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Grand challenges in population dynamics

Daniel Oro*

Department of Biodiversity and Conservation, Mediterranean Institute of Advanced Studies IMEDEA (CSIC-UIB), Mallorca, Spain
**Correspondence: d.oro@uib.es*

Edited by:
Stefano Allesina, University of Chicago, USA

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Stefano Allesina, University of Chicago, USA

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Most multicellular organisms (either metazoan or plants) are grouped in contiguous spatial distributions, where they share genes and common environmental features. These aggregations—the size of which fluctuates in space and time—are called populations. Despite the fact that population dynamics has historically attracted the interest of many scientists, we are still far from understanding how and why populations fluctuate in natural ecosystems. The main reason is that populations are complex systems, with emergent properties that are impossible to determine by the sum of their parts. The components of population dynamics, including processes and patterns, are numerous and have multifaceted dimensions. Here, I will highlight some of them—unavoidably, in a subjective manner.

THE MULTIDIMENSIONALITY OF POPULATION DYNAMICS

The size of a population integrates many factors, from the individual to the ecosystem levels, such as behavior, physiology, host-parasite and predator-prey interactions, diseases, nutrients, among others. Those processes also interact with physical drivers (e.g., climate) to influencing basic fitness components: survival, reproduction and dispersal. In most cases, these topics have been studied independently and in a simple manner; for instance, can the dynamics of a population be understood from pairwise interactions between two competing species? Thus, disentangling the influence of each of the numerous factors influencing population fluctuations remains a great challenge, due to the complexity of integrating the genetic, biotic and physical interactions giving raise to population dynamics. The challenge is even greater because most studies deal with mean-species-level-values, whereas individual variation and how this variance translates into population dynamics is far from being well-understood (Bjørnstad et al., 1994). Working directly with fitness components, together with their variance, and simultaneously having robust estimates of population size over time may partially overcome those challenges, but the challenge is then shifted to time-consuming field monitoring work. Experiments at the microcosm-level are a valid alternative mainly to test specific hypotheses, but they do not solve the challenge of understanding population fluctuations in a holistic manner, given that experiments represent a simplified and altered version of reality.

THE SPATIAL DIMENSION OF POPULATION DYNAMICS

Compared to population fluctuations over time, the spatial scale of population dynamics has historically been ignored because it can greatly complicate research. Collecting spatially-structured population data is highly demanding, but studying population processes that are inherent to the spatial scale are crucial, because the world is unavoidably spatially heterogeneous (Tilman and Kareiva, 1997). Pioneering studies on simple predator-prey systems already stressed that a patchy, subdivided environment is necessary to maintain coexistence between two species (Huffaker et al., 1963). The study of dispersal and connectivity between populations has much advanced in recent decades, particularly with the development of island biogeography and metapopulation theory (MacArthur and Wilson, 1967; Hanski, 1999). There is still a considerable lag between theoretical advances and empirical results testing specific hypothesis, though new approaches and technologies, such as individual mark-recapture and telemetry (e.g., GPS, geolocators) are partially filling in the gap (Clobert et al., 2012). For example, we are now aware of the importance of disturbances (both natural and anthropogenic) in dispersal, or of the many individual traits associated to dispersal (such as morphology, behavior, physiology or life-history), but some issues still remain little-known, such as the role of trophic level, mating strategy, niche breath and plasticity of organisms on dispersal.

THEORETICAL MODELS AND EMPIRICAL STUDIES

Many of the challenges described above have been solved by working with theoretical modeling. These models simplify complexity and concentrate on reproducing specific population processes to describe new patterns, to test hypotheses, or to set up new ones (Bascompte and Solé, 1998). One paradigmatic example is the logistic curve of population growth first described by Verhulst back in 1838. Even for this broadly accepted pattern of population growth, the empirical evidences of this pattern are few, because of the difficulty of studying a population since its foundation (colonization) and over a sufficient amount of time, and also because not all the assumptions of the model can be properly tested in nature. The growth of theoretical models in population dynamics has been huge in recent decades, favored by the enormous capacities of computers to simulate complex scenarios. But, in general, theoretical and empirical ecologists working on population dynamics seldom engage in interdisciplinary studies and hence are not taking advantage of potential collaborations and inputs. This remains an issue that should be tackled in the future. At the same time, some models in widespread use, such as biogeographical models (e.g., niche, invasion-spread, distribution range) and the complex network models (e.g., networks of mutualistic relationships) would gain reliability by including population dynamics at vertices.

SOME PROPERTIES OF POPULATION DYNAMICS

Why do populations remain relatively stable or able to persist over time? This is one of the most difficult challenges confronting ecologists (Cappuccino and Price, 1995). The role of density-dependence, age composition, competition at intra- and inter-specific levels, predation, dispersal between local populations, and other drivers and processes are still far from being understood as a whole, ever since the founding works on population regulation by Hutchinson (1948). We know that populations have resilient properties that allow them to rebound after perturbations have ceased, and maintain numbers around a dynamic equilibrium. But we also know that populations can crash and collapse following extreme values of environmental and demographic stochasticities or due to deterministic factors. What are the factors allowing population resilience? The roles played by the hidden components of populations (e.g., non-breeders, dormant seeds, larvae), by demographic buffering (e.g., the compensatory capacity of some traits) or by dispersal, still need much more attention and are central issues for understanding population stability and persistence.

POPULATION DYNAMICS IN APPLIED DISCIPLINES

The bridge between population dynamics and conservation biology still remains weak. Some processes, like extinction and colonization of empty patches, or concepts, like habitat quality heterogeneity, are commonly misunderstood in conservation. Thus, there is a need for a stronger background in population dynamics properties for the curricula of conservation practitioners. Concepts such as the minimum viable population or quasi-extinction probabilities in forecasting population trajectories (see below) still remain vague and allow for an extra dose of scientific subjectivity. There is still a lot to investigate on early-warning signals of population crashes and on regime shifts from rich to impoverished ecosystems, to inform conservation managers about the impacts of global change and the capacity of populations to cope with those impacts (Solé, 2007).

Another important application of population dynamics is on the harvesting of populations and their sustainability. Some fisheries collapses recorded in the literature are important examples of non-linear population dynamics that challenge our knowledge on these dynamics, and highlight once again the importance and potential of interdisciplinary work between biologists and other scientists, including physicists or oceanographers. The influence of ecosystem maturity on harvested fish populations (and in general in the study of natural populations and communities) was already pointed out by Margalef (1963) but has been seldom considered in studies on anthropogenic perturbed systems and their resilient capacity.

From an applied point of view, forecasting the fate of a population (threatened or exploited) is one of the greatest challenges for scientists, and crucial in the contexts of both sustainable exploitation and biodiversity conservation. Predictions increase their reliability with the amount of data available, but collecting robust data sets is consuming especially at large spatio-temporal scales. When data on population size is available, application of time series analysis, including data mining, pattern recognition and machine learning can be a fruitful pathway, together with the identification of non-linear behaviors, time-lags, extinction vortices associated to Allee effects, and regime shifts among others. There is an interest also from theoretical studies to understand and predict the dynamics of populations and communities, thus encouraging once again interdisciplinary work with field ecologists.

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