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Population dynamics: Nature's dynamical complexity

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

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 deterministic¹. As a consequence it is notoriously hard to understand and predict population dynamics. Writing in this issue of *Nature Ecology and Evolution*, Clark and Luis² 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 nature³. 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 models⁴ and lab experiments with insect populations⁵ 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 characterised 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 timeseries across 228 different taxa including mammals, bony fish, birds, and insects. Second, they analysed the dynamical complexity of each timeseries using nonlinear forecasting⁶. Nonlinear forecasting is a set of nonparametric time series modelling techniques that is based on Takens' embedology theorem⁷. The idea is that instead of parameterising a specific model, the timeseries is used to build a map by plotting (embedding) the time points of a timeseries in a phase space made up of time delayed coordinates (Fig. 1). Takens' theorem states that the embedded timeseries 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 timeseries 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

timeseries. In this way, they quantified for each population timeseries three properties⁶: dimensionality, predictability, and nonlinearity.

Their results are revealing. In three out of the four taxonomic classes, they found strong prevalence of nonlinear dynamics. Only bird populations were characterised 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 methods⁷, and they seem to confirm our intuition that most systems are in a 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.

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 ecology⁹.

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 models¹⁰) to map dynamics and understand processes. Nonlinear nonparametric forecasting represents an alternative equation-free approach¹¹. 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 approaches¹¹, 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 standardised methodologies are being developed. The opportunities of such advancements for conservation management especially under current trends of global change should not be missed.

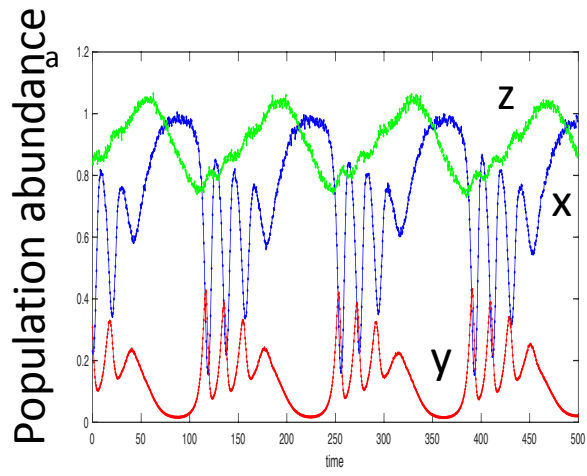
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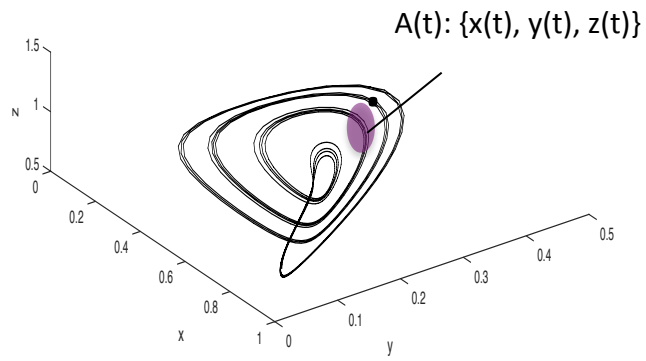
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Fig 1. Estimating dynamical complexity of population trajectories

(a). Hypothetical timeseries of population abundances of three species (x, y, z) belonging to a trophic chain. (b) Plotting in phase-space the abundances of each species measured at the same point in time (black dot highlighted in purple, $A: \{x(t), y(t), z(t)\}$) produces a „map“ with a particular structure that is unique signature of the 3-species system. (c) Based on Takens' theorem⁷, using the single timeseries of species x (blue line in panel a) and „embedding“ it in phase-space using lagged coordinates (black dot highlighted in red $x(t)$ vs $x(t+\tau)$ vs $x(t+2\tau)$, where τ is the time delay) reveals another „map“ that resembles the “true” map of the original 3-species system in panel b. Based on such reconstructed maps one can forecast the future evolution of the system state and infer the dimensionality (i.e. the number of dimensions of the embedded phase space), predictability (i.e. the forecasting skill), and nonlinearity (i.e. the weighing of a nonlinear model used for producing the highest forecasting skill) of an ecological system.



b



c

