POPULATION DYNAMICS

Nature's dynamical complexity

A large-scale, cross-taxa analysis reveals high nonlinearity and limited long-term predictability in the dynamics of animal populations.

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Dynamics of animal populations fluctuate in a variety of ways. They may periodically oscillate, wax and wane irregularly, boom-and-bust, or alternate between periods with different types of fluctuations. All these complex patterns are driven by a combination of biotic and abiotic factors, either stochastic or deterministic[1]. As a consequence, it is notoriously hard to understand and predict population dynamics. Writing in this issue of *Nature Ecology & Evolution*, Clark and Luis[2] analyse the temporal dynamics of a large collection of animal populations to demonstrate that, in more than half of the cases, their dynamics are nonlinear and difficult to predict.

Understanding nonlinearity and predictability has always been a fascinating subject for ecologists, especially as it relates to identifying chaotic dynamics in nature[3]. Nonlinearity emerges when interactions among system components are not directly proportional. This could mean threshold or saturating relationships, or multiplicative interactions that combined give rise to complex dynamics. Simple population models[4] and lab experiments with insect populations[5] showed how chaotic dynamics could arise due to such nonlinear intrinsic processes like overcompensatory density-dependence where population growth is strongly affected by population abundance. Chaotic dynamics are characterized by high sensitivity to initial conditions, which means that even a slight difference at the start of two trajectories will exponentially diverge in time. This implies that chaotic, and in general nonlinear, systems are inherently hard to predict far ahead into the future — just like it is hard to forecast the weather several days in advance.

But just how nonlinear and unpredictable are natural populations? Clark and Luis attempt to answer this question.

To do so, they first collected 747 datasets of population abundance time series across 228 different taxa including mammals, bony fish, birds and insects. Second, they analysed the dynamical complexity of each time series using nonlinear forecasting[6]. Nonlinear forecasting is a set of nonparametric time series modelling techniques that is based on Takens's embedology theorem[7]. The idea is that instead of parameterizing a specific model, the time series is used to build a map by plotting (embedding) the time points of a time series in a phase-space made up of time delayed coordinates (Fig. 1). Takens's theorem states that the embedded time series should produce a geometric object that resembles the characteristics of the 'true' system, which in their study is every population and its supposed interactions with all other populations and abiotic factors. Such mapping becomes more reliable if a time series is sufficiently long, so Clark and Luis only used records of more than 30 observations to perform the nonlinear forecasting. They then used these embedded maps to estimate how accurately they can forecast population densities taken out-of-sample for each time series. In this way, they quantified three properties for each population time series[6]: dimensionality, predictability and nonlinearity.

Their results are revealing. In three out of the four taxonomic classes, they found strong prevalence of nonlinear dynamics. Bird populations were characterized as the least nonlinear (35% of bird populations), while insects were the most nonlinear group (74% of insect populations). They also found that nonlinearity was negatively correlated with predictability, which means that less predictable populations were probably more affected by stochastic processes. Nonetheless, when they tried to forecast more than a single time step into the future, predictability declined exponentially in all cases.

To a large extent, these results are in line with previous studies that have identified nonlinear dynamics using similar methods[8], and they seem to confirm our intuition that most systems are in non-equilibrium state that is hard to predict. But which, when, and how? What can we conclude when looking at these 'macro-ecological' patterns to infer what drives nonlinear dynamics? Clark and Luis take a step towards that direction by linking the three elements of dynamic complexity to species life-history traits, phylogeny and trophic level as well as other elements of the observed records.

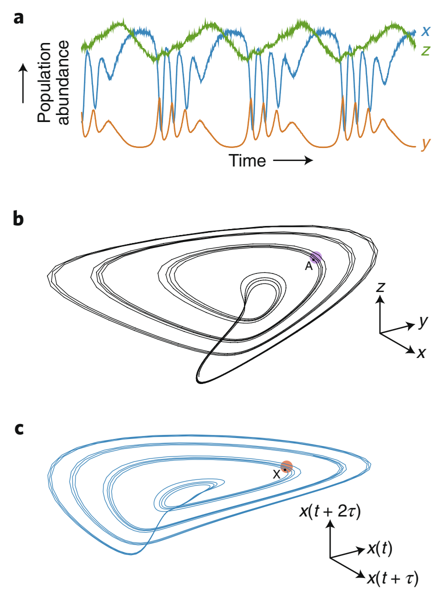

Fig. 1 | Estimating dynamical complexity of population trajectories. a, Hypothetical time series of population abundances of three species (x, y and z) belonging to a trophic chain[11]. **b**, Plotting the abundances of each species measured at the same point in time (t) (point A: $\{x(t), y(t), z(t)\}$ highlighted by the purple circle) in phase-space produces a 'map' with a particular structure that is a unique signature of the three-species system. **c**, Based on Takens's theorem[7], using the single time series of species x (blue line in **a**) and 'embedding' it in phase-space using lagged coordinates (point X:$\{x(t)$ versus $x(t+\tau)$ versus $x(t+2\tau)\}$ highlighted by the red circle where τ is the time delay) reveals another 'map' that resembles the 'true' map of the original three-species system in **b**. Based on such reconstructed maps one can forecast the future evolution of the system state and infer the dimensionality (that is, the number of dimensions of the embedded phase-space), predictability (that is, the forecasting skill), and nonlinearity (that is, the weighing of a nonlinear model used for producing the highest forecasting skill) of an ecological system.

They found no significant phylogenetic relationships, but they did consistently find a positive relationship between nonlinearity and predictability for animals that had fast life-history traits (reflected by their short body size, early age-at-first-reproduction and short longevity). Although the relationships are rather weak and the authors themselves conclude that "no matter the species or ecosystem studied, the underlying systems may be hard to predict", they do point in the right direction for exploring the possibilities and limitations of building a more predictive ecology[9].

Most of our understanding in this direction has focused on improving mathematical population models (like the Ricker model), or better fitting statistical parametric models (like autoregressive models) to map dynamics and understand processes. Nonlinear nonparametric forecasting represents an alternative equation-free approach[10]. Without relying on specific equations, it can produce predictions simply based on the observed dynamics of the system. Its forecasting skill at times outperforms other approaches[10], but it comes at the expense of lacking a mechanistic background. By applying nonlinear forecasting to such a large dataset, Clark and Luis have only scratched the surface to start understanding the extent to which such equation-free approaches could help build better models at least for predicting animal populations.

This work does not, of course, solve the old spell of the 'equilibrium world' that haunts ecologists in their quest to understand and predict nature, in which ecological systems are assumed to have regular dynamics around a stable steady state. But it does make us think of the potential to test the limits of predictability of our ecological systems as more and better resolved data are becoming available and novel standardized methodologies are being developed. The opportunities of such advancements for conservation management, especially under current trends of global change, should not be missed. ❐

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Competing interests

The author declares no competing interests.