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Complex dynamics in ecology

Ecological systems are complex, and the complexity has two principal forms: intricate interactions among numerous species[1] (ecosystem complexity) and changing patterns of observed abundances[2] (dynamical complexity). What are the mechanisms that cause complex patterns? Which complexities are important? Does natural selection favour complexity? These are some of the fundamental questions that have attracted the attention of ecologists and evolutionary biologists for decades.

At the Seventh International Congress of Ecology last July (Florence, Italy) a full-day session organized by Charles Godfray (Imperial College at Silwood Park, Ascot, UK) and Marino Gatto (Politecnico di Milano, Italy) was devoted to the origins and forms of ecological complexity.

Dynamical complexity

Empirical data vary enormously in their degree of dynamical complexity. Some populations do not appear to change in size, apparently maintaining a stable equilibrium[3], but the population dynamics of many species are more complicated. Temporally, some populations show cyclic trends[4], whereas others can even be chaotic[5]. Spatially, some populations undergo frequent, local extinctions and recolonizations[6] and some seem to show coherent spatial patterns[7,8]. Explaining the mechanisms responsible for generating these observed patterns remains a major challenge for population biologists.

The source of dynamical complexity is an important and hotly debated subject. Complex ecological dynamics can arise from ‘intrinsic’ or ‘extrinsic’ influences on populations. The nonlinear response of population growth rate to increases in population density is an intrinsic feature, whereas the effects of the weather, for example, are extrinsic. Either intrinsic or extrinsic forces might be more important in given systems but commonly they interact; for example, seasonal changes in climate (or some other factor) might induce complex population dynamics in species that are intrinsically stable.

At the Intecol meeting, Robert May (University of Oxford, UK) introduced the subject of ecological complexity by reviewing how complex dynamics can often arise from extremely simple processes[2]. The overall themes of his review were that dynamical complexity in population fluctuations can arise from density-dependent population growth, simple rules can generate fractal patterns, and localized dispersal in a spatially homogeneous environment can give rise to spatially heterogeneous patterns.

William Schaffer (University of Arizona, Tucson, USA) presented a series of numerical analyses showing how dynamical complexity can arise in predator–prey systems as a consequence of seasonal forcing. This follows influential work on the effects of seasonality (in disease transmission rates) on the dynamics of host–parasite systems, which are strongly analagous to predator–prey systems[9,10]. Fundamental, qualitative features of real ecological dynamics are often exposed by very simple models, but such caricatures are unlikely to correspond quantitatively to any particular system. Schaffer presented some results of very detailed simulations, which are sometimes appropriate when they can be reliably parameterized using relatively high resolution data.

Marino Gatto argued that it might be most fruitful to study models incorporating some intermediate level of biological detail, because they capture the key features sufficiently well to be reasonably realistic without precluding rigorous analyses. Gatto’s model predicts the mean and variance of population abundance in each occupied patch, not just the probability of occupation (as in the classic metapopulation model of Levins[11]). Related presentations considered the effects of local disturbances on the joint evolution of dispersal and reproductive effort (Ophélie Ronce, Université de Montpellier, France) and potential influences of ocean currents on marine predator–prey systems (Alfredo Ascioti, University of Reggio Calabria, Italy).

Evolutionary forces: simplicity or complexity?

A growing controversy concerns the influence of selective pressures on the character of population dynamics. Some models predict evolution to chaos[12], whereas others predict evolution to stability[13]. Karin Johst (Centre for Environmental Research, Leipzig, Germany) added to this debate, arguing that spatial structure, and perhaps age structure too, favours the evolution of chaotic dynamics.

In situations where population dynamics *are* complex, we may well ask whether there are any important biological implications[10]. Why should we care about chaos? Robert Holt (University of Kansas, Lawrence, USA) argued that chaotic dynamics favour high dispersal rates, even though dispersal is usually selected against[14], and chaos favours the persistent use of low quality (but stable) habitats. Greater dispersal implies a higher degree of global mixing, so chaos might resist the evolution of local adaptation. Régis Férrière (Ecole Normale Supérieure, Paris, France) noted that it is not clear how to define the meaning of ‘fitness’ and ‘invasability’ in populations with complex dynamics. Different types of mutant might be able to invade at different parts of a population cycle or on different dynamical attractors. Hans Metz (Institute of Evolutionary and Ecological Sciences, Leiden, The Netherlands) discussed a framework for dealing with these problems: he defines fitness as the asymptotic average relative rate of increase of a population[15].

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Observed complexity

It is possible that these theoretical analyses have missed something fundamental. In particular, Alan Hastings (University of California, Davis, USA) emphasized that the ecological systems we observe might often be in a transient phase of dynamics[16]. This contrasts with most theoretical work, which focuses almost exclusively on long-term dynamics after systems have 'settled down' (asymptotic states of models). Consideration of the relevant timescale is crucial because transients can often be longer than typical ecological observations or experiments. As an extreme example, Hastings pointed out that since the last ice age there have been only 100 generations of redwood trees (*Sequoia sempervirens*), probably far too few for redwood density to have reached a dynamical equilibrium, if one exists. In general, we can see complex dynamics even in systems that would behave very simply if given long enough to reach an asymptotic state or 'converge onto a dynamical attractor'.

Experiments that test ecological theories are exceedingly difficult to perform. A painstaking, long-term study of population cycles in southern pine beetles (Scolytidae) was presented by Peter Turchin (University of Connecticut, Storrs, USA). In contrast to conventional wisdom, Turchin showed that delayed density dependence is the main driving mechanism for these cycles. He also argued convincingly that to understand cycles in ecological systems we must combine mechanistic models with field experiments and time-series analysis.

Bryan Grenfell (University of Cambridge, UK) discussed the extraordinarily detailed data set for measles incidence in England and Wales since the Second World War. The medical community has systematically collected and compiled these data since 1939. From an ecological perspective, several manipulative experiments have also been conducted (e.g. changes in birth rate, introduction of vaccination, and drops in immunization levels in response to vaccine scares). These spatiotemporal data provide a remarkable and largely untapped resource for theories of host–parasite population dynamics, potentially allowing us to unravel complex interactions between nonlinearity, external forcing and dispersal.

Ecosystem complexity

Of course, the above discussion of population dynamics concerns communities that have already formed. How can we predict which species should be expected to live together in a community? Richard Law (University of York, UK) argued that theoretical studies of community ecology should focus on species assemblages, ignoring the detailed population dynamics of individual species. The problem is hard enough even if we simply ask whether a group of species can coexist. Law's preliminary work using Lotka–Volterra systems suggests that succession is indeterminate (the history of species assemblages in a community depends on initial conditions) but that the number of possible endstates is small (all initial conditions lead eventually to one of a few species assemblages).

Although it is certainly true that simple systems can produce complex dynamics, it is also true that systems that are inherently very complex can show simple dynamics, as emphasized by Simon Levin (Princeton University, NJ, USA). The notion of 'simplicity from complexity', first popular in the physical sciences, has led to recent controversy about the importance of self-organization in biological systems and the possibility of evolution to 'the edge of chaos'[17]. These concepts concern dynamics that arise from numerous, locally interacting agents in a hierarchy. In ecology, the hierarchy involves individuals, populations, metapopulations, communities, ecosystems and ultimately the whole planet. This is an area that seems bound to receive a great deal of attention from theoretical ecologists in the future.

Sergio Rinaldi (Politecnico di Milano) proposed the existence of another simple 'rule', which seems to be followed in tritrophic food chain models that he has studied: top-predator mean density is maximized in the region of transition to chaos. Although Rinaldi's approach was very theoretical, this work has possible implications for conservation of top predators (e.g. Project Tiger[18]).

Surprisingly, there was very little discussion of stochastic (as opposed to deterministic) ecological models. In practice, demographic and environmental stochasticity can both be important. Stochastic processes form a major area of theoretical interest, not least because distinguishing between dynamical chaos and stochasticity is difficult (some say impossible) in ecology[19]. It remains possible that many ecological systems might show complex dynamics because of external, stochastic forces that many models ignore[20]. Much further work will be required to isolate the distinct or synergistic effects of intrinsic, extrinsic, deterministic and stochastic processes in ecology.

Given the breadth of topics that were discussed in the session, it is perhaps not surprising that no single 'take home message' emerged. Nevertheless, we both left Florence feeling that most fruitful further progress on ecological complexity is likely to come from studies that forge strong links between models and data.

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