Synchronicity, chaos and population cycles: spatial coherence in an uncertain world

The Canadian lynx (*Lynx canadensis*), with its regular oscillations in abundance, has held a special fascination for generations of ecologists. One of the most striking features of these oscillations, noted by Elton in his seminal studies of the fur catches of the Hudson's Bay Company[1], is the remarkable extent to which the population cycles in geographically distant regions are synchronized. Elton's work on the lynx, together with studies of similar oscillations in a wide range of species (including oscillations in the incidence of various childhood infections before the advent of vaccination), have proved to be a rich vein for population biologists, leading to several long-standing debates concerning the nature and origins of population cycles, and the mechanisms by which synchrony is achieved[1–5]. Although these debates have tended to be treated as separate issues, a new paper by Blasius and co-workers[6] uses recent developments in nonlinear dynamics to bring the strands back together. In so doing, these authors bring new theoretical insights into the ecological discussion of synchrony as well as introducing powerful new techniques for the study of synchrony in field data.

What causes synchrony?

One explanation, indeed suggested by Elton himself, for the synchronous nature of the cycles is that changing climatic conditions in different geographical regions are correlated: if one region experiences a harsh winter, other regions are likely to suffer similarly. Although less regular than the conductor's baton which keeps an orchestra playing to the same tempo, Moran demonstrated that the effects of weather can be sufficient to give rise to the kind of correlations observed in the field[3]. Another mechanism by which synchrony can arise is purely dynamical, with the coupling of populations by migration. Studies of rhythmic phenomena in biological and physical systems[7,8] have shown that even fairly weak interactions between several oscillators (usually modelled as limit cycles) can lead to 'collective' behaviour of the whole system, including synchronization – as witnessed most dramatically by the synchronous flashing that emerges amongst a population of fireflies[8]. The debate over the relative importance of these two mechanisms in maintaining synchrony even in the face of random effects, such as demographic noise, which would tend to desynchronize cycles, has continued until the present day. Surprisingly, a convincing demonstration of the Moran effect appeared only recently, when Grenfell and co-workers showed that two isolated island populations of sheep exhibited a large degree of synchrony in their fluctuations[9].

Time series analyses of population data have been employed not only to elucidate the biological mechanisms underlying population cycles[5], but also to shed some light on the nature of the cycles. Although the period of oscillations in lynx numbers shows little variability about its mean of approximately ten years, there are large variations in the amplitude, that is, in the numbers of lynx seen at the peaks of each cycle. Although this large variability was first attributed to stochastic effects buffeting the population about either an equilibrium level or an underlying cycle, other studies (for instance, by Schaffer and Kot, in only the third issue of *TREE*[4]) have suggested that the fluctuations in peak amplitude might be as much a part of the 'signal' as is the period, with both regularities and apparent irregularities arising as a consequence of deterministic chaos. In reality, the truth is likely to lie somewhere between these two positions, with fluctuations being caused partly by stochastic effects and partly by nonlinear dynamics, as well as by the interaction of the two.

At first sight, chaotic fluctuations in populations at a local level might seem to be at odds with the highly synchronized nature of the cycles between regions. After all, the sensitivity to initial conditions, which typifies chaotic systems, should amplify any differences (arising, for instance, if populations are not synchronized at some point, or even from the effects of randomness on closely synchronized populations) between the numbers of individuals in different regions. Surprisingly, this need not be the case, as was demonstrated almost ten years ago in an influential paper by Pecora and Carroll, which showed that synchronization can result even when individually chaotic systems are coupled[10].

Phase synchronization

A natural way of discussing synchrony in periodic systems is in terms of the relationship between the phases of oscillators (for instance, in the classic work by Winfree[7]). Rosenblum and co-workers extended this discussion to coupled chaotic oscillators[11] and demonstrated (using a model of two coupled Rössler systems) that phase locking, often seen when periodic oscillators of different frequencies are weakly coupled, can occur in weakly coupled chaotic systems. They dubbed this phenomenon 'phase synchronization', because a constant phase difference (or, equivalently, a constant time lag) is maintained between the oscillations although the amplitudes remain largely uncorrelated. [Because phase differences are maintained, rather than vanish, the term 'phase synchronization' is somewhat of a misnomer; the phenomenon is one of the entrainment of oscillators that would separately oscillate at different frequencies.] The strength of coupling required to achieve phase synchronization depends on the size of the mismatch between the frequencies of the individual oscillators, and the resulting phase difference depends both on the size of the frequency mismatch and on the strength of coupling. Stronger coupling leads to complete synchrony, where the individual systems become completely entrained, although remaining chaotic.

These ideas have now been brought into the ecological arena, with Blasius and co-workers providing, in terms of phase-synchronized chaotic oscillators, an alternative description for both the cycles seen in lynx dynamics and the synchrony of cycles between different regions. They employ a patch (metapopulation) model, with weak coupling between non-identical patches, to model diffusive migration of predator and prey. The dynamics within each patch are described by a tri-trophic food-web model, the uniform phase evolution and chaotic amplitude (UPCA) model, which mimics the interactions between lynx, snowshoe hare (*Lepus americanus*) (the main prey of the lynx) and vegetation. A three-dimensional plot of the dynamics of the UPCA model, which is qualitatively similar to that of the Rössler system, resembles a reconstruction of the attractor (the solution to which a system tends after a period of time) underlying the lynx time series. (However, it should be noted that this is far from being a watertight demonstration, either that the lynx dynamics are truly chaotic or that the UPCA model is a good description of reality.) As the coupling between patches increases, the phase synchronization phenomenon can be seen, with the model exhibiting phase-synchronized oscillations, which are suggestive of the lynx abundance time series. Importantly, this observation does not depend on the precise form taken for the within-patch dynamics, confirming that phase synchronization is a robust phenomenon in such systems.

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Synchrony and persistence

Synchrony between fluctuations in population numbers in different regions has important implications for the persistence of populations; asynchrony allows for the global persistence of a population through rescue effects, even when there are local extinctions. Indeed in certain circumstances, the highly desynchronizing effects of chaos have been shown to enhance the global persistence of model populations, even though the large population swings often (but not always) associated with chaotic dynamics increase the chance of local extinction. Because phase differences persist between patches, possibly in the form of travelling waves when the patches are arranged on a lattice, phase synchronization need not be detrimental to population persistence. Indeed, the complex spatial structures that can arise might play an important rôle in enhancing population persistence.

Ecologists should not be surprised by the synchronization of chaotic populations in light of work on the dynamics of metapopulation models (although most of this work has centred on discrete time models). However, this demonstration of collective behaviour, arising from weak local coupling between chaotic populations, shows that such phenomena are not restricted to a set of models that make fairly restrictive assumptions of non-overlapping generations and the strict separation of dynamics and dispersal.

Another situation in which synchronization can occur naturally is in the presence of strong periodic forcing, such as is the case for the recurrent epidemics seen in childhood diseases, such as measles, in which the congregation of children during school terms increases rates of transmission relative to rates during vacations. Understanding the patterns of synchrony in measles outbreaks provides a particularly exciting challenge, because the synchrony results from a complex interplay between seasonal forcing and spatial coupling in the face of strong stochastic effects, which arise during the deep troughs seen between epidemics[12]. Most importantly, there is a wealth of available data from which information about the mechanisms underlying synchrony can be gleaned, and against which model predictions can be tested.

Although there has been much interest in the dynamics of spatially extended systems in ecology and epidemiology, most of the work has been simulation-based, giving rise to a literature littered with disparate descriptions of behaviour seen in models, few of which are underpinned by general principles. With some notable exceptions, there have been few successful theoretical descriptions of spatial phenomena observed in ecology, and even fewer practical tools for the analysis of ecological data sets containing both spatial and temporal data. Given the powerful results derived in the study of rhythmic phenomena in other areas of biology (not only concerning the synchrony of oscillations, but also the response of oscillations to perturbations), one might hope that in directing attention towards the analysis of the phase of population cycles, Blasius and co-workers might provide the much-needed new tools for population biologists to study their well-worn data sets.

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How soil food webs make plants grow

Historically, much of the ecological research that has focused above-ground has tended to ignore those associations occurring below-ground, while much below-ground ecological research has paid scant attention to the ecology of the associated above-ground biota. However, there is currently a growing interest in exploring the interface of population-level and ecosystem-level approaches to ecology[1]. Such approaches require us to acknowledge the significance of both the above-ground and below-ground compartments of terrestrial ecosystems (as well as the feedbacks between them), because the former is responsible for most of the production (carbon input) in an ecosystem, whereas the latter is responsible for most of the decomposition (carbon loss) in the system. The above-ground and below-ground compartments are dependent upon one another because of the role of plants as the source of carbon for soil biota, and because the soil biota in turn release nutrients bound up in relatively recalcitrant compounds into simpler forms that are more readily taken up by the plant.

The decomposer food web has a primary role in altering the availability of nutrients for plants. Although most mineralization of nutrients is directly governed by the basal consumer trophic level of the soil food web (bacteria and fungi), their activity is profoundly affected by soil animals of higher trophic levels (e.g. protozoa, nematodes, mites, springtails, millipedes and earthworms), and the feeding activities of these animals therefore have important indirect effects on availability of nutrients in soils. Those studies that have sought to manipulate key functional faunal components of the decomposer food web have invariably detected responses of both microbial activity and key microbially mediated processes to feeding by soil animals, and some have identified important effects of these types of trophic relationship on plant productivity[2,3] and plant nutrient acquisition[4]. Although there is recent theoretical evidence to suggest that soil food web structure can influence nutrient availability[5], there is a dearth of experimental data on the ecosystem-level consequences of soil food-web architecture, and much remains unknown about how soil food-web structure affects plant growth or ecosystem productivity.

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