcations) of the number of points in the cycle until the modeled behavior of the population becomes extremely complex, i.e., chaotic [4]. The bifurcation diagram of the model analyzed by May has since become one of the visual stereotypes of complexity and chaos.

In population models, complex dynamics can only occur if the population does not approach the carrying capacity monotonically, but “overshoots” it [5]; hence the name overcompensation for such behavior. The mechanism is easy to envisage: assume a population of annual insects below its carrying capacity. Because resources are abundant, the number of eggs laid can be extremely large, leading to a population that is well above the carrying capacity in the next year. Then, calamitous competition may preclude reproduction, again sending the population back to a negligible density. In simple continuous-time models, where the population regulates itself instantaneously in response to changes in density, such behavior is unlikely. Time lags may nevertheless occur. As I write this, children in the Mexican population are less numerous than teenagers as a happy result of a reduction in birth and population growth rates. However, when the current demographic wave of teenagers becomes reproductive, Mexico’s population growth is expected to accelerate again as a time-lagged echo of larger birth rates in the past. Thus, time lags may induce models that resemble overcompensation and thus result in very complex dynamics [6]. Overcompensation can only arise if the function relating N_{t+1} to N_t reaches a maximum for some value of N_t [2]. Nevertheless, it must be noted that density-dependence in one of the vital rates of a demographic model may result in very complex dynamics regardless of whether it is over- or undercompensating [7].

Allee effects are ubiquitous in nature and result necessarily in a non-linear behavior. Allee effects occur when populations perform poorly when density is low because of inbreeding, low probability of finding mates, collapse of social systems, lowered capability to deter predators, etc. This means that the population growth rate may increase with density, but, because of intraspecific competition, growth must eventually decline if density is high enough. In models, the interaction between these opposing forces may result in chaos [8]. Such models also show another trait of complex systems: critical transitions. If the population is large enough it may persist indefinitely, but if its density falls below a critical threshold, the population becomes trapped in an “extinction vortex” and disappears [9].

Interspecific competition is similar to intraspecific competition in many respects, and the mathematical models used to study both of them are frequently the same, displaying the same range of complex responses. However, things become complicated when many species are considered. For instance, the Lotka-Volterra model with two species converges to a unique stable point, or else to one of two stable attractors depending on the initial conditions. However, if four species interact, chaos may appear, and with five species any complex behavior is possible [10].

The coexistence of several competing species has been the subject of a long-lasting

debate in ecology. As early mathematical and experimental research demonstrated, in simple systems one or a few species outcompete the others. Temporal or spatial variability in environmental conditions have been proposed to preclude such extinctions, and may thus explain the high diversity observed in natural communities. Peter Chesson has shown that variability can only promote coexistence among competitors through two mechanisms: storage effects and relative non-linearities. The former occur if the effects of competition and environment are non-additive. Life-cycle stages that endure adverse conditions also promote storage effects by establishing strongly non-linear relationships between environmental conditions and population growth. Relative non-linearities permit coexistence in models when a species that would be displaced competitively under average environmental conditions has the most concave response to the environment. If so, this species becomes the strongest competitor under extreme events, which, if occur frequently enough, may rescue the species from imminent extinction [11]. Despite the (biological) simplicity and generality of Chesson's theory, storage effects and relative nonlinearities have seldom been tested in nature.

The population dynamics of predator-prey systems also relies heavily in non-linear phenomena. Perhaps the most important of these is the functional response of the predator, i.e., the number of prey consumed as a function of prey density. On one hand, increased prey density reduces the time that the predator invests in searching for food, thus increasing the consumption rate. On the other hand, there is a minimum time required to handle and assimilate food items, setting an upper limit to the number of prey that the predator may eat per time unit. The balance between these opposing trends imposes a strong non-linearity on functional responses. The specific form of these functions depends on the biological attributes of the system such as the capability of many predators to switch between different prey items. Several models have been proposed to describe functional responses, such as the popular Holling equations in all their variants [12, 13].

The form of the functional responses determines the dynamics of predation models in several ways. It affects coexistence: it is easier for animals preying on the same items to coexist if their functional responses are different. Also, models with type-III functional responses (in which predators ignore specific prey items when their density is low) may easily result in the growth of the prey population when it has a low density, allowing it to recover when it becomes scarce. This does not happen when the functional response is type II, making coexistence more difficult. Functional responses also determine whether the model's dynamics shows damped oscillations, cycle limits, or is unstable [12, 13].

Traditionally, models assume that the vital rates or the density-dependent interactions are averaged across all the individuals in the population. More sophisticated approaches that simulate the behavior of each organism are becoming increasingly popular [15]. One of the reasons why individual-based models have a remarkable predictive power in plant ecology is that they explicitly incorporate space. Interactions between plants in a population depend non-linearly on the space between them, and the dispersal kernels of seeds are frequently non-monotonic functions of distance [16]. Limited dispersal causes the ag-

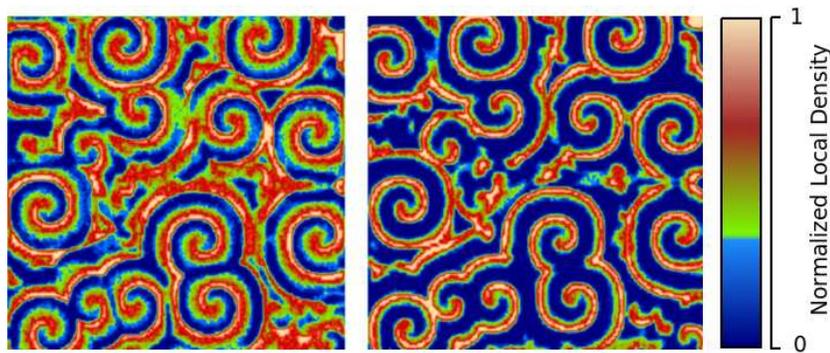


Figure 1: Self-organized spiral spatial patterns that emerge in a predator-prey system. Colors correspond to different predator (in this case a parasitoid; right panel) and prey (host; left panel) local densities. Modified from Rohani & Miramontes 1995 [14]. Image courtesy of the authors.

gregation of individuals, increasing the demographic importance of intraspecific interactions inordinately relative to their per-capita intensity [17]. Spatial patterns also determine the population-level outcome interspecific competition, which may not be proportional to the competitive ability of species [18].

One of the most appealing emergent properties of non-linear, spatially-explicit models is self-organization. Mosaics of areas dominated by different competitors permit coexistence in models that otherwise predict extinction. Beautiful spirals characterize the landscape when predation drives population dynamics [19](see Figure 1). At least that is what theory says: the empirical evidence for such phenomena in real populations is still weak. Nevertheless, some intriguing results have arisen from these models: for instance, a minimal area is required for self-organization to permit coexistence. Such insights are most relevant when designing natural preserves or assessing the conservation value of vegetation remnants .

4 Concluding remarks

By now it must be obvious that non-linearity is omnipresent in population ecology, and that perhaps every conceivable form of complexity may arise from it. I would like to finish stressing some points that hopefully are also apparent by now. 1) The outcome of non-linearity is heavily dependent on its functional form. Theoretical ecology is ripe with non-linear models, but such corpus is rarely confronted with the data in a direct, quantitative manner: empirical studies are full of proxies and indirect indexes that preclude direct tests of the theory. It is encouraging that this panorama has been changing in the last couple of decades thanks to potent statistical techniques and computational tools. It is critical to know which non-linear models are appropriate and under which circumstances.

2) Perhaps because of the hypnotic beauty of complexity, much emphasis has been placed on searching for complexity in our models. However, we need to test if the observed complexity in real populations actually arises from the mechanisms assumed in our models. Let's assume that we observe a complex population-dynamics: does this complexity arise from specific parameters in a simple model such as May's? Or is it the result of interactions between several populations as in the Lotka-Volterra model? We need to build models that comprise the intricacies of nature [20], parametrize them with real data, and then analyze if the dynamics of the model is truly complex and why. 3) That deterministic systems may be inherently complex must not blind us from the fact that populations are also driven by external factors that ecologists envision as stochastic (e.g., climate, disturbances). In practice, stochasticity and chaos produce similar patterns that are difficult to tell without very large data sets. Methods such as the analysis of non-linear time series are becoming available for such task, but are still cumbersome or unable to deal with high-dimensionality problems. We need to understand how complexity interacts with environmental noise in model and real populations. This interaction may itself be complex, as it happens with resonance [21]. Population biology needs to link the complexities in the mathematical and the real worlds –and exemplar efforts are currently under way.

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